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Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession

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Introduction

Modeling forest landscape change is challenging because it involves the interaction of a variety of factors and processes, such as climate, succession, disturbance, and management. These processes occur at various spatial and temporal scales, and the interactions can be very complex on heterogeneous landscapes. However, simulation models make it possible to examine assumptions about landscape change explicitly by defining complex processes and their interactions logically and mathematically. More importantly, modeling allows us to deduce results that otherwise cannot be investigated due to their complexity, such as landscape change over long time periods and the ecological ramifications of large disturbances, or diverse management regimes.

The variety of approaches taken to model forest landscapes reflect the diverse backgrounds and objectives of individual researchers (Mladenoff and Baker, Chapter 1). LANDIS has been refined (Mladenoff *et al.*, 1996) as a forest landscape model that integrates forest succession, windthrow, fire, and forest management. LANDIS is a tool to study species-level responses and changes in forest landscape pattern with varied natural and anthropogenic disturbances. LANDIS addresses several needs, including to (i) simulate large (10^4–10^6 ha) landscapes that are heterogeneous in terms of site conditions or environment (landtypes), and initial vegetation conditions at the tree species level, (ii) simulate interaction of dominant forest disturbance regimes, such as fire, windthrow, and harvesting, with species-level forest succession, (iii) adapt to a range of possible scales and map input-data of varied resolutions, and (iv) include spatially explicit ecological interactions, and mechanistic realism, while having modest input parameter needs. These requirements are similar to a degree for most forest landscape models, and cannot all be optimized. The particular needs being addressed by the model drive how these requirements are balanced. These needs are framed by temporal and spatial scale (landscape extent and resolution), data availability, and parameter information for large areas.

The LANDIS model

General characteristics

LANDIS is a spatially explicit and stochastic model that simulates forest landscape change over long time domains and large, heterogeneous landscapes. LANDIS has several key characteristics (Mladenoff *et al.*, 1996; He and Mladenoff, 1999). LANDIS uses a cell-based, or raster data format, a widely used data structure for spatial analysis and modeling (e.g., Green, 1989; Baker *et al.*, 1991; Turner *et al.*, 1994; Keane *et al.*, 1996; Gardner *et al.*, 1996, Chapter 7; Urban *et al.*, Chapter 4). In general, the raster data format is more efficient computationally than the vector, or polygon format (Gao *et al.*, 1996). This makes it possible to incorporate greater mechanistic complexity (Mladenoff *et al.*, 1996). Raster data allow direct input of large-scale, satellite-based forest classification maps (e.g., Wolter *et al.*, 1995), a major source of species input data for large-scale simulations (He *et al.*, 1998). With the raster data format, cell size can be controlled and varied to reflect different spatial resolutions. This is of particular interest, since very often either the question investigated or input data availability imply a certain appropriate cell size. Also, the corresponding operations on vegetation pattern and environmental data layers allow multi-scaled issues to be examined, since aggregating or disaggregating cells are among the standard operations of raster GIS data (e.g., Arc/Info Grid (ESRI, 1996; ERDAS, 1994).

Spatial interactions, such as seed dispersal based on potential distances rather than polygon neighborhoods, can be more accurately simulated with raster data format than vector data (Mladenoff *et al.*, 1996). The LANDIS model is conceptually related to two existing approaches, the plot-level JABOWA-FORET "gap" models (Botkin *et al.*, 1972; Botkin, 1993; Shugart, 1984), and the landscape-scale LANDSIM model (Roberts, 1996; Roberts and Betz, Chapter 5). Both of these previous approaches simulate species succession, although their scale and mechanistic detail differ considerably (Mladenoff and Baker, Chapter 1).

Within each cell, LANDIS tracks the presence/absence of species age cohorts at 10-year time steps rather than the actual number of individual trees. This differs from most gap models, except FORCLIM (Bugmann, 1996), that track individual trees. Use of FORCLIM suggests that realism is not significantly reduced by tracking age cohorts rather than individuals for large-scale applications. Additionally, computational loads are greatly reduced, because actual species abundance, biomass, or density are not being simulated. If such detailed information is desired, it can be added to model output from the growth and yield relationships available in the literature, through a lookup-table relationship, or by linking with an ecosystem process model. In this context, species presence/absence information is relatively more scale-independent than quantitative data. Varying cell sizes has less effect on the way that species information is recorded than does tracking individuals, up to certain model design limits. This provides the basis for the model to be useful at different scales by varying cell size and appropriately scaling spatial interactions such as seed dispersal. A major purpose of LANDIS is to simulate large landscapes,

Table 6.1. *Species life history parameters that drive the model*

Species	sLong	sMat	sC	fireT	effD	maxD	vegP	spAge
Abies balsamea	150	25	5	1	30	160	0	0
Acer rubrum	150	10	3	1	100	200	0.5	150
Acer saccharum	300	40	5	1	100	200	0.1	240
Betula alleghaniensis	300	40	4	2	100	400	0.1	180
Betula papyrifera	120	30	2	2	200	5000	0.5	70
Carya cordiformis	300	30	3	2	30	1000	0.5	220
Fraxinus americana	200	30	4	1	70	140	0.1	70
Picea glauca	200	25	3	2	30	200	0	0
Pinus banksiana	70	15	1	2	20	40	0	0
Pinus resinosa	250	35	2	4	12	275	0	0
Pinus strobus	400	15	3	3	100	250	0	0
Populus grandidentata	90	20	1	2	−1	−1	1.0	90
Populus tremuloides	90	15	1	2	−1	−1	1.0	120
Prunus pensylvanica	30	10	1	1	30	3000	0	0
Prunus serotina	200	20	2	1	30	3000	0.5	140
Quercus alba	400	40	3	4	30	3000	0.5	300
Quercus ellipsoidalis	200	35	2	4	30	3000	1.0	300
Quercus macrocarpa	300	30	2	5	30	3000	1.0	220
Quercus ruba	250	25	3	3	30	3000	0.5	250
Quercus velutina	300	30	2	3	30	3000	1.0	220
Thuja occidentalis	350	30	4	1	45	60	0.5	400
Tilia americana	250	15	4	2	30	120	0.5	250
Tsuga canadensis	450	30	5	3	30	100	0	0

sLong – longevity (years), sMat–age of sexual maturity (years), sC – shade tolerance class (1–5), fireT – fire tolerance class (1–5), effD – effective seeding distance (m), maxD – maximum seeding distance (m), vegP – vegetative reproduction probability, spAge – maximum age of vegetative reproduction (years).

where available input data may be coarse or parameters poorly estimated. A species presence/absence approach avoids any false precision of predicting species abundance measures that may occur with inadequate input data or parameter information.

Our model is similar to LANDSIM (Roberts, 1996) in that successional dynamics are based on species vital attributes or life history characteristics, along with other ecological parameters relating to disturbance and site characteristics (Table 6.1). Similarly, the model is currently based on a 10-year time step. The LANDIS model differs from LANDSIM in several ways that opt for greater mechanistic detail in spatial interactions, with some corresponding increase in computational load. LANDSIM operates on fixed polygon maps, and spatial interactions such as seed dispersal operate on fixed polygon neighborhoods rather than actual distances (Roberts, 1996). This approach is well suited to areas such as mountainous regions where large and steep environmental gradients are amenable to mapping of relatively discrete vegetation patches and habitats, and where such polygons may constitute management units. The LANDIS model was designed to also operate in an environment where vegetation patterns and environmental gradients are less discrete, and to allow flexibility in spatial representation. Because LANDIS operates in a cell-based mode, vegetation patches are not fixed polygons, and can aggregate and disaggregate in response to spatial patterns of stochastic disturbance and succession.

LANDIS simulates disturbances in addition to simulating succession (He and Mladenoff, 1999). Any simulated disturbance is a result of spatially explicit interactions of environment variables, vegetation information, and the nature of the disturbance itself. Simulating windthrow disturbance, an important factor in many forest systems, in combination with fire, appears not to have been previously modeled (Mladenoff *et al.*, 1996). The interaction of these two disturbance types can provide feedbacks in the model and influence resulting successional pathways.

C++, an object-oriented programming language was used in developing LANDIS (Mladenoff *et al.*, 1996; He *et al.*, 1996, He *et al.*, 1999*b*). Programming of the model using hierarchical classes provides flexibility in model design and computational efficiency. The modeling system also includes a graphical user interface (GUI), as well as a freestanding spatial analysis package (APACK) that can be used with map output from LANDIS or other sources (Mladenoff and Dezonia, 1997).

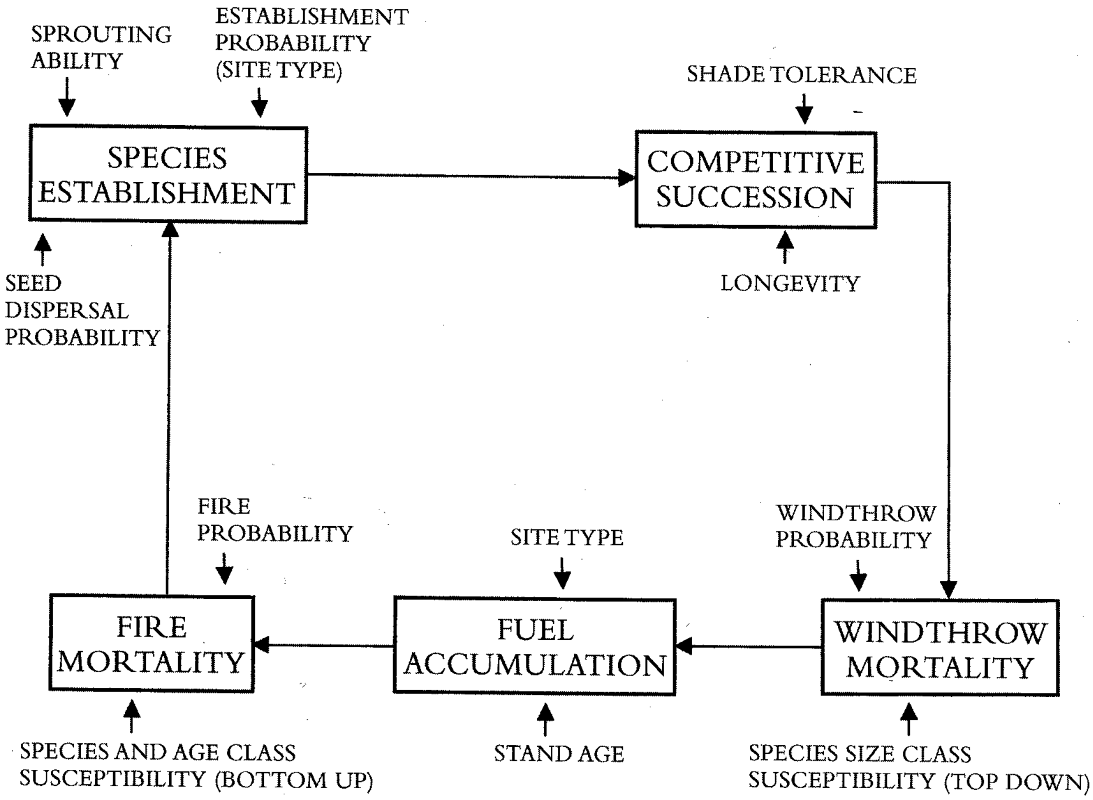
Ecological dynamics

Site (cell) level representation

In LANDIS, a landscape is conceptualized as a lattice or grid of cells of equal size. These cells can be conceived of as an array of sites making up the larger landscape. Any given cell is unique in terms of the environment or landtype (defined below) on which it resides, the species present, the age cohorts of the species, the disturbance history, and fuel regime. Either cell or site is used in our discussion to refer to these units, depending on whether an ecological or map format emphasis is intended. It is also important to keep in mind that the cell size is user defined and can vary. Various ecological processes may simultaneously occur in each cell through time, including species establishment through competitive succession and seeding, wind and fire disturbances, fuel accumulation and decomposition. These processes constantly alter the species information and drive the vegetation dynamics in the cell (Fig. 6.1).

In succession, several parameters are treated as categorical inputs, rather than modeled explicitly, similar to LANDSIM (Roberts and Betz, Chapter 5; Table 6.1). In addition, each species has an *establishment coeffcent*, that expresses species relative ability to grow on different site categories or *landtypes*, and are differentiated based on species relative responses to soil moisture, climate, and nutrients. The species establishment coefficients are not themselves modeled within

Fig. 6.1. Succession and disturbance dynamics of LANDIS model at a given site.

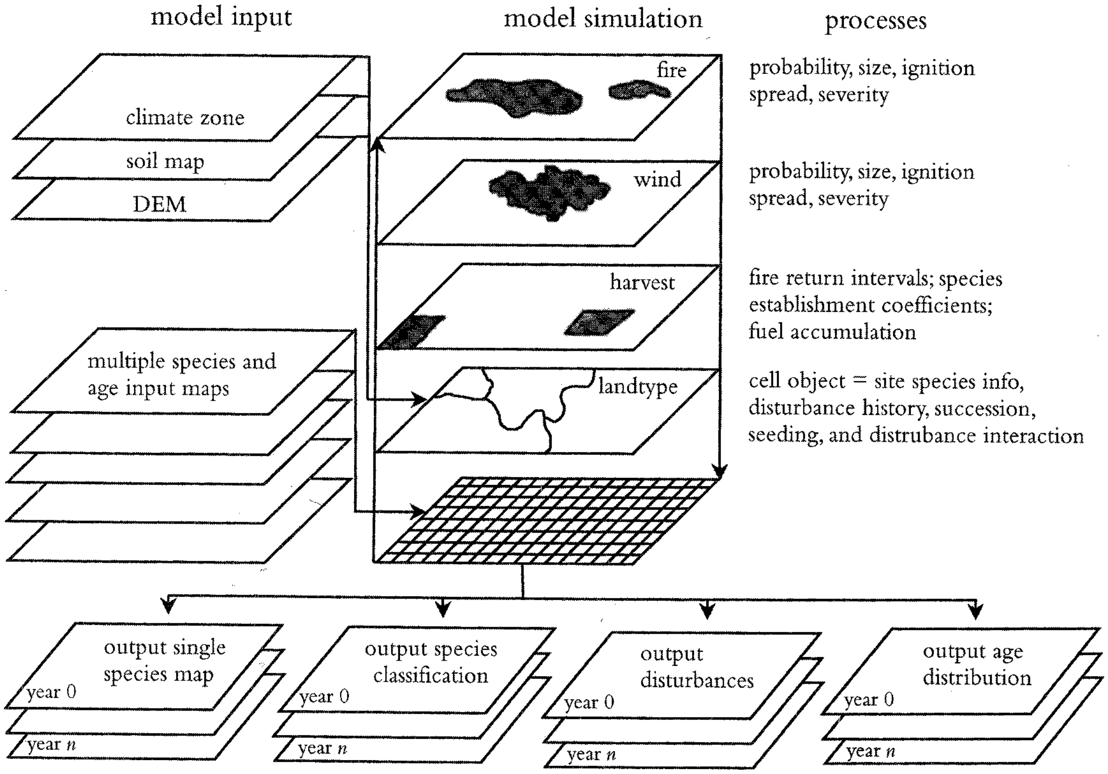


LANDIS. They can be estimated empirically or derived from a gap model with ecosystem-process drivers (He *et al.* 1999a). Similarly, fire characteristics such as severity vary with landtypes, and are based on interactions of productivity, decomposition, and time since last fire. These are also represented as categorical variables. The use of categories at the landscape-scale to represent more computationally complex phenomena at the site level allows the effects of ecological processes to be scaled-up (Roberts and Betz, Chapter 5; He and Mladenoff 1999).

