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Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm

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Abstract

Insects and diseases are common disturbance agents in forested ecosystems. Severe outbreaks can cause significant changes in tree species composition, age structure, and fuel conditions over broad areas. To investigate the role of biological disturbances in shaping forest landscapes over time, we constructed a new "biological disturbance agent" (BDA) module for a landscape-level forest succession and disturbance simulator, LANDIS. The BDA module is designed to simulate tree mortality following major outbreaks of insects and/or disease. Major outbreaks are defined as those significant enough to influence forest succession, fire disturbance, or harvest disturbance at landscape scales. Module design is flexible to accommodate a diversity of life history traits characterizing destructive insects and diseases, and more than one BDA can be simulated to examine their interactions. Five main elements control the probability of biological disturbance within the module: (1) local host dominance on a given site; (2) host value modifiers that reflect environmental conditions and recent disturbance history; (3) host dominance within a user-specified neighborhood; (4) the temporal outbreak pattern characteristic of the BDA, and (5) BDA dispersal in cases where the annual dispersal range of the BDA is small relative to the study area. In this paper, we describe the first four elements of the BDA module, and present the initial testing of the module on a variety of neutral landscape patterns, using Eastern spruce budworm as a test case. Our results are consistent with published successional patterns of spruce-fir and mixed forests affected by spruce budworm, but also highlight areas of uncertainty in the spatio-temporal patterns of budworm-caused tree mortality and biological disturbances in general. We suggest that the behavior of the module is consistent with the design and intended purpose of LANDIS as a probabilistic landscape-level simulator of forest disturbance and succession.

Keywords: Biological disturbance agents; Forest insects and disease; Spatially explicit landscape model; LANDIS; Succession; Eastern spruce budworm; *Choristoneura fumiferana*

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1. Introduction

Biological disturbances, such as insect and disease outbreaks, are critically important agents of forest change, causing tree mortality at scales ranging from individual trees to entire regions. Damage caused by biotic agents such as Eastern spruce budworm (*Choristoneura fumiferana*) and mountain pine beetle (*Dendroctonus ponderosae*) can dwarf other natural disturbances (Fleming et al., 2000; Samman and Logan, 2000), and interact synergistically with fire disturbance by greatly enhancing fuel loading and the risk of high-intensity fires (Hessburg et al., 1999; Fleming et al., 2002). Due to their host-specificity, biotic disturbances are also sensitive to host abundance and landscape distribution, and therefore likely respond to feedback associated with forest succession and change (Bergeron and Leduc, 1998; Hessburg et al., 1999). Depending on their severity and extent, these disturbances have important and long-lasting consequences for long-term forest composition and pattern at landscape scales (Hessburg et al., 1999).

There are few examples of landscape-level biotic disturbance–succession models published in the literature (see Rykiel et al., 1988 and Fall et al., 2001 for notable exceptions). Nonetheless, decades of research and forest monitoring provide some insight into some of the essential elements required to simulate interactions between biotic disturbance agents and their hosts in forested landscapes. For example, forest ecologists have quantified many of the local stand characteristics (e.g., host abundance, age, stand structure, soil moisture, etc.) that determine the relative vulnerability of a stand to an outbreak should one occur (Batzer, 1969; Wulf, 1985; Shore and Safranyik, 1992; Bergeron et al., 1995; Chojnacky et al., 2000; Orwig et al., 2002). Intermediate scale factors affecting forest vulnerability are less understood, but expert opinion (e.g., Wulf, 1985) and empirical evidence suggests that characteristics of the surrounding landscape can also influence stand vulnerability to a given biotic disturbance (Cappuccino et al., 1998; Radeloff et al., 2000). At the regional scale the regularity, periodicity, and synchronicity of insect outbreaks have been well documented through aerial survey programs (Erickson and Hastings, 1978; MacLean and MacKinnon, 1996) and dendrochronology studies (Blais, 1983; Swetnam and Lynch, 1993; Bergeron, 2000). Collectively, these monitoring efforts provide important insights into the spatio-temporal patterns of biological disturbances in forest ecosystems.

The vast majority of modeling studies investigating forest insects have focused on their population dynamics. These models include conceptual models (e.g., Holling, 1986), models based on life tables (e.g., Royama, 1984; Dale et al., 1991), and highly sophisticated time-series analysis designed to elucidate the mechanisms driving insect population dynamics (Turchin, 2003). Most of these population-based approaches do not consider spatial processes affecting population dynamics in heterogeneous environments. An exception is the use of reaction–diffusion models to elucidate mechanisms underlying population viability in heterogeneous environments (Flather and Bevers, 2002) and regional synchronicity (Bjornstad and Bascompte, 2001; Bjornstad et al., 2002). Nonetheless, the behavior of spatially explicit population models is complex, even within homogeneous environments (Kareiva and Wennergren, 1995).

Holling (1986, 1992) noted that the dynamics of insect outbreaks are complex because they are controlled by multiple constraints operating at vastly different temporal and spatial scales. For example, endemic spruce budworm populations are held in check by a complex of natural enemies that can respond quickly to minor fluctuations in budworm populations (Royama, 1984). During endemic periods, food resources for the budworm slowly increase to a level that can sustain an outbreak. Once the system has reached this threshold state, a relatively minor event (e.g., weather conditions or budworm immigration from neighboring forests) can rapidly shift the control of budworm populations to their food resource, and their population growth becomes exponential (Holling, 1986). While predicting the triggering event or the specific year of an outbreak is nearly impossible, predicting whether an outbreak will occur within a larger temporal window (e.g., a decade) becomes more feasible (Allen and Hoekstra, 1992).

Since forest succession is very slow relative to insect population dynamics, the fine-scale temporal details of pest populations are less important than the more general temporal pattern of damage (i.e., mortality) that they cause. Thus an alternative approach to simulating forest-pest interactions is to use the characteristic patterns of biotic disturbance from the past to predict their behavior in future landscapes. This is analogous to using the statistical properties of past fire regimes to

simulate interactions between fire disturbance and forest succession in future landscapes, an approach that has been widely and productively applied in the past (e.g., Baker, 1992; He and Mladenoff, 1999). The idea is not to accurately predict the dynamics of a given site on the landscape, but rather to capture the essential patterns of disturbances at landscape scales. This approach is consistent with the design and philosophy of LANDIS, a landscape-scale forest succession and disturbance simulator that trades mechanistic detail for the ability to simulate large areas over long periods of time (Mladenoff, this volume).

This paper provides a detailed description of a new biological disturbance agent (BDA) module designed to complement the LANDIS simulation framework. The BDA module is designed to simulate tree mortality following major outbreaks of insects and/or disease, where major outbreaks are defined as those significant enough to influence forest succession, fire disturbance, or harvest disturbance at landscape scales. The module is flexible enough to accommodate several types of destructive insect and disease species, and more than one BDA can be simulated concurrently to examine their interactions. For clarity, we focus our presentation of the module and its behavior using a case study forest-pest – Eastern spruce budworm. For the initial testing, we evaluate the relative influence and interactions between the spatial pattern of the environment, neighborhood effects, and tree species diversity on the abundance, severity, and pattern of budworm-caused tree mortality on neutral landscapes. We then discuss the limitations and future development directions of the module in the context of other types of destructive forest insects and diseases.

1.1. LANDIS overview

The purpose of LANDIS is to simulate the reciprocal effects of disturbance processes and patterns of forest vegetation on each other across large (10^4–10^7 ha) landscapes and long time scales (50–1000 years). The current version of LANDIS (v3.7) simulates differential reproduction, dispersal, and succession patterns using the vital attributes of species, and incorporates effects of natural disturbance (fire and wind) and environmental heterogeneity interacting spatially across the landscape (Mladenoff and He, 1999). Vital attributes influencing forest succession include shade tolerance, fire tolerance, seed dispersal, ability to sprout vegetatively, and longevity. The forest harvest module of LANDIS simulates forest management disturbance using a suite of ranking algorithms that can be related to specific management goals (Gustafson et al., 2000). The model operates on a raster (grid) map, where each cell contains information on the presence/absence of tree species and their 10-year age-cohorts (species-age list), but not information about the density or size of individual stems. Model input includes mapped land types/ecoregions, initial species-age conditions, mapped stands and management areas, as well as parameters for species establishment, fire characteristics, and fuel accumulation regimes for each landtype/ecoregion. Several new improvements to LANDIS, described in this paper and others in this special issue (He et al., this volume; Shang et al., this volume; Scheller and Mladenoff, this volume; Yang et al., this volume) will be integrated into subsequent versions of the model.

2. Biological disturbance agent module

2.1. Overview

The temporal resolution for a given BDA is limited by the time step of LANDIS, currently fixed at ten years. Given this temporal resolution, only tree mortality, rather than defoliation or infection, is simulated. Biological disturbances are probabilistic at the site (i.e., cell) scale, where each site is assigned a probability value called *Site Vulnerability* (SV), and compared with a uniform random number to determine whether the site is disturbed or not. Disturbance causes species- and cohort-specific mortality in the cell. In the simplest case, site vulnerability equals *Site Resource Dominance* (SRD), a number that ranges from 0 (no susceptible host) to 1 (most susceptible host) based on the tree species and age-cohorts present in the site. While the presence of susceptible host is required for disturbance, four other factors may also modify site vulnerability: (1) environmental and/or other disturbance-related stress (*Site Resource Modifiers*); (2) the abundance of host in the neighborhood surrounding the site (*Neighborhood Resource Dominance*) (NRD); (3) user-defined temporal functions (e.g., cyclic, random, or chronic) that affect the temporal pattern of

Table 1
Host preference look-up table example using spruce budworm, where the age range listed represents the ages at which the species exists within the host preference class

Species	Minor host (min–max age)	Secondary host (min–max age)	Primary host (min–max age)
Balsam fir	0–10	20–40	50–120
Black spruce	0–40	50–200	999–999
White spruce	0–10	20–40	50–200

A value of 999 indicates that the species never reaches a given host preference class, and species not listed (e.g., trembling aspen) are considered non-hosts by default.

disturbances across the entire spatial domain of the simulation (*Regional Outbreak Status*) (ROS); and (4) spatial epidemic zones defined via simulated dispersal of a BDA through a heterogeneous landscape (*Dispersal*). Any combination of the optional factors can be simulated to capture the essential dynamics for a given BDA; multiple BDAs can be simulated simultaneously for a given landscape; and interactions between BDAs may be simulated via disturbance-related stress. This model description starts by describing the simplest case (i.e., site-level resources), and then builds further complexity into the module by adding optional elements 1–3 above (dispersal algorithms will be described in a forthcoming manuscript). A flow diagram for the module is shown in Fig. 1.