Landscape-scale representations and dynamics

Ecological dynamics such as seeding, and fire and wind disturbances, occur at spatial extents that exceed a single cell, and cannot be defined at the site level. At landscape scales, heterogeneous landscapes are often stratified as ecoregions or landtypes (Fig. 6.2). Landtypes are processed from other GIS layers, and are scaleable corresponding to the question investigated and the data availability. At coarser regional scales (e.g., 10^4–10^6 ha), climatic zones, soil series associations, and general physiography can be used to delineate landtypes, while at finer scales (< 10^4 ha), high resolution data such as digital elevation models (DEMs) and finer soil maps can be used. In LANDIS, landtypes are used to stratify the environment

Fig. 6.2. Ecological processes, data input and output in LANDIS.



into areas with relatively consistent species establishment, fire characteristics, and fuel accumulation regimes.

Unlike most gap models that assume constant or random seed rain (Shugart, 1984), seed dispersal is explicitly simulated across the landscape in LANDIS. The available seed source is calculated from vegetation patterns by the model, and species seeding distances are explicitly defined. Seed dispersal curves (negative exponential) depict the probability of seed to travel certain distances based on existing literature. These derived curves are implemented in the model as simplified categorical parameters, again reflecting the presence/absence representation of species in cells. The dispersal categories represent effective and maximum seeding distances for each tree species. Within effective seeding distance, seed has high probability of dispersal. On the other hand, the chance for seed to travel farther than its maximum seeding distance is very low (He *et al.*, 1996).

In LANDIS, fire and wind disturbances are simulated based on the historical distribution of disturbance sizes and mean return intervals. This information can be derived from the literature on the region or can be explicitly studied (e.g., Canham and Loucks, 1984; Frelich and Lorimer, 1991; Heinselman, 1973, 1981). Fire and windthrow disturbances may occur at various locations on the landscape, with each event varying in time and form (e.g., extent, shape, severity). Neither the time when a disturbance occurs nor the pattern and shape of the disturbance is deterministic. However, in real landscapes fire and wind disturbances are not purely stochastic events since some landtypes may be more susceptible to disturbance than others. At the landscape scale, spatial interactions between disturbance processes, environment and vegetation dynamics can be more precisely defined, and patterns of re-occurrence based on assigned distributions can be more realistically portrayed over time (He and Mladenoff, 1999).

Fire is simulated as a bottom-up disturbance; fires of increasing severity affect smaller tree age-classes first. Fires of increasing severity affect increasingly larger age-classes. Fire severity is determined by fuel availability, which is based on time since the last fire and landtype characteristics that influence production and decomposition.

Windthrow is predominately a top-down disturbance; with probability of tree cohorts being affected by a wind event increasing with tree age and size. Therefore generally the oldest, tallest canopy tree are affected first by windthrow, and increasingly more severe wind events can remove more of the canopy (younger cohorts lower in the canopy). The time since a windthrow event can also influence the potential fire severity class, depending on decomposition dynamics of the particular landtype. Interactions between these two disturbances can be interesting and complex. Generally, windthrow becomes more important on landtypes with longer-lived species, and where fire frequency is low.

Model structure and object-oriented design

The challenge in designing a model like LANDIS is balancing the representative ecological processes affecting landscape change at appropriate spatial resolutions, with computational efficiency in order to simulate large, heterogeneous landscapes. One relatively new and useful approach involves object-oriented modeling and design (Rumbaugh *et al.*, 1991; Coad and Yourdon, 1991; Varhol, 1992; Paepcke, 1993; Sigfried, 1996; Yourdon and Argilar, 1996). Object-oriented modeling and design techniques allow conceptualizing problems by using objects organized around real-world concepts. It facilitates the modeling process through several important features, including *modularity*, *abstraction*, and *encapsulation*. This approach may also result in a program that is easier to maintain or modify than computer code using more conventional, iterative programming and modeling approaches.

Modularity

The best way to simplify the problem-solving process is to divide a large problem into small, manageable parts or modules. One way to achieve a modular solution is by identifying within a problem various smaller components, called objects, that combine both data and the operations on the data. For example, the problem of forest landscape change can be broken down into species, succession, disturbance, management, environment, etc. An object-oriented approach produces a modular solution, that is, a collection of objects that interact, rather than a sequence of actions (Carrano, 1995).

Abstraction

Abstraction separates the purpose of a module from its implementation. This feature makes it easy to focus on the essential, inherent aspects of an entity and ignores its incidental properties. In model design, this means focusing on what an object is and does, before deciding how it should be implemented. Subsequently, the use of abstraction preserves the freedom to make decisions as long as possible by avoiding premature commitments to details (Rumbaugh *et al.*, 1991). When designing a modular solution to a problem, each module begins as a box that states what it does, but not how it does it. No one box may "know" how any other box performs its task; each box may know only the task of other boxes (Fig. 6.1). Therefore, modularity and abstraction complement each other. Modularity breaks a solution into modules; abstraction specifies each module clearly before implementing it in a programming language.

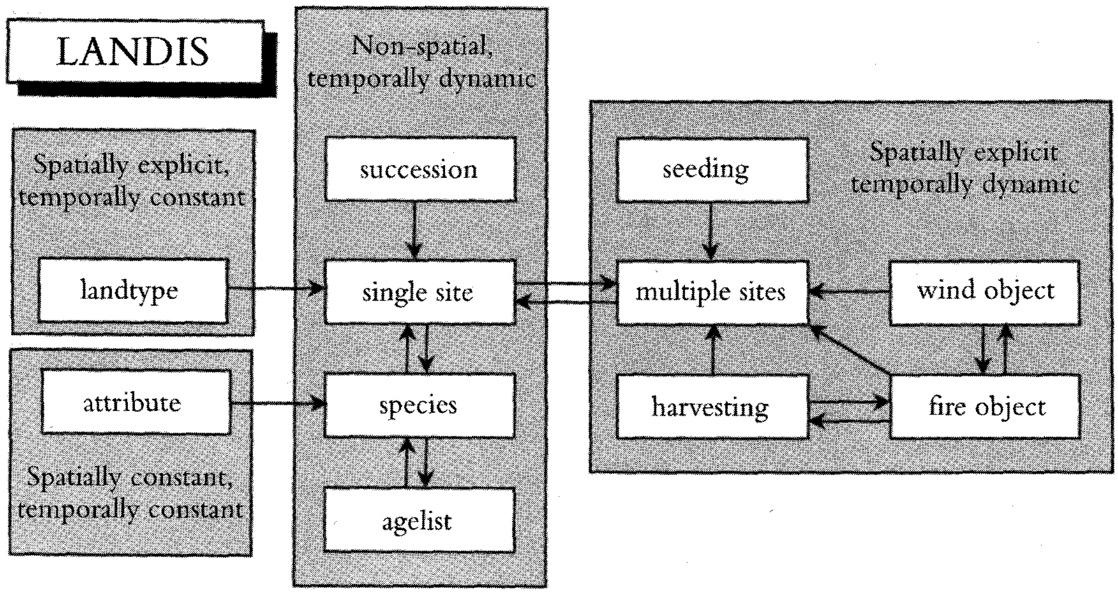
Encapsulation

Encapsulation consists of separating the external interface from its internal state. The external interface allows objects to communicate with other objects. The internal state of an object is used by that object to perform its duties (Fig. 6.1). Encapsulation prevents a program from becoming so interdependent that a small change has massive ripple-effects (Rumbaugh *et al.*, 1991). The implementation of an object can be changed without affecting the applications that use it. In object-oriented design, encapsulation is facilitated through the design of the *abstracted data type* (ADT). The ADT allows us to define a unique data structure for a specific object, and implement operations on the data. This is important since different objects require different data structures and operations. For example, a fire object may use fire probability, mean fire return interval, disturbance size, mean, maximum and minimum disturbance size as its data structure, and ignition and spread as its operations (He and Mladenoff, 1999). Encapsulation is not unique to object-oriented languages, but the ability to combine data structure and behavior in a single ADT makes encapsulation cleaner and more powerful than in designs using conventional languages that typically separate data structure and behavior.

Model structure

Two issues are often involved in landscape model design: spatial scale and representing the objects to be modeled. No model can comprehensively address all scales. Usually the scale range is decided at the model design stage, and this will affect the way we represent the real world objects in the model (He *et al.* 1999b). Assumptions often have to be made at various levels such as among objects and within objects. For example, between species and fire objects, there are multiple causes that result in mortality. However, in modeling assumptions have to be defined

Fig. 6.3. LANDIS overall modular design. LANDIS modules within white boxes are grouped as shaded blocks representing model components that can be spatially explicit or non-spatial, and temporally dynamic or constant.



which simplify the removal of a certain species from the landscape. Within an object, the data type of a given parameter is another type of assumption, since ecological parameters are in the form of nominal (e.g., presence/absence), ranked, interval, or continuous numeric forms. Choosing a logical or mathematical representation for these parameters also entails assumptions and must be based on available information.

Due to the need for simplification and various stochastic components, landscape models are often not designed to predict particular events in a local and deterministic sense; rather they are designed to examine general patterns produced due to different sets of assumptions and interactions. Thus for a given landscape model, having the ability to update assumptions with new knowledge and re-calibrate each component of the model is essential. The objected-oriented design approach facilitates calibration, modification, and testing of the model through modular manipulation (He *et al.*, 1999b).

The overall LANDIS design includes objects and components that may be of several types: they may be spatially explicit or non-spatial, and temporally constant or dynamic (Fig. 6.3). For example, fire, wind, harvest, and seeding are processes operating at spatial extents larger than a single site, especially when operating at smaller cell sizes. These processes are both spatially explicit and temporally dynamic. Succession occurring on every site where forest species exist is a temporally dynamic process. Through succession, the species list and agelist change with time. Landtype is spatially explicit and temporally constant. Usually landscape attributes encapsulated by landtype do not change within the simulation time span. The species attributes are non-spatial and temporally constant (Fig. 6.3). Since the actual interaction among these objects can be fairly complex, it is difficult to present all the possible interactions among all processes. Rather, an endeavor is made to conceptualize the integration of ecological processes at the site or cell level and to scale up to landscape levels.

LANDIS basic components and objects

Succession

Succession dynamics in each cell is a spatially constant, temporally explicit component of LANDIS, but interacts with several spatial components. For each cell or site, *succession* interacts with *species*, species *attributes*, and species age cohorts (*agelist*) objects for every simulation step (Fig. 6.3). *Succession* is a competitive process driven by species life history parameters (Table 6.1). It comprises a set of logical rules modified from the LANDSIM model (Roberts, 1996; Mladenoff *et al.*, 1996). Species competitive ability is mainly the combination of shade tolerance, seeding ability, longevity, vegetative reproduction capability, and the suitability of the landtype to a given species. Within *succession*, species birth, growth, and death are performed under the rules. For example, shade-intolerant species cannot establish on a site where more shade-tolerant species are present. On the other hand, the most shade-tolerant species are delayed in being able to occupy an open site. Without disturbance, shade tolerant species will dominate the landscape given that other attributes are not highly limiting and the environmental condition is generally suitable.

Seeding

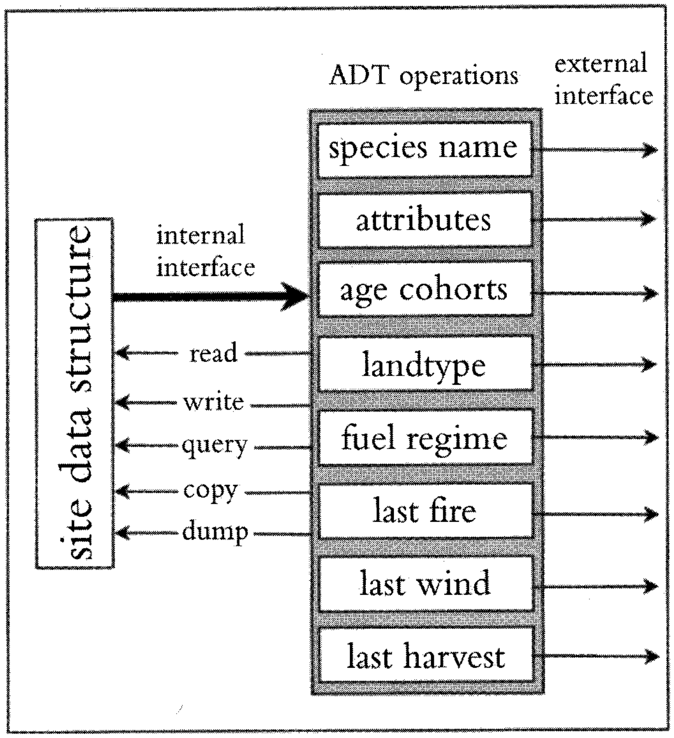
Seeding is a spatially and temporally explicit component of LANDIS involving multiple sites or cells. *Seeding* interacts with *species*, *attributes*, *agelist*, and *landtype* objects for every model iteration (Fig. 6.3). Seeding activity can be conceptualized as the following expression:

$$Seeding = f(sMat,\ effD,\ maxD,\ rD,\ sC,\ eC,\ rP)$$

where *sMat* is the species sexual maturity age, *effD* is effective seeding distance, *maxD* is maximum seeding distance, *rD* is the actual distance of a site from the seed source, *sC* is the species shade tolerance class, *eC* is the species establishment coefficient (Table 6.1) (Mladenoff *et al.*, 1996), *rP* is a random probability 0–1.

Seed can disperse from any cell or site on the landscape where a seed source is available, and a cell can receive seed from other cells. For any given cell, the *seeding* routine checks if any species' *agelist* contains a cohort older than its *sMat*. If such a species exists, *seeding* then looks up the *effD* and *maxD* stored in species *attributes*. In general, seed has a high probability of reaching sites within *effD*, one of the

Fig. 6.4. LANDIS site object, showing abstracted data type (ADT) operations.



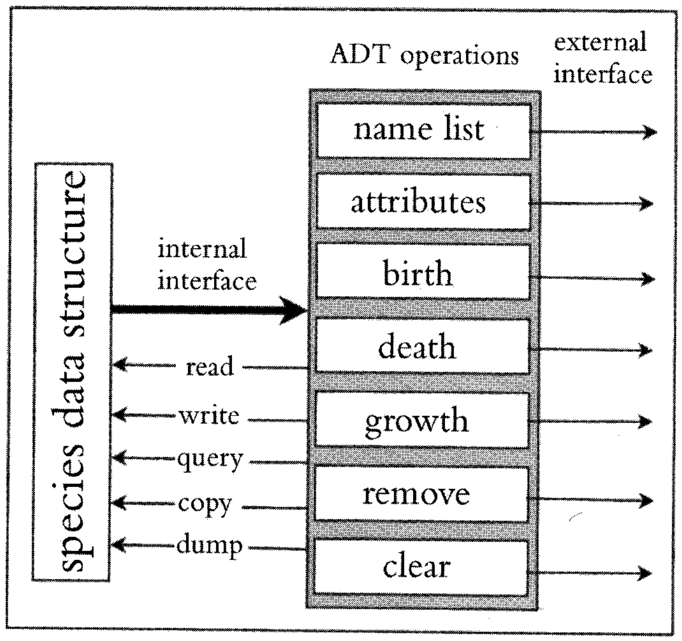
attributes measuring species seeding ability. Beyond this range, seed dispersal probability decreases exponentially with distance, but is expressed in the model as discrete distance classes rather than continuously. Once seed successfully arrives at a given cell at distance *rD*, *rP* is drawn from a uniform random number pool, and comparison between *eC* and *rP* is then made. The seed can establish in that cell only if $eC > rP$. Several seeding routines are available in LANDIS emphasizing various seeding parameters, and they can be chosen for the appropriate cell sizes (He *et al.*, 1996).

Site object

The *site* object is a conceptual representation of the basic landscape unit (cell) being modeled (Fig. 6.3). The landscape is composed of multiple *sites* or cells with each containing unique information. *Site* interacts with all other objects and components querying site specific information. Responses to the queries are implemented as the operations on the object or external interface of *site* (Fig. 6.4).

Succession, *seeding*, *wind* and *fire* disturbance, and *harvesting* all interact with *site*. The *succession* routine queries the *site* for the information related to species list, age cohort, species *attributes* including mature age, longevity, shade tolerance class, and vegetative reproduction probability. The *fire* object queries for information such

Fig. 6.5. LANDIS species object, showing abstracted data type (ADT) operations.

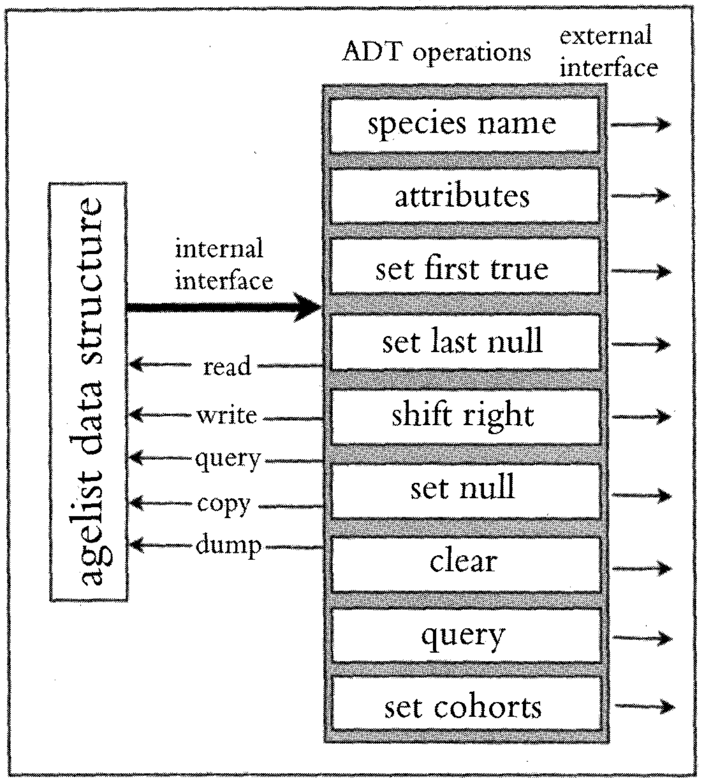


as the mean fire return interval on the site (encapsulated by *landtype*), the time since last fire, current fuel accumulation regime, and species fire-tolerance class. The *seeding* routine queries for the species list, current age cohorts, effective seeding and maximum seeding distance, species shade-tolerance class, species vegetative reproduction probability, and species establishment coefficients on the site. The *site* object uses its internal interface to work with its internal data structure to respond to each external query. The internal interface includes read, write (update), query, copy, and dump functions that are also standard for other objects. These internal operations and the internal data structure of the object are described elsewhere (He *et al.*, 1999b).

Species object

Species is a spatially constant, temporally explicit object (Fig. 6.3). Operations defined for *species* include "query" (for species name and attributes), "birth", "death", "grow", "remove", and "clear" (Fig. 6.5). The "query" operation is site specific since each site may contain a unique species list. The "birth" operation simulates either a new species seeding in, or on-site species regeneration. The latter usually applies to species with high shade tolerance. For some species with vegetative reproduction ability, "birth" simulates vegetative reproduction. The "death" operation typically simulates species reaching maximum longevity. It applies only to the particular age cohort which reaches longevity. "Grow" simulates the species age-class increment during each model iteration. "Remove" simulates one or more

Fig. 6.6. LANDIS agelist object, showing abstracted data type (ADT) operations.

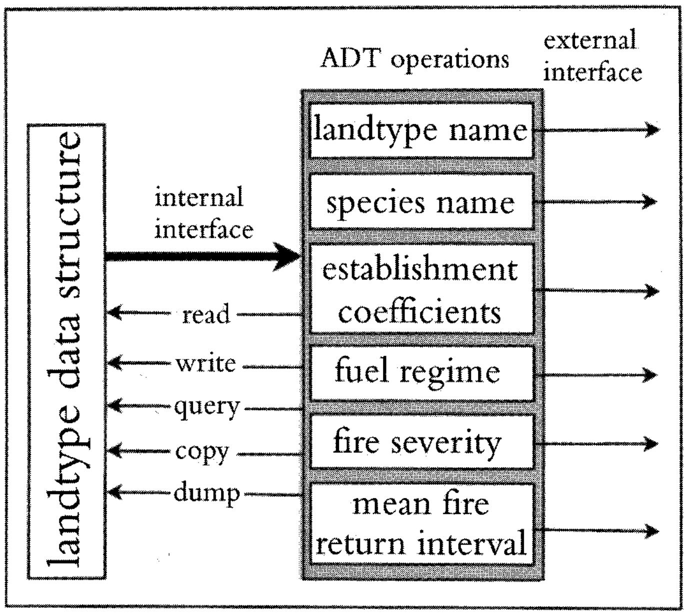


age-cohorts of a species removed from the site due to various causes. Disturbances, harvest, and background mortality can all result in removal of certain species age-cohorts. For example, wind disturbance tends to remove older age cohorts, while fire disturbance tends to remove younger age-cohorts. The "remove" operation differs from "death", and can remove any age-cohort of the species. "Clear" simulates the removal of entire age-cohorts of a given species on the site, and usually accompanies severe fire disturbances or clearcut harvest.

Agelist object

Agelist is also a spatially constant, temporally explicit object in the model (Fig. 6.3). *Agelist* can be considered a lower level *species* operation (Fig. 6.6), containing a bit-level data structure of species age-cohorts (He *et al.* 1999b). In programming, *agelist* is the base class of *species*, and *species* inherits the features defined for *ageclass*. "Set first true" simulates "birth", when a new age-cohort is set present at 10-year-old. "Set last null" simulates "death", when the last age-cohort of a species is set to null. "Shift right" simulates "grow", when all age-cohorts increase 10 years by moving rightward in the bit-level data structure. "Set null" simulates "remove" of certain species age-cohorts. "Clear" simulates the removal of entire species

Fig. 6.7. LANDIS landtype object, showing abstracted data type (ADT) operations.



age-cohorts. Other *agelist* operations include "query age-cohort", a query frequently made by many processes, and "set age-cohorts", used to set the initial age information. With data *abstraction*, *agelist* is only accessible through *species*.

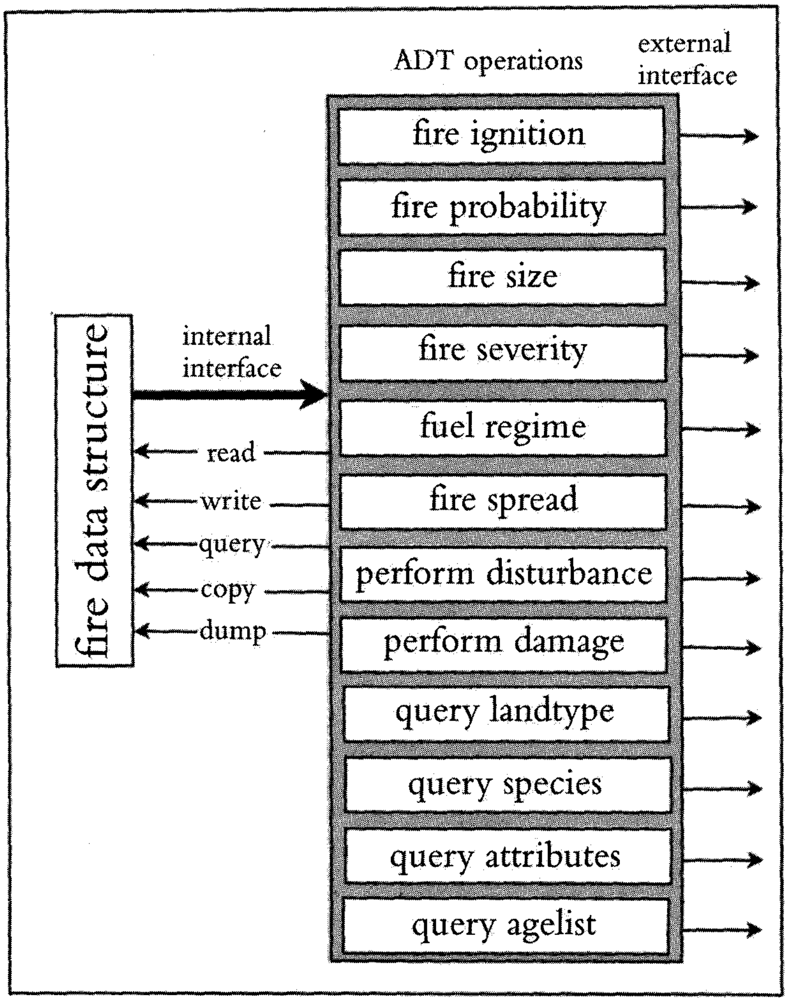
Landtype object

Landtype is a static, spatial object (Fig. 6.3). Several parameters are contained within the landtype object (Mladenoff *et al.*, 1996), including: (i) species establishment coefficients, (ii) disturbance characteristics such as mean fire return interval, and (iii) fuel accumulation and decomposition features (Fig. 6.7). These can vary among landtypes, but are homogeneous within a landtype. As previously discussed, landtype is a spatially scaleable object. More explicit simulations can be conducted if more differentiable environmental information is available in finer-grained *landtypes*. For example, if lightning is a primary driver of fire, terrain units which are more likely to have lightning can be processed from high resolution digital elevation models (DEMs). These units can be assigned shorter mean fire return intervals than less susceptible landtypes. Operations requested by other objects to *landtype* include establishment coefficients queried by *seeding*, and fuel regime, fire severity, and mean fire return interval queried by the *fire* object (Fig. 6.7).

Fire object

Fire is a spatially explicit and stochastic object (Fig. 6.3). *fire* simulates disturbance size, probability, ignition, spread, and severity using mathematically defined distri-

Fig. 6.8. LANDIS fire object, showing abstracted data type (ADT) operations.



butions in combination with various algorithms. The fire disturbance module and its interaction with succession is described in detail in He and Mladenoff 1999).

Fire size (*S*, Fig. 6.8), is a function of mean disturbance size (*MS*) based on the following distribution:

$$S = a\ (10.0)^r \times MS \tag{1}$$

MS is the estimate of the mean disturbance patch sizes; *r* is a normalized random number. The parameter *a* is called the *fire disturbance size coefficient*, and is used for model calibration (He and Mladenoff, 1999). With $r \sim N(0,\sigma^2)$, *S* follows the log-normal distribution with small disturbances being more frequent than large disturbances. Since *r* is randomly generated, *S* bears stochastic features.

Fire probability (*P*, Fig. 6.8) follows a negative exponential distribution (Eq. 2) based on the mean fire return interval (*MI*), and is a distribution used in other similar studies (Johnson, 1992; Johnson & Gutsell, 1994; Baker *et al.*, 1991; Turner *et al.*, 1993).

$$P = b \times lf \times MI^{-(c+2)} \quad (2)$$

MI is the mean number of years for fire to recur on a certain site. A smaller *MI* has higher fire probability. The parameter *lf*, denoting the year since last fire, linearly modifies *P*. With larger *lf*, there is a higher fire probability. The parameter *b* is the *fire probability coefficient* used for model calibration (He and Mladenoff, 1999).

Fire ignition (Fig. 6.8) involves an algorithm to randomly locate sites for starting a fire disturbance. The ignition coefficient, a function of map size, determines the number of sites checked during each model iteration. In LANDIS ignition does not necessarily result in a fire. Once a site is chosen for ignition, the fire probability *P* is computed (Eq. 2), and compared to a uniform random number *p* (0–1). Ignition results in a fire if $P>p$.

Once ignited, the fire spread algorithm (Fig. 6.8) is activated. Fire can spread randomly to adjacent sites based on susceptibility, but is more likely to spread in the wind direction that was randomly determined at the time of ignition. Fire spread is more computationally intensive, involving: (i) computing *P* of any new site to which the fire spreads, (ii) generating a random number *p*, and (iii) comparing *P* with *p* to determine if the site can burn. If disturbed, species data and the fuel regime of the site will drive the extent of fire damage. Fire-related mortality is determined from species-specific fire tolerance classes (retrieved from species attributes), fire susceptibility (retrieved from agelist), and fire severity class (He and Mladenoff, 1999). Thus, there can be cases of low severity fires where no species are killed, or high severity fires where all species are killed. If damage (species killed) occurs, the time since last fire on the site is set to 0.

The parameter *lf* (Eq. 2) defines the fuel regime on the site (Fig. 6.8). A larger *lf* implies more fuel accumulation and corresponding higher fire severity class. The relationship between *lf* and severity classes is defined for each landtype with the assumption that the fuel accumulation and decomposition rates are homogeneous within a landtype. Windthrow occurring within the previous decade or last several decades can increase fire severity class by adding more fuel to the *site*. On mesic landtypes for example, as time since last windthrow increases, fire severity class returns to a lower level, assuming greater fuel decomposition (Mladenoff *et al.*, 1996).