2.2. Site resource dominance

Site resource dominance indicates the relative quantity/quality of food resources on a given site and is a combined function of tree species composition and age-cohorts present on that site. The relative food resources provided by a given tree species in a particular age class is defined by its host preference. Four host preference classes are rank-ordered according to their relative resource value: primary, secondary, minor, and non-host. A host preference parameter look-up table provides a flexible method for defining the age range at which a given species exists within a given host preference class. Tree species not listed in the look-up table are assumed non-hosts. For example, in a simple boreal forest system disturbed by Eastern spruce budworm (Table 1) balsam fir and white spruce are minor hosts in the youngest cohort, secondary hosts at ages 20–40, and reach primary host status by age 50 (Montgomery et al., 1983). Since black spruce (*P. mariana*) is considered a secondary host (MacLean, 1980; Montgomery et al., 1982), it never reaches primary host status (i.e., minimum primary host age > longevity).

SRD for a given site varies between 0 and 1, and represents the relative resource value of a site for the BDA. The relative resource value of a given species cohort is defined by its host preference class, where preferred host = 1.0, secondary host = 0.66, minor host = 0.33, and non-host = 0. While these rank-ordered host values logically correspond with published host susceptibility rankings for many forest pests (e.g., MacLean, 1980; Hall et al., 1998; Chojnacky et al., 2000), we caution that disturbance probability is not necessarily a linear function of host susceptibility. The BDA module compares the look-up table with the species cohort list generated by LANDIS to calculate SRD using one of three methods: (1) the maximum host preference class present, (2) an average resource value of all tree species present, where the resource value of each species is represented by the cohort with the maximum host preference, and (3) an average resource value for all tree cohorts present. When the biomass option becomes available in LANDIS (Scheller and Mladenoff, this volume), a fourth option will use the biomass of each tree species' cohort to weight its relative resource value.

SRD is required to calculate a site's vulnerability that ultimately dictates the probability and severity of biotic disturbance on a given site. Though other contributing factors may be simulated, the simplest calculation of SV is:

$$\mathrm{SV} = a \times \mathrm{SRD} \quad (1)$$

where a is a user-defined calibration parameter. By default, $a = 1$. BDA disturbance events are determined for each site by comparing SV with a uniform random number ranging from 0 to 1.

Once a site is disturbed, the disturbance severity is calculated for the site to determine which species cohorts die, based on their tolerance as a host. While host tolerance (species susceptibility to BDA disturbance) is typically related to related to its host preference (value as a food resource), there are often differences between the two that are significant enough to warrant a new set of parameters. For example, all cohorts of a species may be equally sensitive to a disturbance, even though older cohorts provide greater food resources.