Wind object

The wind object is similar in design to the fire object (Fig. 6.3) and will not be fully discussed here. Species wind susceptibility classes are approximated based on species' life-spans. Species life-span is divided into five classes according to its respective life-span proportion: 20%, 50%, 70%, 85%, 100%. Thus, susceptibility class one (with age <20% of species life span) is the youngest age class and least susceptible; susceptibility class five (with age >85% of species life span) is the oldest age class and most susceptible. Wind disturbance severity class is categorical from 1 to 5, corresponding to the susceptibility class. Differential windthrow susceptibility by landtype is not currently included in the model.

Program and hardware characteristics

Data format and hardware requirements

LANDIS currently inputs and outputs popular raster GIS file formats, that can be converted either to or from various GIS platforms. LANDIS is a platform-independent application implemented for MS-Win32 families and UNIX operating systems (He *et al.*, 1996). An important advantage of LANDIS is the ability to simulate fairly large landscapes in a reasonably short time. LANDIS can simulate a 500 by 500 pixel landscape for 500 years in minutes. Processing time will vary depending on machine configuration and the complexity of the simulation task (He *et al.*, 1996).

Graphic interfaces

LANDIS has two graphic interfaces, the LANDIS *viewer* and an Arcview™ based graphic user interface (GUI). The LANDIS viewer is a stand-alone program that can display and analyze GIS files created by LANDIS. It can be used to display species' spatial information, fire or wind disturbance patterns, species age-class groups, and forest type maps at each time-step of a simulation. The LANDIS viewer is easy to use, fast, and requires less memory than GIS interfaces. However, the tradeoff is that it cannot perform complex spatial operations, query-by-example, or view large maps (e.g., larger than 500 × 500 pixels). The other optional LANDIS graphic interface, Arcview™ GUI, uses Avenue scripts from Arcview™. By incorporating all of the functions of the LANDIS viewer, this interface is able to integrate maps, tables, and charts. It also has more sophisticated GIS functions.

Spatial analysis program

APACK is a statistical analysis software package useful for calculating various landscape indices. It was initially designed to analyze LANDIS output maps, but it now can be applied to any raster GIS map with various formats (Mladenoff and Dezonia, 1997). APACK can be run under both PC and UNIX platforms. Numerous landscape indices can be individually selected for calculation, including fractal dimension, perimeter/area ratio, average polygon area, diversity, total area by type, average polygon perimeter, dominance, contagion, edge electivity index, electivity for overlays, percolation ratio, angular second moment, inverse different moment, and lacunarity (Mladenoff and Dezonia, 1997).

Model behavior and sensitivity analysis

Methods such as sensitivity analysis or error analysis are commonly used to evaluate ecological models (e.g., Dale *et al.*, 1988; Woodward & Rochefort, 1991; Botkin & Nisbet, 1992). These methods attempt to analyze the model behavior by ranking the parameters according to their contribution to the overall model response. Such an evaluation is useful for a model like LANDIS since it assists evaluation of model results and provides feedback to model design.

Methods

We created a random landscape of 100 × 100 cells (sites), each cell 30 m × 30 m size. Sugar maple (*Acer saccharum*), quaking aspen (*Populus tremuloides*), northern red oak (*Quercus borealis*) and open space were created as four categories randomly distributed on the landscape in approximately equal proportions. This design ensures that seed sources are not limiting anywhere on the landscape for purposes of the tests. In this case, seed of the three species can disperse to any site regardless of which seed dispersal routine is selected. To simplify the simulation, the three species were assigned as 10-year-old age cohorts, and included only one active landtype across the entire landscape. The designed mean fire return interval is 800 years and mean fire disturbance size is about 1 000 000 m^2 (100 ha or 1111 cells).

Model calibration and result verification

Sensitivity tests were performed by adjusting individual parameters ± 10 and 20% in separate model runs, and the results compared to the standard run with unmodified parameter values. These were done for most LANDIS parameters, but our discussion here will focus on two fire-related variables, mean fire return interval (standard run value of 800 years) and mean fire disturbance size (standard run value of 100 ha); and the species establishment coefficient (standard run value of 0.5), which responds to landtype and disturbance. Our discussion will also be limited to one measurement, species areal abundance on the landscape, as the most important response variable in the simulations.

Various stochastic components are built into LANDIS including disturbance, seed dispersal, and seedling establishment. Simulation results from independent runs are presumably different from each other unless a fixed random number seed is used (He *et al.*, 1996). In simulating disturbance, LANDIS uses either empirical or assumed means according to the defined distributions. As reported elsewhere, the variation of the simulated mean fire disturbance size for 20 different runs can be as high as ± 50% at the 85% confidence interval (He and Mladenoff, 1999). Therefore, model calibration and verification are important to ensure that either the empirical or the assumed means are correctly simulated. Conducting multiple, replicate simulations is often not feasible due to the large spatial data sets and long time spans involved. Furthermore, algorithms creating new maps from the multiple, replicate maps are not yet available. Thus, verification and calibration of a single run is important for stochastic models as discussed elsewhere for LANDIS (He and Mladenoff, 1999).

Simulation verification and model calibration were performed following the routine discussed in He and Mladenoff (1999). In this procedure, sensitivity analysis is based on comparisions of output from a model run with a single modified parameter against a base model run. A fixed random number seed is used for both simulations, so that change between the two runs is attributable to the degree of parameter modification and not stochastic effects.

Results

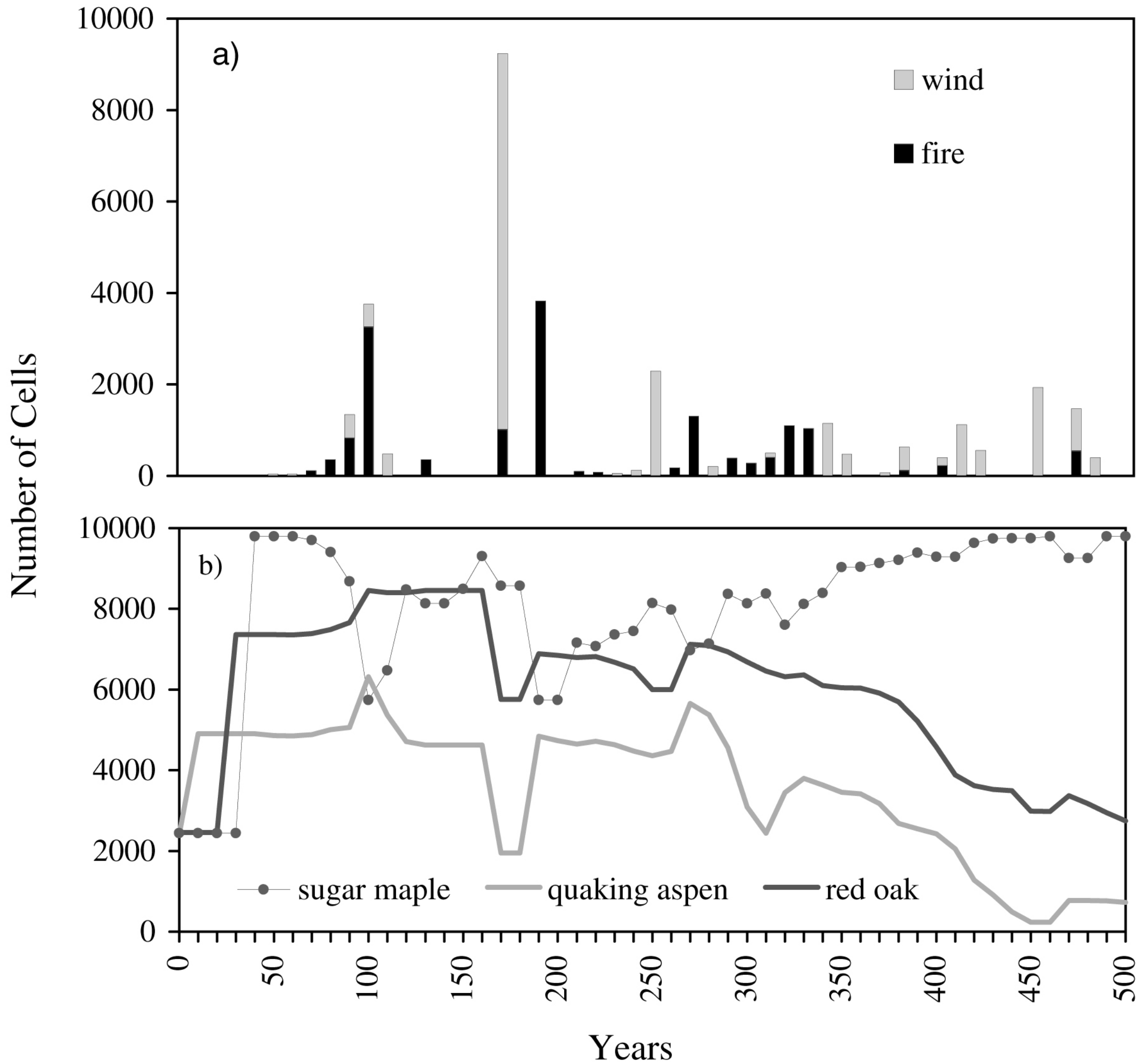
Standard run

A 500-year LANDIS run was conducted with the standard parameters, generating fire and windthrow disturbances based on the assigned return interval parameters. The model randomly generated 19 fires and 20 windthrow disturbances with varied sizes (Fig. 6.9(*a*)). Fires at years 100, 190, 270, 320, and 330 were relatively large. A very large windthrow event occurred at year 170, with several significant wind disturbances at years 250, 340, 450.

The disturbances interact with other processes such as establishment, and background mortality (when maximum longevity is reached), to affect trajectories of species abundance. Dominant influences on succession for different factors can be observed from the trajectories (Fig. 6.9(*b*)). At year 0, all species have equal abundance at about one-quarter of the total area. At year 10, aspen reaches its sexual maturity first (20 yr) and begins to seed into the quarter open area. Aspen is not able to seed into cells where oak or maple reside due to its lower shade tolerance. At year 10, aspen abundance doubles, but oak and maple remain unchanged since neither are mature. Red oak is less shade tolerant than sugar maple but more than aspen. At year 20 oak is mature and seeds into the aspen dominated area. Oak abundance then reaches three-quarters of the landscape by year 30. Sugar maple reaches sexual maturity (40 yr) at year 30 of the simulation, and is able to seed into other areas at year 40. Fuel has accumulated and small fires occur at years 70 to 90. These fires reduce the sugar maple, which is most susceptible to fire of the three species. The area of the other species remains relatively unchanged, since red oak and aspen either survive or resprout under these low severity fires. Fire at year 100 removes a significant amount of sugar maple and creates open space. Red oak and aspen both benefit from the fire as shown by the increase in their trajectories for a few decades at year 100.

From year 110 to 160, sugar maple gradually recovers from the major fire, but does not reach its former levels due to small fires elsewhere on the landscape. Red oak and aspen remain relatively stable with oak increasing slightly over aspen. At year 170, the average age of the second generation aspen has reached 60 years old, and first generation red oak reaches 170 years. Oak and aspen are now older and more susceptible to windthrow disturbance. The large windthrow at year 170

Fig 6.9. (a*) Year and size of fire and wind disturbance under assigned standard parameters. (* b*) The abundance of sugar maple, quaking aspen, and red oak under the assigned standard disturbance regime parameters.*



removes a significant amount of aspen and oak from the landscape. Sugar maple in the understory is younger and not greatly affected by the wind. Shortly after the large windthrow, fire susceptibility is enhanced by the greater level of fuels present and a large fire significantly reduces sugar maple at year 190. Aspen benefits most from the fire disturbance and quickly occupies the open space. For the remainder of the simulation several small fires occur, but sugar maple largely out competes red oak and aspen with this disturbance regime, fully occupying the landscape. Red oak substantially declines in abundance, and aspen is nearly removed from the landscape (Fig. 6.9(*b*).

Altered mean disturbance size

Responses of sugar maple and aspen are examined for the test runs with altered parameters, although red oak also was included in the simulations. As in the standard run, the response of red oak to disturbance generally remains intermediate to the other two species. Compared with the standard run, fire disturbance size fluctuated as mean disturbance size was adjusted ±10% (Fig. 6.10(*a*), Eq. 1). In these tests, the dominant roles of each factor (except fire) discussed in the standard run still play approximately the same roles at their respective time steps. To avoid confusion, we will describe the parameter changes as raising and lowering, and the species abundance responses as increases and decreases.

Lowering mean disturbance size by 10% results in an average 1.5% increase in sugar maple abundance, since it is the most shade tolerant and fire sensitive among the three species (Fig. 6.10(*b*, Table 6.2). Compared with the standard run, quaking aspen decreases in abundance by an average 5.7% (Fig. 6.10(*c*), Table 6.2). In the second test run, lowering mean disturbance size by 20% (Fig. 6.11(*a*)), both sugar maple and quaking aspen respond more strongly compared to the +10% scenario. Sugar maple abundance increases an average 3.4% (Fig. 6.11(*b*)), 1.9% more than the +10% scenario, and quaking aspen decreases 11.9% (Fig. 6.11(*c*)), a 6.2% greater response than the +10% scenario (Table 6.2).

Raising mean disturbance size by 10% (Fig. 6.10(*a*)) results in sugar maple abundance decreasing on average 5.0% (Fig. 6.10(*b*)). Quaking aspen benefits from this decrease, with its abundance increasing an average 8.5%. But the change of abundance of aspen is more obvious than that of maple (Fig. 6.10(*c*)). Raising mean disturbance size by 20% (Fig. 6.11(*a*)) results in sugar maple abundance decreasing an average 6.6% (Fig. 6.11(*b*)), or 1.6% greater decrease than the +10% scenario. Quaking aspen benefited from this decrease, its abundance increasing an average 13.4% (Fig. 6.11(*c*)), 4.9% more than +10% scenario (Table 6.2).

Altered mean fire return interval

Raising the fire disturbance interval decreases fire probability, and lowering fire disturbance interval increases fire disturbance probability. The results of the changes are not as direct as found in changing mean disturbance sizes (Table 6.3). Mean return interval is used to calculate disturbance probability P, according to Eq. 2, which is site specific.

There is little obvious change between the standard run and the simulation with the mean fire return interval raised 10% (Fig. 6.12(*a*)). There is one fewer fire over the simulation, with a fire dropped at year 340. The effect of that drop can be observed by the slight increase in sugar maple abundance at year 340 (Fig. 6.12(*b*)) and a small decrease in aspen abundance at year 340 (Fig. 6.12(*c*)). Overall, these changes reflect an average abundance increase of 0.9% for sugar maple and 3.5% decrease for aspen (Table 6.2). Raising mean fire return interval by 20% resulted

Fig 6.10. (a*) Simulated disturbances with mean disturbance size +/- 10%. (* b*) and (* c*) are abundance of sugar maple and quaking aspen responding to (* a*).*

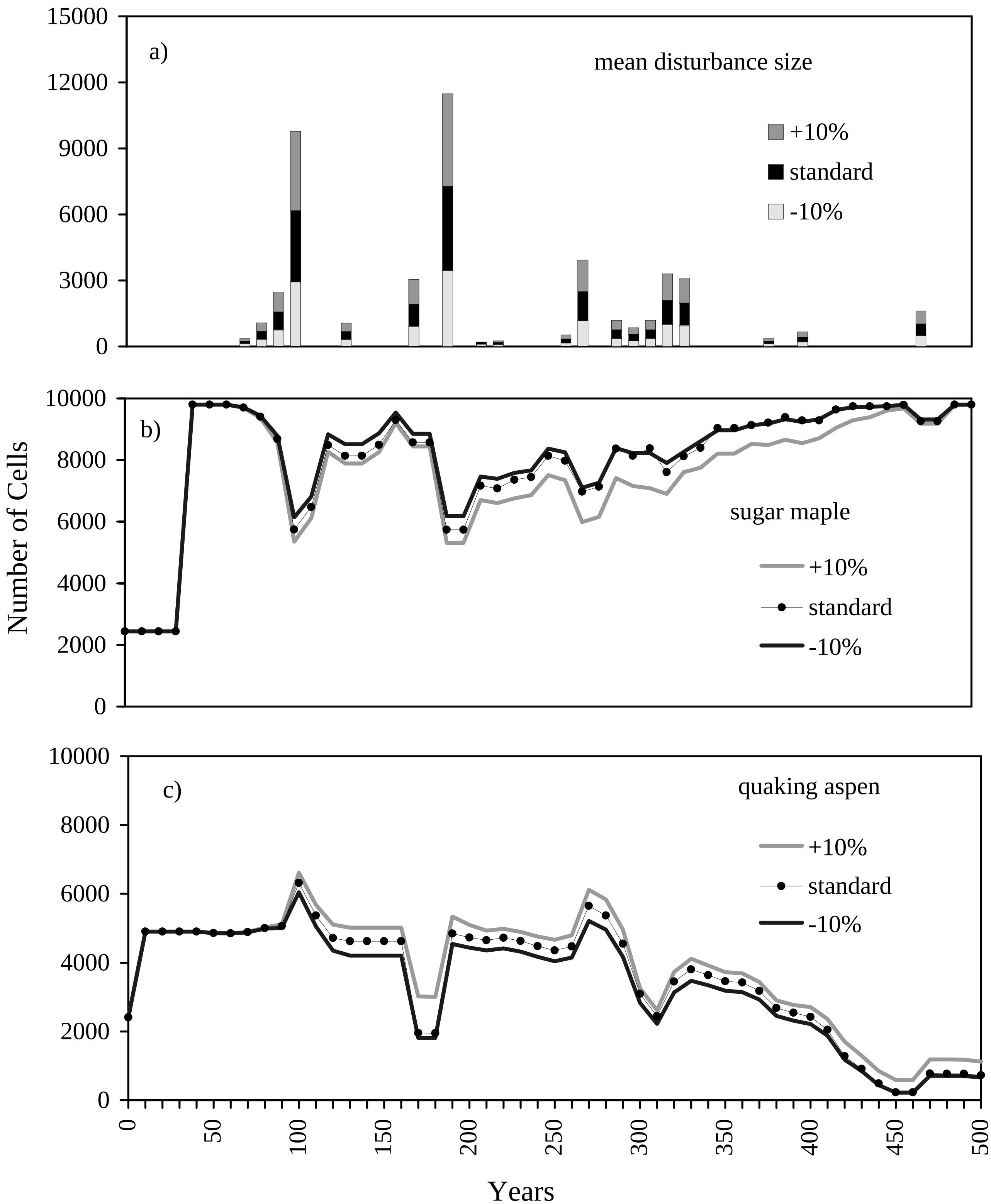


Table 6.2. *Species abundance changes between standard run and simulations with altered fire parameters at the end of 500-year simulations*

	Sugar maple		Quaking aspen	
Parameter altered	Cells	Change (%)	Cells	Change (%)
MS–10%	8158	+1.5	3335	–5.7
MS+10%	7636	–5.0	3834	+8.5
MI–10%	7337	–8.7	4378	+23.8
MI+10%	8107	+0.9	3412	–3.5
MS–20%	8311	+3.4	3115	–11.9
MS+20%	7503	–6.6	4009	+13.4
MI–20%	7330	–8.8	4378	+23.8
MI+20%	8805	+9.6	2310	–34.7

MS – mean fire size, MI – mean fire return interval. Change (%) is based in comparison of simulations with modified parameters with the standard parameter value run.

in four fires dropped at years 190, 260, 340, and 470 respectively (three more fires dropped comparing with the +10% scenario) (Fig. 6.13(*a*)). Sugar maple largely responds to these changes, especially from the drop of a relatively large fire at year 190 (Fig. 6.13(*b*)). Sugar maple mean abundance increases substantially by 9.6%, 8.7% greater compared with the +10% scenario (Table 6.2). Aspen, on the other hand, responds more abruptly at year 190 (Fig. 6.13(*c*)). Its average abundance decreases significantly by 34.7%, 31.2% more than the +10% scenario.

For the –10% return interval scenario, there are four more fires generated at years 30, 210, 420, and 450 (Fig. 6.12(*a*)). These four extra fires remove substantial amounts of sugar maple (Fig. 6.12(*b*)), resulting in the average abundance of sugar maple decreasing about 8.7% (Table 6.2). Again quaking aspen substantially benefits from the fires with its average abundance increasing 23.8% (Fig. 6.12(*c*), Table 6.2). For the –20% scenario, only a small fire at year 30 was added over the –10% scenario. Both sugar maple and aspen abundance trajectories change little in response to this single disturbance increase (Fig. 6.12(*b*), (*c*) and Fig. 6.13(*b*),(*c*)).

Altered species establishment coefficient

Average species abundance responses reflect the same directional trend expected from increasing or decreasing their establishment coefficients. Raising the species establishment coefficients by 10% results in 1.5, 4.3, and 11.5% increases of sugar maple, red oak, and quaking aspen, respectively (Fig. 6.14(*a*), (*b*), (*c*)). Raising them by 20% results in 3.0, 6.9, and 13.9% greater increase for these three species respectively (Fig. 6.15(*a*), (*b*), (*c*)). A 10% lowering of species establishment coefficients results in 4.7, 4.3, and 7.8% decrease of sugar maple, red oak, and quaking aspen respectively (Fig. 6.14(*a*), (*b*), (*c*)), while greater magnitudes of change were observed for all species with the –20% alteration of establishment coefficients (Fig. 6.15(*a*)–(*c*)).

Fig 6.11. (a*) Simulated disturbances with mean disturbance size +/- 20%. (* b*) and (* c*) are abundance of sugar maple and quaking aspen responding to (* a*).*

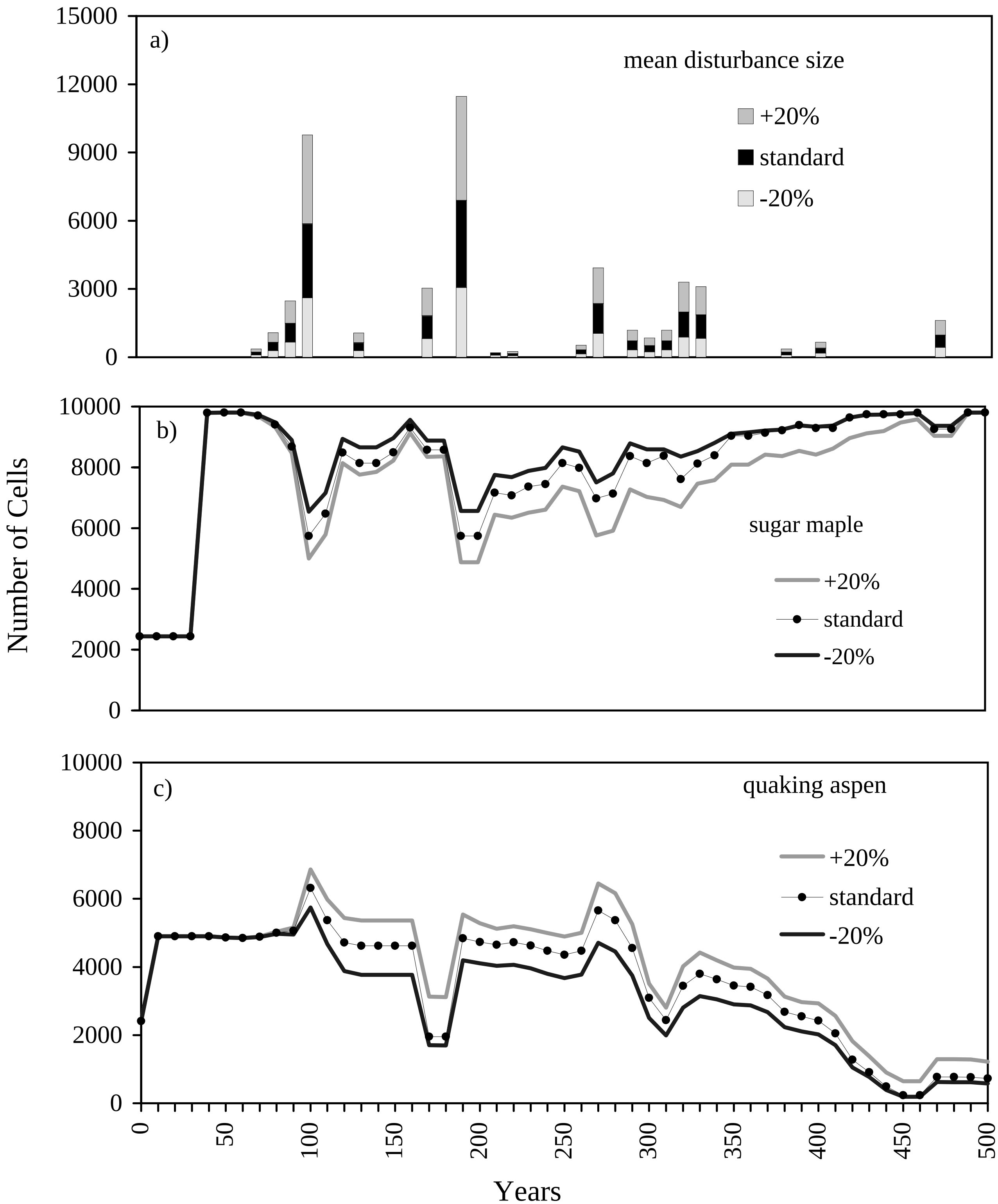


Table 6.3. *Species abundance changes corresponding to altered establishment coefficient (e) sensitivity at the end of 500-year simulations*

Establishment coefficient	Sugar maple (%)		Red oak (%)		Quaking aspen (%)	
	Abundance	Change	Abundance	Change	Abundance	Change
e+10%	71.5	+1.5	59.3	+4.3	25.2	+11.5
e–10%	67.2	–4.7	54.5	–4.3	20.8	–7.8
e+20%	72.6	+3.0	60.8	+6.9	25.8	+13.9
e–20%	64.9	–8.0	50.5	–11.3	17.9	–20.6

Summary

Model behavior observed for all scenarios indicate that the model responds reasonably to the parameter changes. The raising and lowering of mean fire return intervals do not produce proportional results in the increase and decrease of species abundance compared with the standard run (Table 6.2). The reasons include both stochastic factors and the mechanism of the fire probability equation (Eq. 2). As discussed in *fire* object, when $P > p$ (a LANDIS generated random probability) disturbance is initiated. But even when P is lowered due to the +10 or 20% altered mean fire return intervals (*MI*) scenarios, P is still generally larger than the random probability p, and therefore most disturbances are still performed. Secondly, linearly changing *MI* does not result in a linear response of P, since P follows a negative exponential distribution (Eq. 2). Generally, raising fire return interval will produce smaller changes than lowering the return interval (He and Mladenoff, 1999). For the same reason, mean disturbance size (*MS*) does not respond linearly to the adjustments. This behavior can be modified by altering the distributions used in the algorithm.

The raising and lowering of species establishment coefficients do not always result in an equal response in species abundance (Table 6.3) due to the differences in species life history characteristics and competition on occupied landtypes. For dominant shade-tolerant species, such as sugar maple, the +10% scenario did not create a significant increase. The response of red oak under +10% falls in the middle. Aspen, the least shade-tolerant species, responds the strongest in all cases. The most shade-tolerant species (sugar maple) is less affected by such changes, and the least competitive but most opportunistic species (aspen) responds the greatest.

Application

A fuller demonstration of the model is provided here by simulating a large, heterogeneous landscape with multiple landtypes and fuller complement of species and age classes. A large portion of northern Wisconsin was simulated, an area within the northern US Great Lakes States. This region has been highly altered by human activity in the last century, and is dominated by young, second- and third-growth

Fig 6.12. (a*) Simulated disturbances with mean fire return interval +/- 10%. (* b*) and (* c*) are abundance of sugar maple and quaking aspen responding to (* a*).*

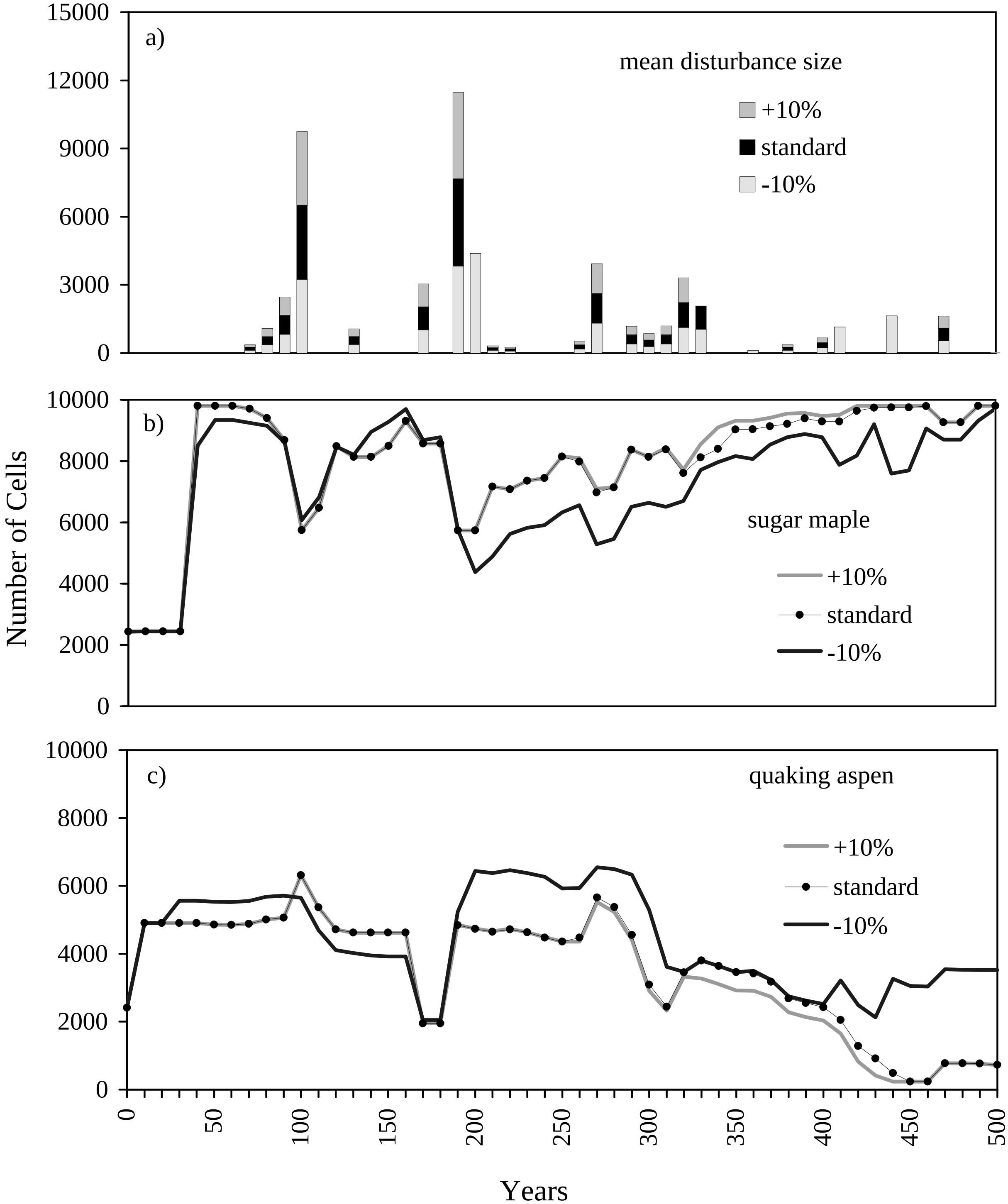


Fig 6.13. (a*) Simulated disturbances with mean fire return interval +/- 20%. (* b*) and (* c*) are abundance of sugar maple and quaking aspen responding to (* a*).*