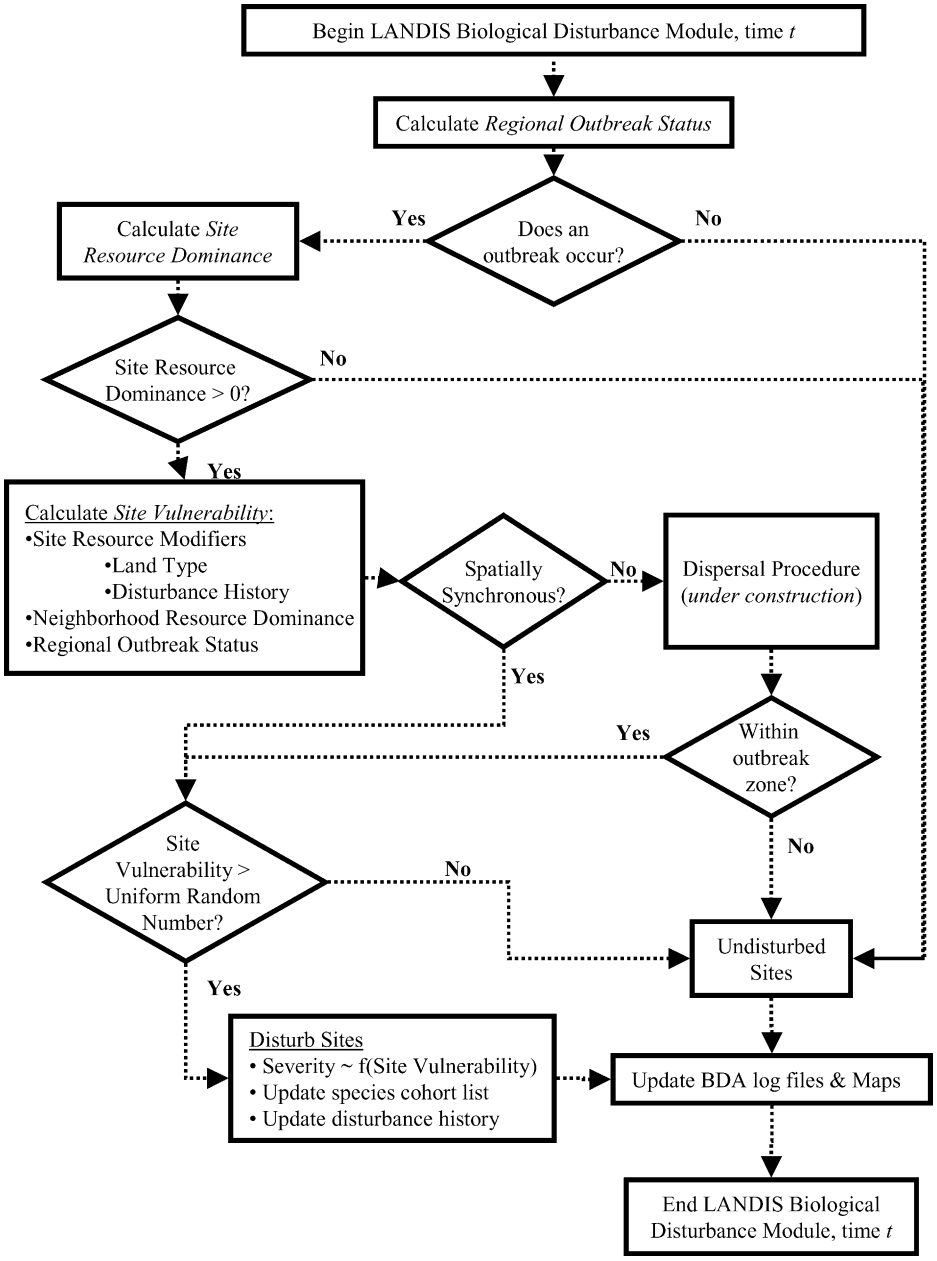

Fig. 1. Logical flow diagram for the biological disturbance agent module.

Disturbance intensity is a direct function of SV, where SV < 0.33 = light; 0.33 < SV < 0.67 = moderate; SV > 0.67 = severe disturbance. Cohort mortality follows the following rules: light disturbance kills all vulnerable cohorts, moderate disturbance kills all tolerant and vulnerable cohorts, and severe disturbance kills resistant, tolerant, and vulnerable cohorts.

If no other BDA options are simulated, the BDA module finishes by updating species cohort lists, updating the time since last biological disturbance, out-

putting a map of BDA disturbance events, and updating the BDA log (Fig. 1).

This algorithm produces landscape patterns of tree mortality with qualities desirable for simulating disturbances by insects and disease. First, the probability of disturbance is a direct function of host value and susceptibility to the BDA (Fig. 2). The resulting disturbance pattern is a logical extension of the stand-level risk factors that are often well documented in the literature. Hence, disturbances are randomly distributed if the host is randomly distributed, and (Fig. 2b) hierarchically distributed when the host is spatially clustered (Fig. 2d). Second, there is no additional autocorrelation in the disturbances other than that caused by spatial autocorrelation of the host. This assumption is due to the paucity of studies quantifying the spatial structure of mortality caused by insects and disease at landscape scales. However this assumption can be relaxed if more information on the drivers of disturbance patterns is known through the use of optional procedures described below.

2.3. Site resource modifiers

Site resource modifiers are optional parameters used to adjust SRD to reflect variation in the quality of food resources introduced by both site environment (i.e., land type) and recent disturbance. For example, dry land types or ecoregions may be more prone to a given BDA due to drought stress (Mattson and Haack, 1987). The modifier need not be positive, as some environmental conditions may either make hosts more resistant to a given BDA, or make the BDA itself less likely to be present (e.g., Van Arsel et al., 1961). Similarly, recent disturbances such as defoliation or fire may weaken the surviving trees, also making them more prone to certain types of biological disturbances (e.g., Wallin and Raffa, 2001), and others (e.g., spray programs via human management) make them more resistant. Hence both land type modifiers (LTMs) and disturbance modifiers (DMs) can range between −1 and +1, and will be added to the SRD value of all active sites where host species are present.

While LTMs are assumed to be constant for the entire simulation, the magnitude of a DM is assumed to decline linearly with the time since last disturbance, and SRD of a given site can be influenced by multiple types of disturbances. To calculate the DM for a given disturbance i:

if $\text{DM\_duration}_i > T_{i,}$

$$\text{DM}_i = \text{DM\_Max}_i \times \frac{\text{DM\_duration}_i - T_i}{\text{DM\_duration}_i} \quad (2)$$

where DM_Max is the maximum modifier for disturbance i, DM_duration_i is the maximum amount of time a disturbance i can influence SRD, and $T_{i,}$ is the time since the last disturbance i experienced on that site. We assume that for those sites experiencing multiple recent disturbances, the modification to SRD is equal to the sum of all disturbance modifiers:

$$\text{DM}_{\text{final}} = (\text{DM}_{\text{dist1}} + \text{DM}_{\text{dist2}} + \ldots \text{DM}_{\text{dist}n}) \quad (3)$$

Disturbances that may affect a given BDA include fire, wind, another BDA, and user-specified harvest prescriptions. SRD is then modified by LTM and DM_{final}:

$$\text{SRD}_{\text{m}} = \text{SRD} + \text{LTM} + \text{DM}_{\text{final}} \quad (4)$$

Site vulnerability is then calculated by substituting SRD_{m} for SRD in Eq. (1). Hence direct effects of environment and recent disturbance on a given BDA are assumed to be additive. Note that both land type and disturbance may also affect the BDA indirectly by modifying the tree species and age structure across the landscape.

The user should calibrate the above modifiers to reflect the relative influence of species composition/age structure, the abiotic environment, and recent disturbance. For example, an LTM value of 0.33 is equal to a full step increase in disturbance intensity above that calculated using species composition alone, and would cause resistant hosts to respond as tolerant hosts and tolerant hosts to respond as vulnerable hosts to a BDA event in that land type. Note that while Eq. (4) allows SRD_{m} to exceed 1.0, by definition SV cannot exceed 1.0 (i.e., 100% probability of disturbance). SRD_{m} values exceeding 1.0 can therefore only enhance the probability of disturbance further if additional variables, such as neighborhoods or temporal disturbance functions (described below) are applied.

2.4. Neighborhood resource dominance

Several recent studies suggest that the landscape context of a site also influences the probability and

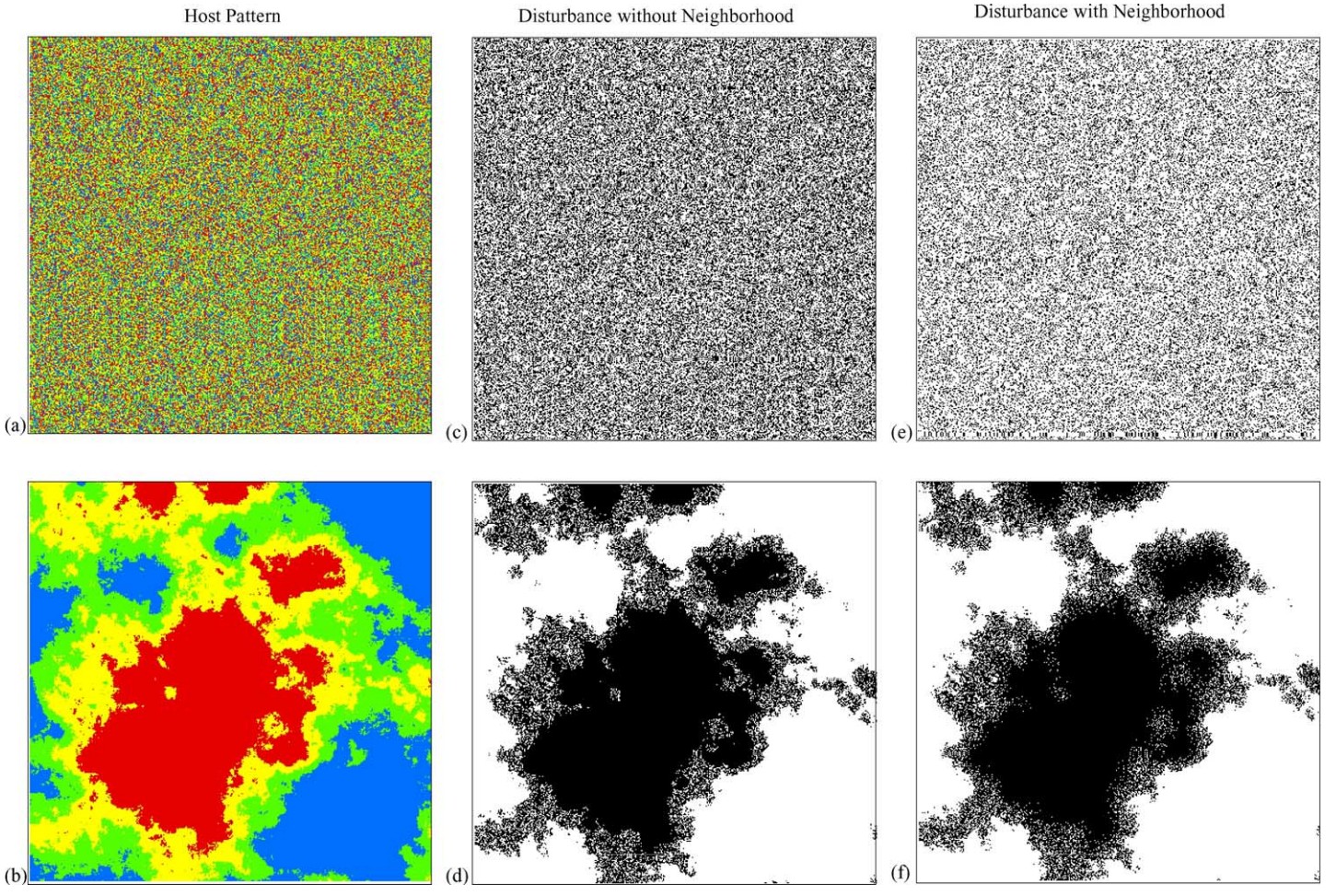

Fig. 2. Effect of host pattern on biotic disturbance. Site resource dominance patterns include hosts of differing susceptibility that are (a) randomly dispersed and (b) spatially aggregated (red = primary host; yellow = secondary host; green = minor host; blue = non-host). If no neighborhood function is applied, then the disturbance pattern is directly related to the spatial pattern of hosts (c and d; black = disturbed, white = not disturbed). If a neighborhood function is applied, disturbance response varies between an overall reduction of disturbed sites when hosts are randomly dispersed (e) to a blending of habitat boundaries if hosts are spatially aggregated (f).

severity of disturbance (Cappuccino et al., 1998; Radeloff et al., 2000). The mechanisms for this "neighborhood effect" are not well-understood, but may include (a) enhanced ability of a dispersing BDA to detect host species when the host trees are embedded within a matrix of host (Greenbank et al., 1980), or (b) reduced natural enemies within landscapes having a low diversity of tree species (Cappuccino et al., 1998). A neighborhood effect is modeled as the mean SRD_m of each cell within a user-defined radius R, using one of three radial distance weighting functions listed in increasing order of local dominance: uniform, linear, and gaussian (Orr, 1996). The linear radial distance function is calculated using the:

$$\text{Weight} = \frac{R - D}{R} \tag{5}$$

where D is the distance from the focal site. The gaussian radial distance function was adapted from Orr (1996):

$$\text{Weight} = \exp - \frac{D^2}{(R/2)^2} \tag{6}$$

Dividing the radius by 2 in Eq. (6) assumes that the radial distance function includes 2 standard deviations of the distribution with a maximum radius of R.