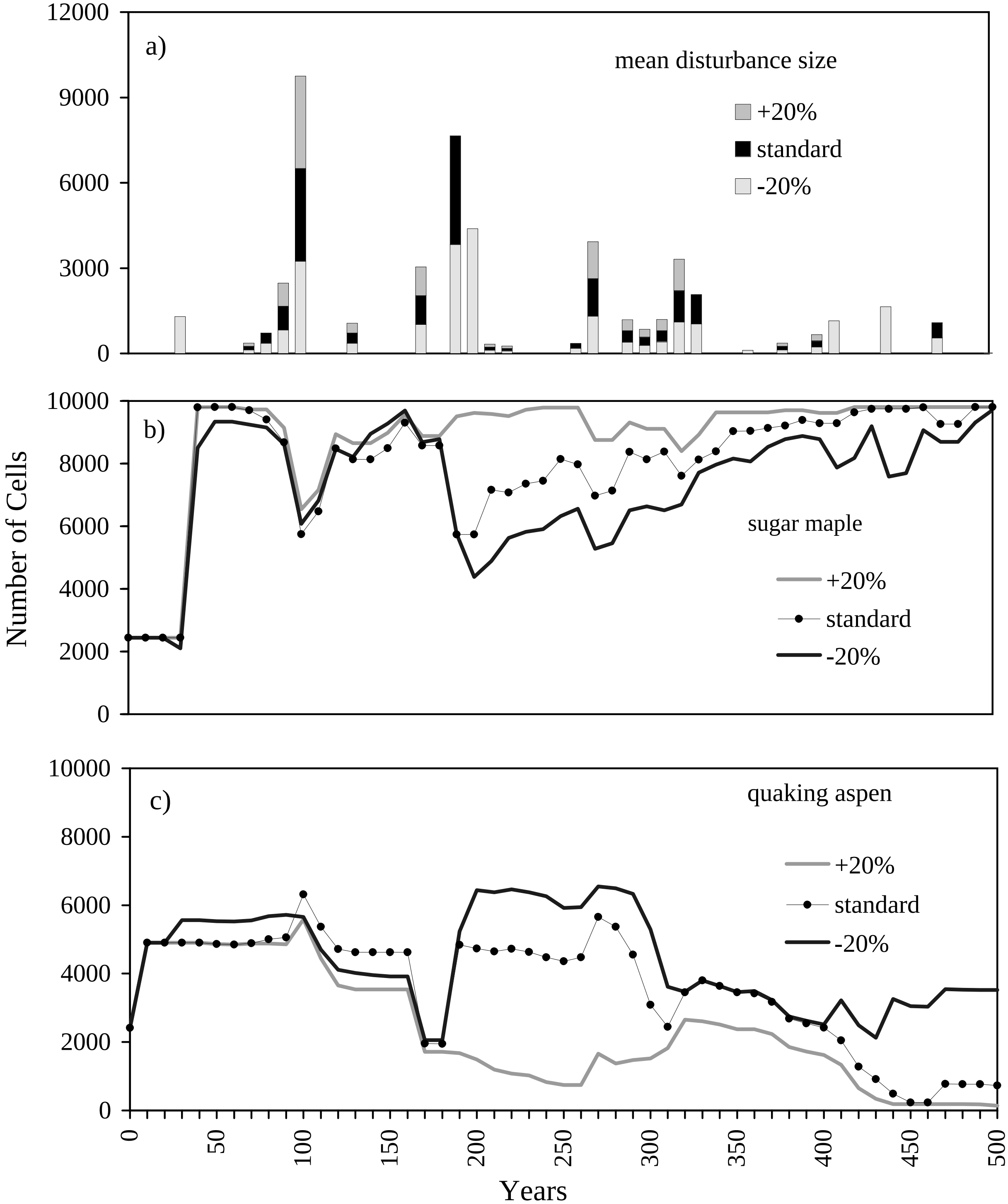


Fig. 6.14 Species abundance reponse to establishment coefficient changes of +/- 10% for (a*) sugar maple, (* b*) quaking aspen, and (* c*) red oak.*

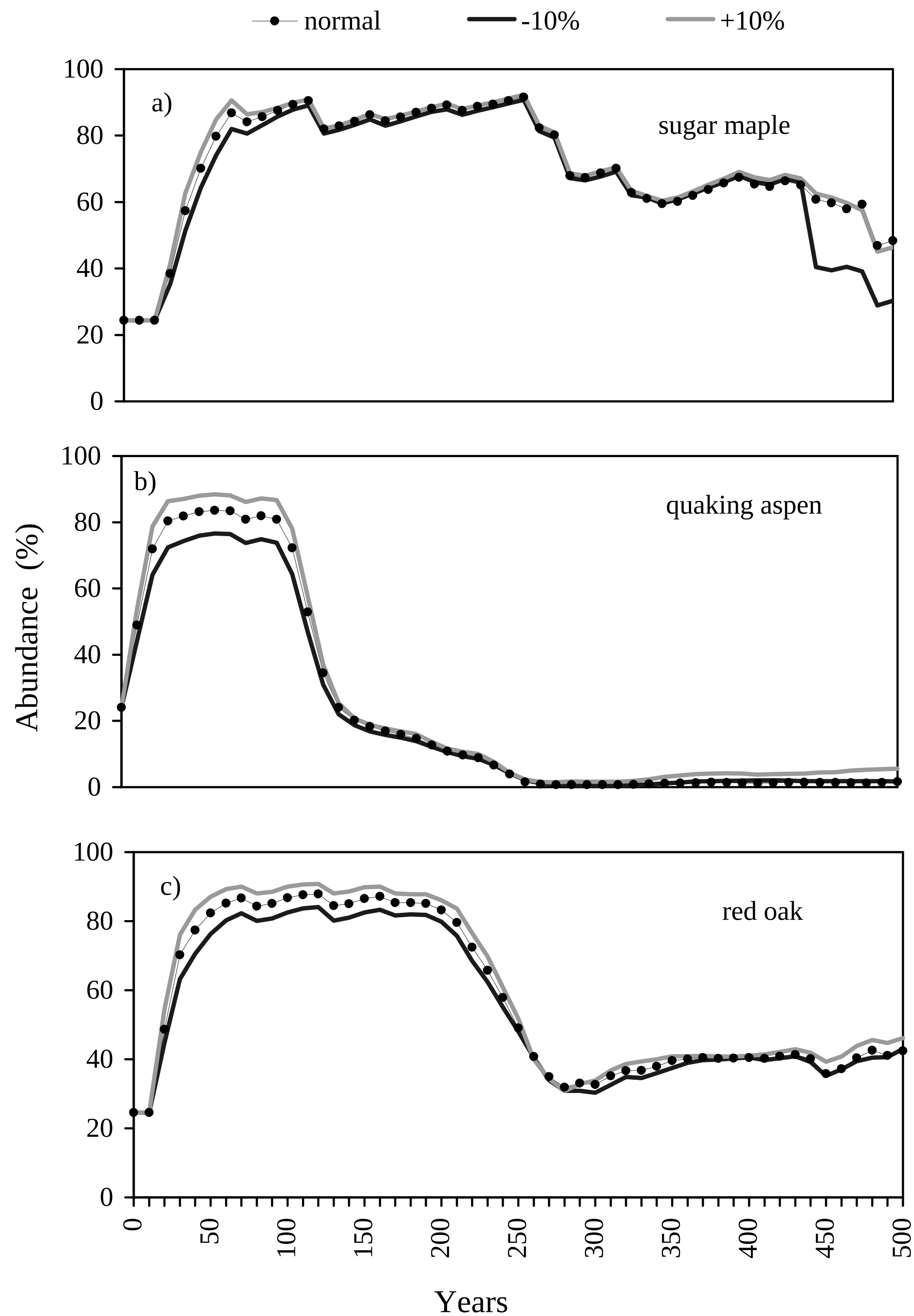
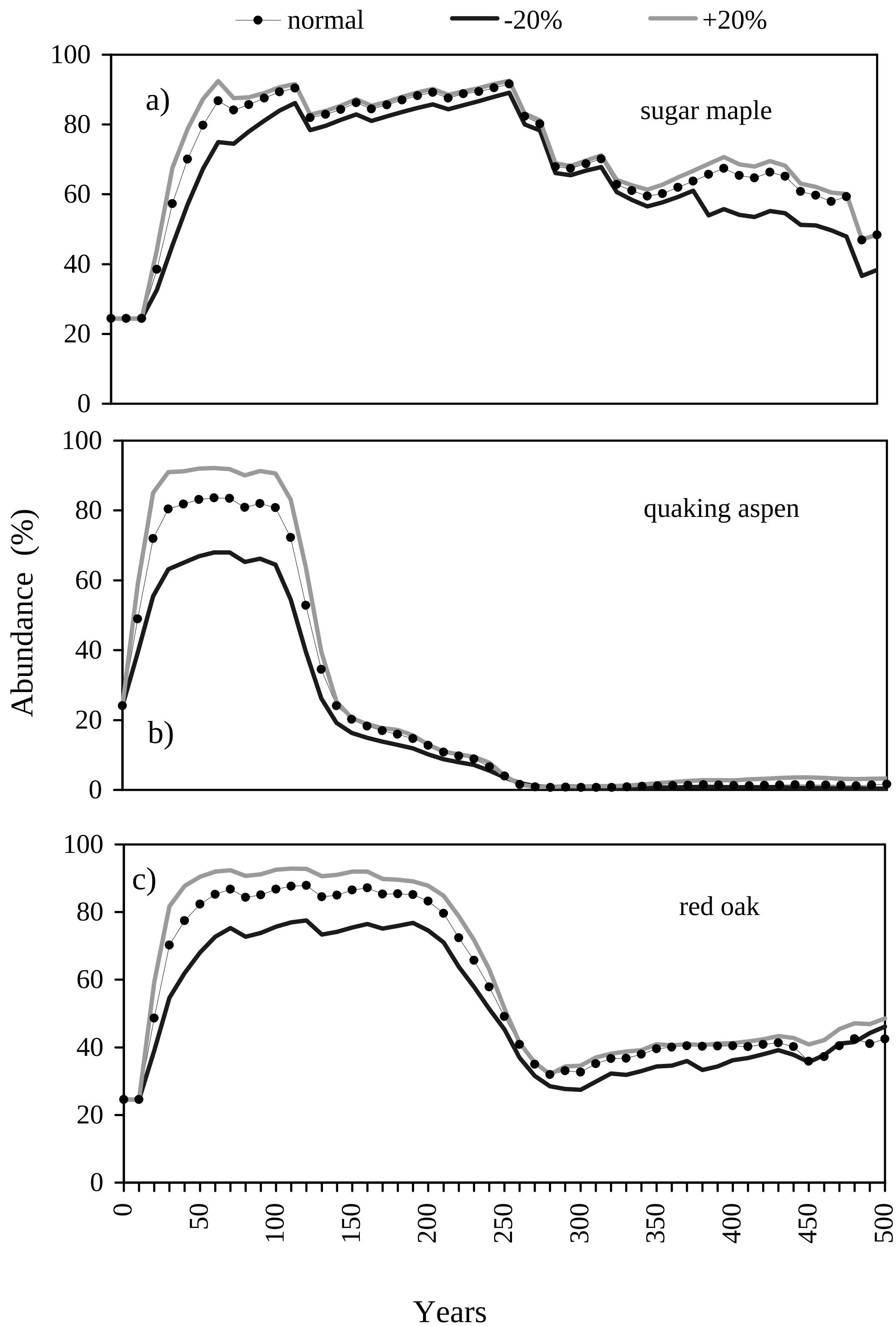


Fig. 6.15. Species abundance reponse to establishment coefficient changes of +/- 20% for (a*) sugar maple, (* b*) quaking aspen, and (* c*) red oak.*



forests (Mladenoff and Pastor, 1993). This application of the model addresses the question of how the regional landscape would recover from the current condition if natural successional processes operated, both with and without fire and wind disturbance. This simulation provides a baseline projection of what could occur without continued forest harvesting.