Neighborhood resource dominance is calculated for all sites containing host species (i.e., SRD > 0). For large neighborhoods (e.g., hundreds of cells), the NRD calculation is computationally expensive, because the SRD value for each cell in a site's neighborhood must be accessed and averaged with the SRD of all other cells within the neighborhood, and this process is repeated for every site containing host. We have therefore added an optional sub-sampling procedure based on the observation that adjacent sites share a significant portion of neighbors. The sub-sampling procedure calculates the NRD for every other site, and the NRD of the remaining sites are estimated by the mean NRD of adjacent sites in the four cardinal directions.

Site vulnerability can now reflect (a) the species and age composition of the site (SRD), (b) modified by land type and past disturbance (SRD_m), and (c) the species and age composition of the neighborhood (NRD):

$$SV = a \times \left[\frac{SRD_m + (NRD \times NW)}{1 + NW} \right] \tag{7}$$

where NW is a parameter designed to define the relative importance between site and neighborhood resources and a is a user-defined calibration parameter defined in Eq. (1).

Importantly, the landscape mean value of SV calculated using Eq. (7) is generally lower than if the neighborhood calculation is not applied (Sturtevant, unpublished data). This effect is observed because sites with low SV decrease the SV of their neighbors, but their own probability of disturbance cannot increase above zero unless the SV of their neighborhood is greater than their threshold tolerance. The neighborhood impact on landscape-level disturbance probability is greatest when hosts and non-hosts are highly interspersed (e.g., Fig. 2c). As the spatial autocorrelation of host increases, the landscape-level probability of disturbance approaches that expected if no neighborhood was applied, though the spatial pattern of disturbances is modified (Fig. 2f).

2.5. Regional outbreak status

Several insect pests fluctuate fairly regularly in time, causing periodic disturbance over broad spatial scales. This type of regional synchronicity is most often observed in highly vagile species such as Lepidopterans (Kendeigh, 1979; Blais, 1983; Swetnam and Lynch, 1993). Several simple temporal patterns may be simulated in the BDA module to represent general outbreak trends for the entire study landscape. Temporal patterns in a given BDA are assumed constant for the length of the simulation, and are defined by a suite of temporal disturbance functions that define the landscape scale severity of the BDA at a given time step. These temporal disturbance functions can vary in complexity from a chronic BDA that occurs with the same severity each time step to cyclic or random temporal patterns that can further vary in severity, and may be parameterized from a variety of historical outbreak records.

We define the regional outbreak status as an estimate of the severity of the regional outbreak, distinguished from disturbance severity at the local scale. Units are integer classes ranging from 0 (no outbreak) to 3 (severe outbreak). The time to the next outbreak is calculated following each outbreak event using either a "uniform" or a "normal" random function. Two user-defined parameters control each function. The uniform random function assumes that the outbreak interval varies between a minimum (*MinI*) and maximum (*MaxI*) with