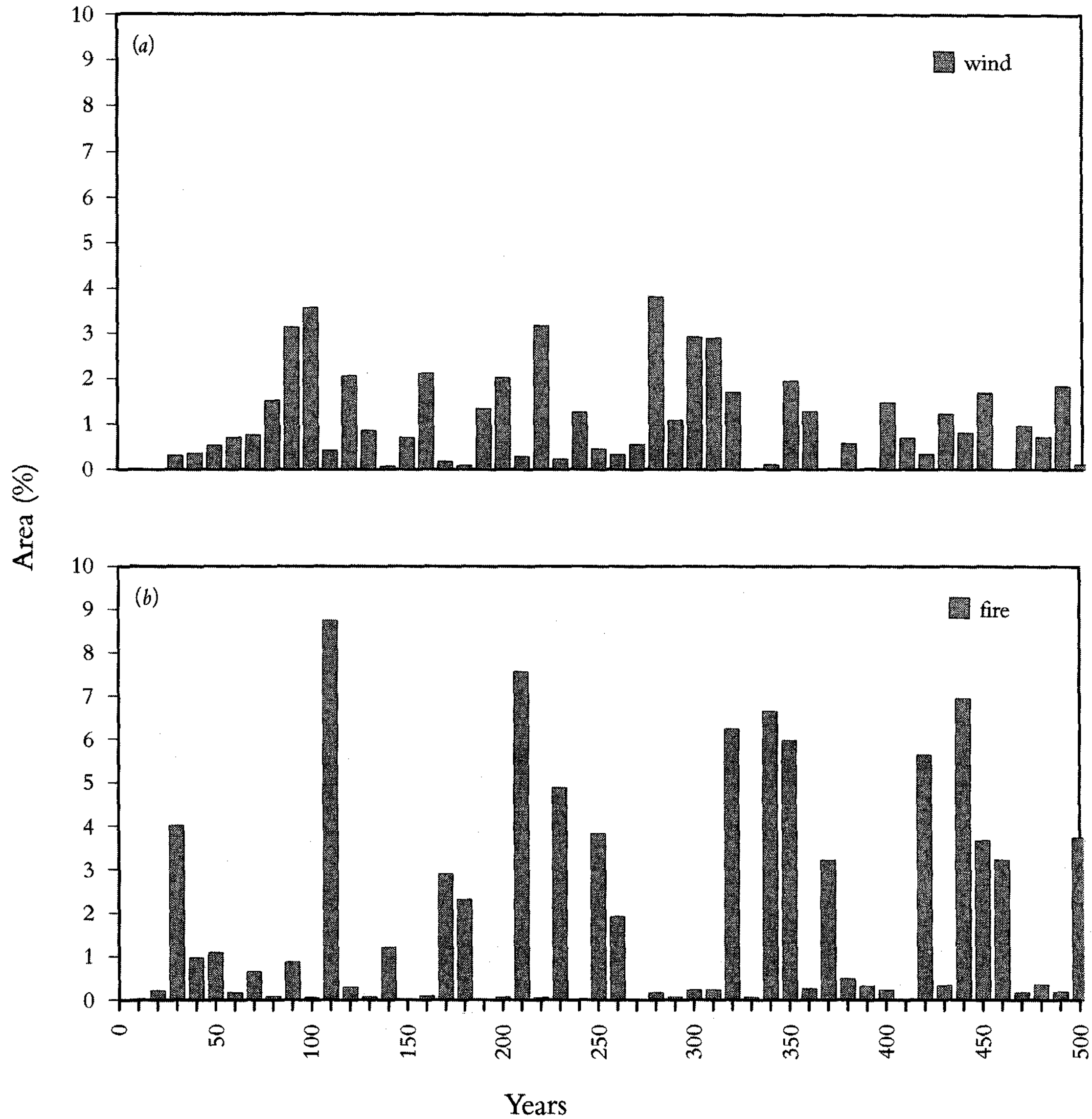
Methods and input data

Our study area comprises about 1.5 million hectares in northwestern Wisconsin. Ecologically, the area is in the transitional zone between boreal forest to the north and temperate forests to the south (Curtis, 1959; Pastor and Mladenoff, 1992). Twenty-three forest species were incorporated in the simulation, with dominant species spatial distributions derived from a species-level classification of Landsat TM imagery (Wolter *et al.*, 1995). This layer maintains dominant species patch structure on the landscape. Secondary species were assigned primarily from their association with the canopy dominants and importance in the US Forest Service Eastwide Forest Inventory and Analysis (FIA) database for the study area (Hansen *et al.*, 1992). Species age class information and associated species spatial distributions were derived by combining TM imagery, FIA, and ecoregions, and assigned probabilistically (He *et al.*, 1998, 1999). Landtype data for this area were available from a quantitative ecoregion classification (Host *et al.*, 1996). The entire study area comprises about 850 × 550 cells with the cell size of 200 m × 200 m, 10 ecoregions (landtypes), and 194 map input classes.

LANDIS runs were conducted with no disturbance (both wind and fire disturbance turned off), and with both disturbances on. When simulating disturbances, moderate disturbance regimes were assumed for both fire and wind. The mean disturbance size (*MI*) for fire is set to about 1.5% of the total area and maximum fire size is <12% of the total area. Mean return intervals (*MI*) for fire vary among landtypes from 200 to 1000 years based on the literature (e.g., Canham and Loucks, 1984; Frelich and Lorimer, 1991; Heinselman, 1973, 1981). Wind disturbance is set more diffuse than fire. Mean disturbance size (*MS*) for wind is set to about 1.0% of the study area, and maximum wind disturbance size is about 4% of the study area. The mean disturbance interval (*MI*) for wind is set at 1000 years.

Model calibration and evaluation was carried out according the procedure described above (see *Model behavior and sensitivity analysis* and *Model calibration and evaluation*) where single model runs are compared using paired simulations with a fixed random number seed (detailed by He and Mladenoff, 1999). For a given parameter, the simulated mean (M') is assessed for the degree to which it approximates the known mean (M) from historical or empirical data of the study area. M' can be described as a proportion (of M) (Guertin and Ramm 1996) where $Accuracy = M'/M \times 100$. For example, disturbance size coefficient a (Eq. 1) and disturbance probability coefficient b (Eq. 2) can be adjusted accordingly to ensure acceptable model accuracy within a predetermined range, and that the model assumptions are being correctly simulated. Percent accuracy (Guertin and Ramm,

Fig. 6.16. Simulated (a) *wind and* (b) *fire disturbances after calibration.*



1996) assesses the similarity of the modified run to the base run (He and Mladenoff, 1999).

Results and analysis

Wind

Various windthrow events occurred during the 500-year LANDIS run (Fig. 6.16(*a*)). The simulated MS is 4034 cells, which is approximately an 85% accuracy based on the known MS set in the simulation. Simulated wind MI is 910 years, which is 91% accuracy of the MI designed for this area. Windthrow has a stronger effect on altering species age structure than it does on species composition, but at some locations stronger windthrow events, such as severity classes 4 and 5, may create gaps in even aged stands. The shapes of windthrow events are not deterministic. Rather, they are the result of interactions of site condition, species age information, and wind severity classes. For example, there are several patches of windthrow at year 160 with different shapes and severity classes (Fig. 6.17(*a*): see color section). The cumulative windthrow map (Fig. 6.17(*b*)) illustrates that windthrow creates a more diffuse, salt-and-pepper pattern throughout the landscape than does fire, which generally spreads contiguously.

Fire

Fire is more difficult to simulate than wind since it has greater variation in disturbance sizes (Fig. 6.16(*b*)) and mean return interval among landtypes. On landtypes with 200-year MI, such as landtype 5, the simulated MI is 271 years (78% accuracy); on landtypes with 500-year MI, including landtypes 4,7, 8, and 11, the simulated MI is 542 years (91% accuracy) on landtypes with 800 year MI including landtypes 3 and 7, simulated MI is 670 years (84% accuracy); on landtypes with 1000-year return interval including landtypes 2 and 6, simulated MI is 1053 years (95% accuracy). The spatially explicit descriptions of fires can be shown as a map of examples (Fig. 6.17(*c*),(*d*): see color section).

Less severe fires can also alter species age structures by removing younger age-cohorts. Stronger severity fires have greater effects on the landscape, which often result in new patches of different species composition. For example, the 420-year fire occurs in several patches randomly located on the landscape, with fire severity classes 2, 3, and 5 (Fig. 6.17(*c*)). Impacts of these fires can be examined at the individual species level. Both red pine and jack pine are fire-intolerant species and common on landtype 5, the pine barrens. Red pine is substantially killed by the severity 3 fire spreading on to the barrens (Fig. 6.18(*a*): see color section). The open space created makes it possible for jack pine, an early successional species, to become established (Fig. 6.18(*b*): see color section). The fire primarily on landtype 9 is a severity class 3 fire (Fig. 6.17(*c*)). The open space created by this fire allows quaking aspen, an early successional species favored on this landtype, to establish itself (Fig. 6.18(*c*)). Northern red oak is also able to seed into the open area due to the surrounding seed source availability (Fig. 6.18(*d*): see color section).

More general fire impacts can be examined at the community level. Before year 420, pine is dominant on the barrens (landtype 5), and maple is dominant on landtype 6 (Fig. 6.19(*a*),(*b*): see color section). At year 420 after the fire occurred, the patch on landtype 5 is still dominated by pine since other species have low establishment probabilities on this landtype (Fig. 6.19(*c*): see color section). On landtype 6, aspen and other hardwoods benefit from the severity 5 fire and are able to invade (Fig. 6.19(*c*)).

Succession dynamics

As discussed in the sensitivity analysis, species abundance trajectories are a result of seeding and establishment, mortality, wind and fire disturbance, and competition. The dominant role of each factor can be observed at different stages of forest succession from the individual species trajectories. In the following, some of the most common deciduous and conifer species in the area are focused on.

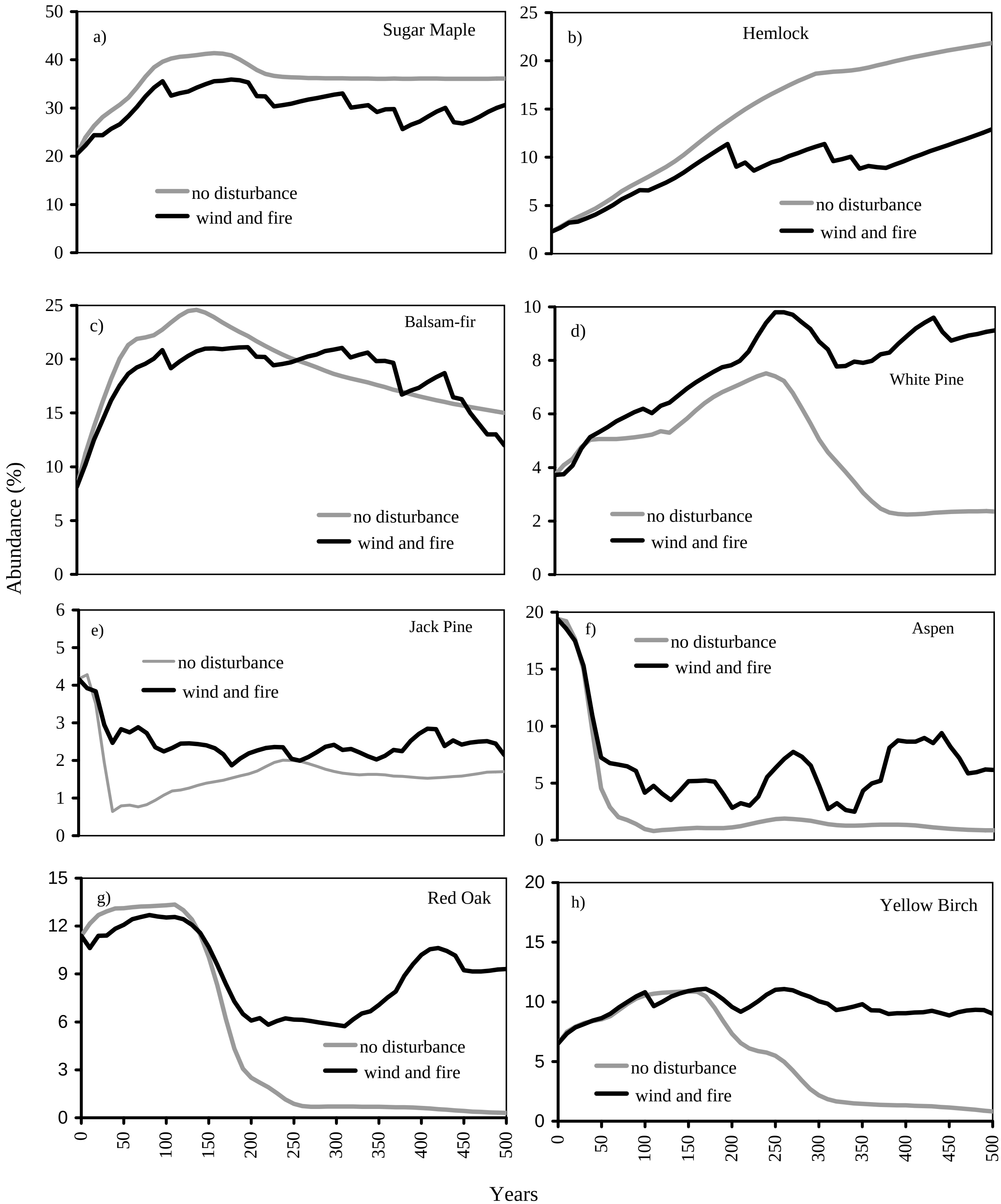
The magnitude of the impact of disturbance on different species varies. The most shade-tolerant species such as sugar maple, hemlock, and balsam fir are not generally favored by fire disturbance (Fig. 6.20(*a*),(*b*),(*c*)). Sugar maple remains dominant on landtypes other than 5 and 9, since the fire return interval on the other landtypes is 500 years and above. At year 500, sugar maple is able to spread to 35% of the landscape without fire, and 25% with fire (Fig. 6.20(*a*)). Hemlock abundance is also usually negatively affected by fires. It generally increases, reaching about 11% of the landscape at year 500, about 10% less than without fire disturbance (Fig. 6.20(*b*)). The low abundance percentage of hemlock at year 0 indicates the historical cutting and current human impacts on this species (Mladenoff and Pastor, 1993; Mladenoff and Stearns, 1993). Our simulation suggests that, even by restoring pre-European disturbance regimes, former dominant species in our region such as hemlock, yellow birch, oak, and pine require 100–500 years to recover their former landscape equilibrium proportions. Human alteration of these landscapes to a degree that limits seed sources contributes to slow species recovery, along with altered disturbance regimes.

White pine, a relatively widespread species, needs fire to become established on most landtypes. With fire disturbance its abundance reaches about 9% of the landscape at year 500 (Fig. 6.20(*d*)). Its low occurrence at year 0 also reflects previous harvesting of this species. Jack pine, a species primarily on pine barrens, responds positively to fires (Fig. 6.20(*e*)). Jack pine depends on fire to remove red pine and oak, which are more shade-tolerant competitors of jack pine on the barrens. Aspen, red oak, and yellow birch all show positive responses to fire throughout the landscape with their abundances reaching around 8% (Fig. 6.20(*f*), (*g*), (*h*)).

Application summary

This demonstration of the LANDIS model illustrates application to a large, heterogeneous landscape, with the simulation based on current forest input. Simulating this northern Wisconsin landscape demonstrates landscape recovery from current conditions, which is a landscape highly altered by human use during the past century (Mladenoff and Pastor, 1993). We simulated the interaction of fire and windthrow disturbances, which are the two dominant disturbance modes operating in this region. Fire and windthrow interact with species distribution, abundance and seed sources to drive successional change on the landscape. The spatial pattern of the current, human-dominated landscape is shown to alter natural dynamics by dramatically reducing and increasing different tree species, their age-class distribu-

Fig. 6.20. Comparison with and without wind and fire disturbances for (a) *sugar maple,* (b) *hemlock,* (c) *balsam-fir, (d) white pine,* (e) *jack pine,* (f) *aspen,* (g) *red oak, and* (h) *yellow birch.*



tion, and seed sources. The simulation suggests that hundreds of years would be required for the forest landscape to return to approximate pre-settlement conditions, even without continued harvesting.