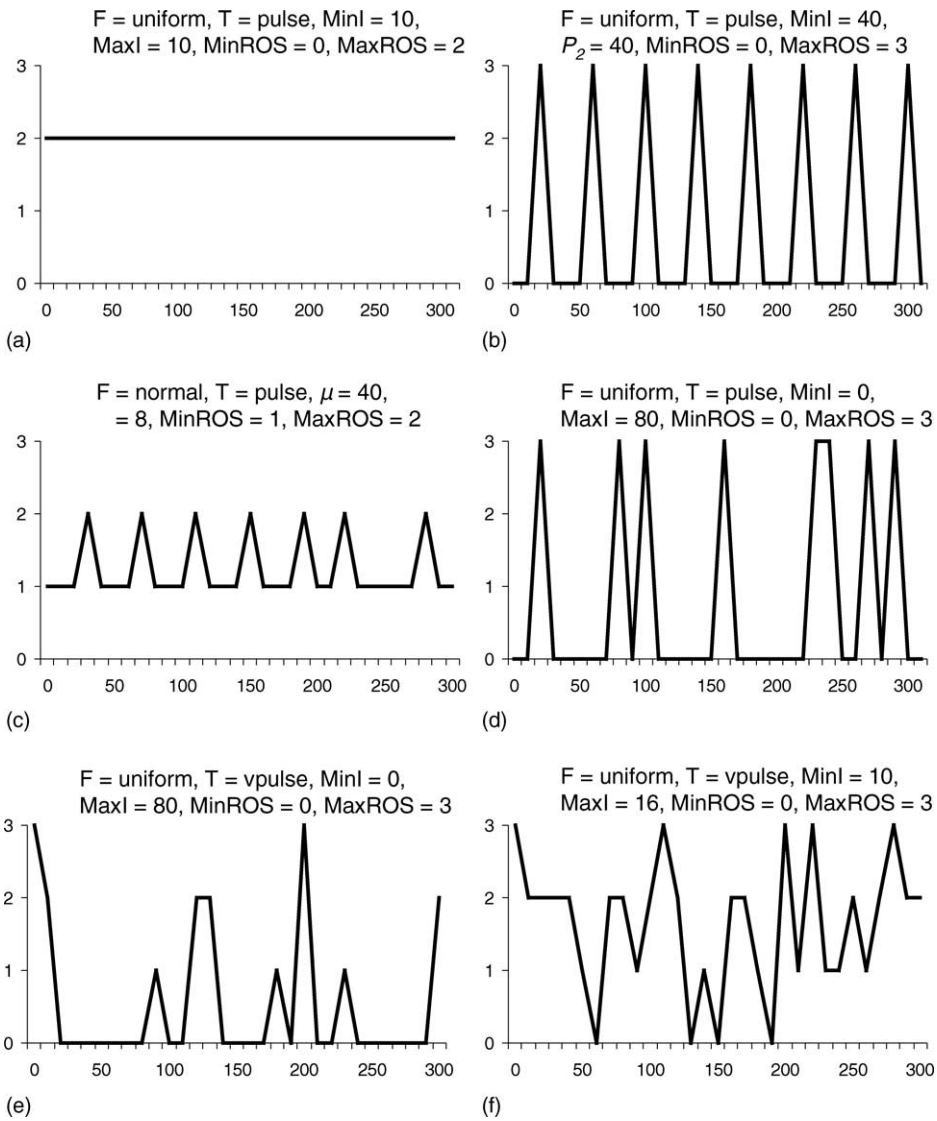

Fig. 3. Examples of temporal patterns in regional outbreak status (ROS) simulated using different combinations of random functions and available parameters. F = random function (uniform, normal), T = outbreak type (pulse, variable pulse), MinROS = minimum ROS, MaxROS = maximum ROS. For F = "random", MinI and MaxI equal the minimum and maximum outbreak interval, respectively. For F = "normal", μ and σ equal the mean and standard deviation in outbreak interval, respectively.

equal probability. The normal random function selects the time to the next outbreak from a normal distribution with a mean = μ and standard deviation = σ. Either of the random functions can be parameterized to produce chronic (i.e., outbreak every time step; Fig. 3a), cyclic (i.e., evenly spaced outbreaks; Fig. 3b), pseudo-cyclic (Fig. 3c), and random (Fig. 3d) outbreak patterns. Though the actual time periods between outbreaks will be constrained by the time step of LANDIS (currently set at 10 years), the random outbreak functions may be used to vary the outbreak interval such that the *average* interval between outbreaks observed during the length of the simulation approximates that expected by the user.

The magnitude of simulated regional outbreak severities is controlled by the MinROS and MaxROS parameters. MinROS defines the "background" outbreak activity that will occur in each time step, and is set to zero by default. Outbreak type determines whether outbreaks are binary (either MinROS or MaxROS; outbreak type = "pulse"; Fig. 3b–d) or if the ROS can range between those values (outbreak type = "variable pulse"; Fig. 3e–f). For the variable pulse outbreak type, the ROS value is randomly selected for each outbreak event from the range between MinROS + 1 and MaxROS. We are currently developing a third outbreak type ("continuous") that will interpolate ROS between outbreak and non outbreak periods.

Site vulnerability can now reflect (a) the species and age composition of the site, (b) modified by land type and past disturbance (SRD_m), (c) the species and age composition of the neighborhood (NRD), and (d) the regional outbreak status (ROS) during any given time step.

$$SV = a \times \left[\frac{SRD_m + (NRD \times NW)}{(1 + NW)}\right] \times \left(\frac{ROS}{3}\right) \quad (8)$$

Since SV controls both the probability of disturbance and the severity of a disturbance once it occurs, ROS <3 will decrease both (a) the probability of disturbance and (b) the severity of the disturbance for the entire landscape.