Conclusions

The design and behavior of LANDIS has been described, illustrating the model ability to integrate fire and wind disturbance with forest succession, and simulate forest landscape change at the tree species level. With object-oriented design, the model provides flexibility of upgrading as our knowledge of ecological processes increases. New modules such as timber harvest, which is completed (E. J. Gustafson *et al.*, unpublished data), insect defoliation, or forest disease can be added to the model without affecting model integrity. The model responded reasonably to the parameter changes in the sensitivity analysis. Changes of ±20% show greater responses than the corresponding ±10% scenario. The model does not produce equal or proportional responses with raising or lowering of some parameters due to both stochastic and non-linear mechanisms built into the model.

With built-in stochastic components and the semi-quantitative method employed to record species age cohort information, LANDIS is not designed to predict the occurrence of a given event or change on a single real location. The model is best viewed as tool for projecting plausible landscape patterns resulting from different simulated assumptions and scenarios. Such models are useful for increasing understanding of the complex interactions that occur on landscapes (Dale, 1998). If realistically parameterized and properly calibrated, LANDIS can be used to examine the trend and pattern of change over long time periods. It can be effectively used to examine forest landscape change under a set of assumptions, such as severe fire disturbance, climate warming, or various management scenarios. The model preserves the flexibility of coping with various input data at a variety of scales. This can be an important feature where not all desired data are available for a study region.

The model application to a real landscape shown above with only natural processes operating, can serve as a useful baseline against which to assess various landscape management or other change scenarios. Current or projected forest harvesting can be simulated to project landscape-scale consequences of forest management scenarios (Gustafson *et al.*, 1999). The model can also be used to assess effects of climate warming on the forest landscape, by linking LANDIS with an ecosystem process model that can directly accept climate variables, producing species establishment coefficients for current and changed climate conditions (He *et al.* (1999a).

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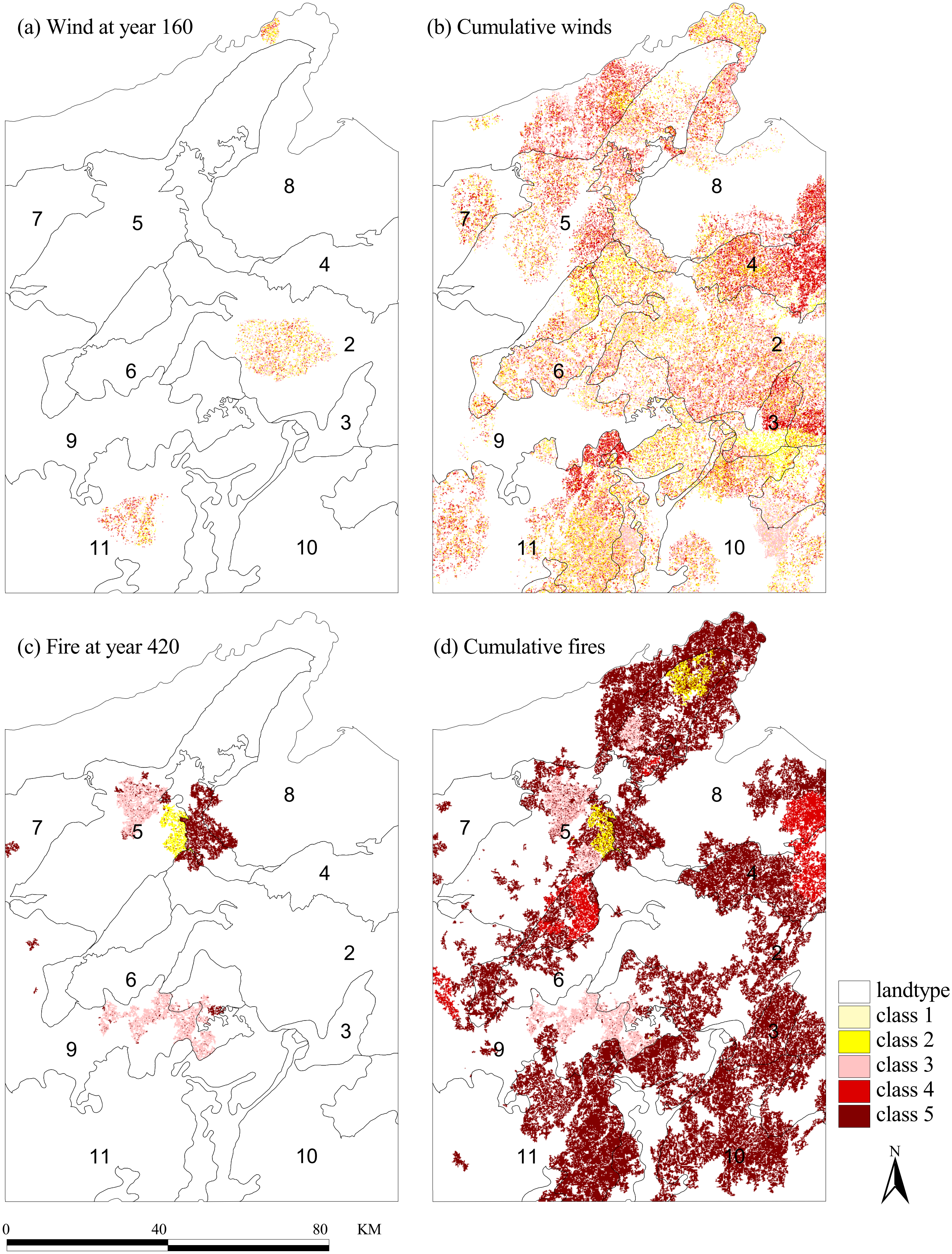

Figure 6.17. (a) Wind disturbances at year 160. (b) Cumulative wind disturbances over 500 year simulation. (c) Fire distubances at year 420. (d) Cumulative fire disturbances over 500 year simulation.

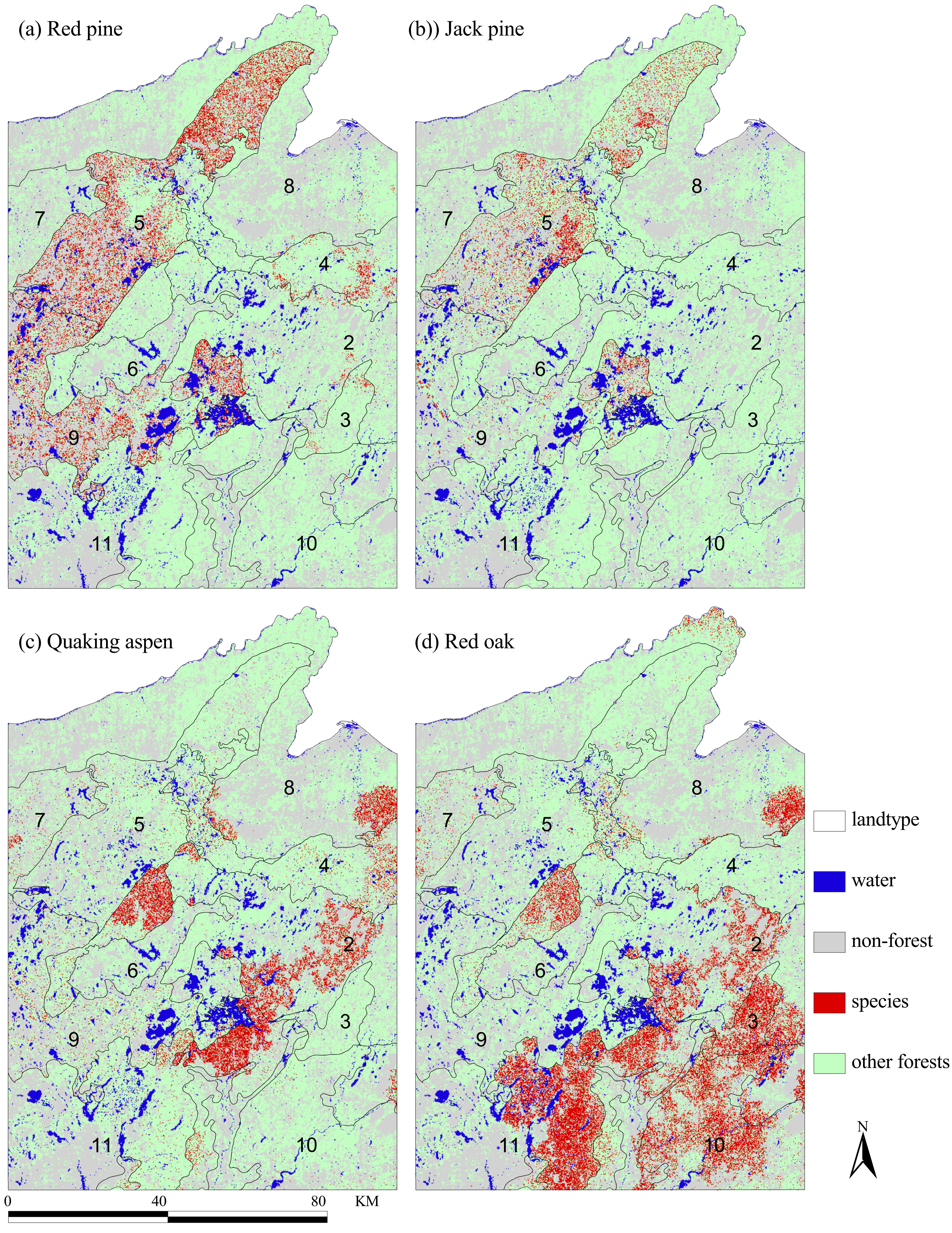

Figure 6.18. (a) red pine, (b) jack pine, (c) quaking aspen, and (d) red oak responses at year 420 after fires.

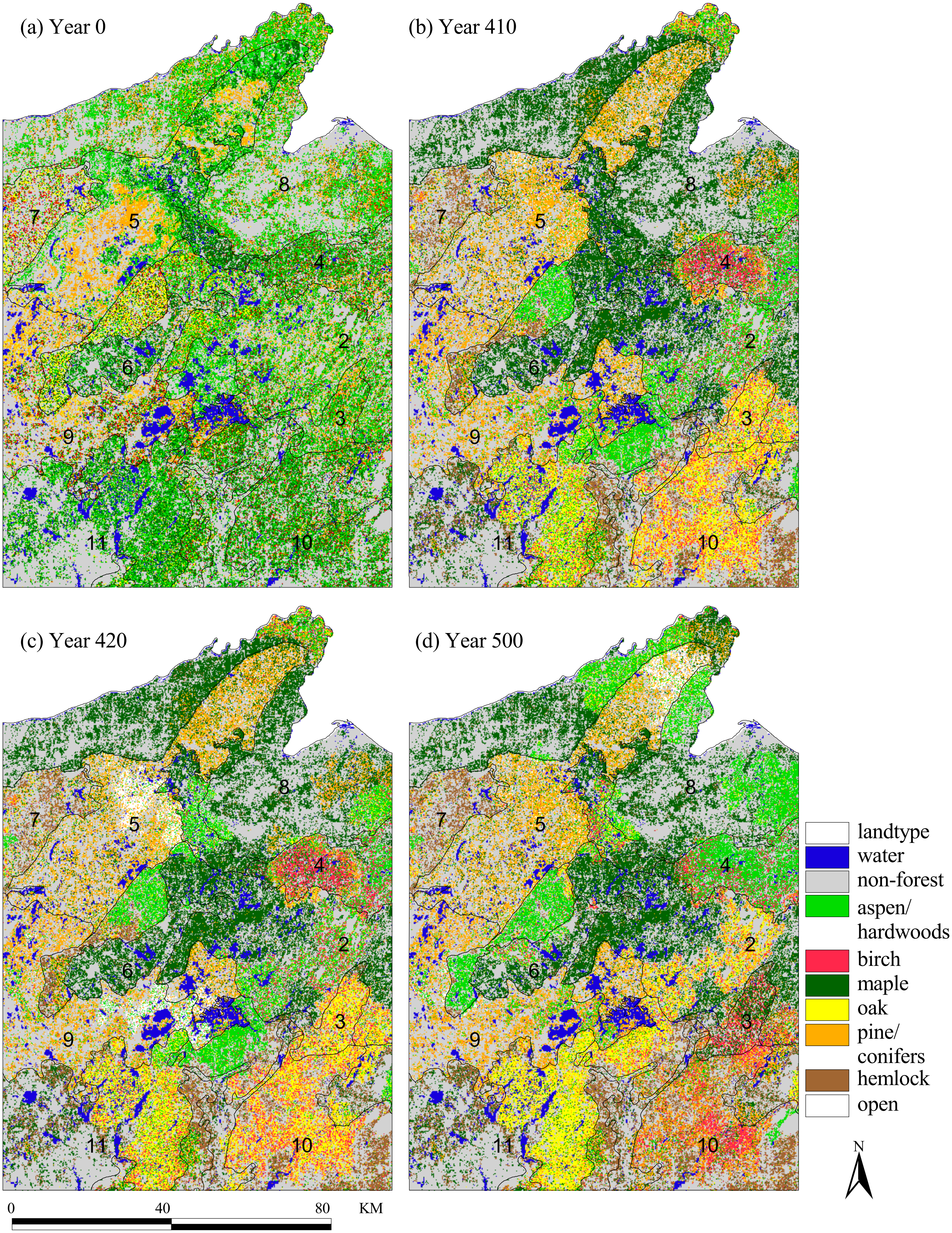

Figure 6.19. Dominant forest types at (a) year 0, (b) year 410 before year 420 fires, (c) year 420 after fires, and (d) year 500, respectively.

Spatial modeling of forest landscape change: approaches and applications

EDITED BY

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK www.cup.cam.ac.uk
40 West 20th Street, New York, NY 10011-4211, USA www.cup.org
10 Stamford Road, Oakleigh, Melbourne 3166, Australia
Ruiz de Alarcon 13, 28014 Madrid, Spain

First published 1999

Printed in the United Kingdom at the University Press, Cambridge

Typeset in Bembo 11/13pt [wv]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data

Spatial modeling of forest landscape change:
approaches and applications/[editors, David J. Mladenoff, William L. Baker].
p. cm.
Papers presented at symposium in Albuquerque, New Mexico, USA, 1997.
Includes index.
ISBN 0 521 63122 X (hardback)
1. Forest dynamics – Computer simulation – Congresses. 2. Landscape ecology – Computer stimulation – Congresses. I. Mladenoff, David J. II. Baker, William L. (William Lawrence)
QK938.F6S668 1999
577.3′01′13–dc21 98-50552 CIP

ISBN 0 521 63122 X hardback

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