2.6. Dispersal

The above disturbance modeling strategies all assume spatial synchrony of the epidemic. Some epidemics occur at spatial scales smaller than the typical simulation area of LANDIS. Accounting for BDA dispersal and spread will be necessary for these cases. The dispersal procedures for the BDA module are still under development and will be elaborated in a future publication. Nonetheless, the objective of the BDA dispersal procedure will be to define smaller spatial zones within the modeled landscape where insect disturbance can actually occur for a given time step (Fig. 1).

2.7. Module performance

Module performance was evaluated using the running time for a single iteration of the BDA module on a personal computer with a 2.53 GHz Pentium IIII CPU and 1 G RAM. Four factors were evaluated for their effect on module performance: map size (500^2, 1000^2, and 2000^2 cells 1 ha in size), neighborhood radius (0, 500, 1000, and 2000 m), neighborhood option (normal or sub-sampling procedure), and number of tree species simulated (5, 10). Iteration time increased as a nearly log-linear function of both map size and neighborhood radius, with a maximum run time of 27 min per iteration when the largest neighborhood was applied to the largest map using the "normal" calculation. The sub-sampling option significantly reduces run time by 42–49%, depending on the neighborhood radius. Doubling the tree species number effectively doubled run time for simulations without a neighborhood calculation, but had very little effect (<5%) on run time for scenarios where neighborhoods were applied.

2.8. Application: spruce budworm disturbance

We tested the behavior and sensitivity of the BDA module in simulated forest ecosystems affected by Eastern spruce budworm. Neutral landscape patterns ranging from random to multifractal maps with high spatial autocorrelation were created using the program RULE (Gardner, 1999) to represent different spatial arrangements of three land types with equal area. The three land types represented xeric, mesic, and hydric environmental conditions, respectively. These land types controlled the distribution and abundance of different host and non-host species through their relative species establishment coefficients and the initial pattern of species and age classes on the landscape. We also evaluated how two other factors, neighborhood effects and tree species richness, affected budworm disturbance behavior.

Table 1 shows the host preference parameters for the three simulated budworm host species: balsam fir, black spruce, and white spruce (Batzer, 1969; MacLean, 1980). All other species were assumed to be non-hosts. The "mean species" option (i.e., host resource value averaged across all tree species present) was used to calculate site resource dominance. Host vulnerability parameters were identical to host preference, except that white spruce was parameterized as a tolerant host instead of a vulnerable host. This is based on observations that, unlike fir, the older needles of spruce are rarely consumed by spruce budworm, and therefore spruce in general are more resistant to bud-

worm damage than are balsam fir (Montgomery et al., 1982).

Simulations were simplified to focus on the behavior of the budworm disturbance as affected by the three variables of interest (i.e., land type pattern, neighborhood influence, and species diversity). No other disturbances were simulated, no land type modifiers were applied, and the calibration parameter *a*, (Eq. (1)) was set to unity. A simple cyclic temporal pattern of disturbance, using the "pulse" outbreak type and a 40-year outbreak interval, was simulated using the parameters shown for Fig. 3b. This pattern roughly corresponds with the periodicity of spruce budworm in boreal ecosystems (Blais, 1983). The time since the last regional outbreak was set at 20 years.

To evaluate the effect of tree species richness on budworm disturbance behavior, we simulated two types of systems, one representing a boreal, species-poor system, and the other representing a subboreal, species-rich system. The boreal system contained nine species (Table 2) typical of Northwestern Ontario (Canada), and the subboreal system contained the same nine species plus an additional nine species typical of mixed forests of Northern Minnesota, USA (Burns and Honkala, 1990). Species attributes were interpreted from the literature (Table 2: Burns and Honkala, 1990). Species establishment coefficients were used to parameterize three land types (xeric, mesic, and hydric) representing a moisture gradient (Table 2). Establishment coefficients were estimated using presence/absence patterns and successional pathways described by Kotar and Burger (2000) for three representative habitat types of North Central Minnesota. To focus the comparison on species diversity rather than climate, establishment coefficients for boreal species were identical in both boreal and subboreal systems.

Initial conditions for simulations were populated as a function of land type. For each land type, one of six communities were randomly assigned to a given site, representing common or rare early successional communities, common or rare mid-successional communities, and common or rare late successional communities, based on their current distribution in North Central Minnesota (Table 3: Kotar and Burger, 2000). For each land type, the three common communities were randomly assigned in equal proportions to 90%

Table 2
Species parameters used in the test simulations

Scientific name	Lng[a]	Mat	Shd	Fire	EffD	MaxD	Species establishment coefficient		
							Xeric	Mesic	Hydric
Abies balsamea	**120**	**25**	**5**	**1**	**30**	**160**	**0.25**	**0.5**	**0.05**
Acer rubrum	150	10	3	1	100	200	0.25	0.25	0
A. saccharum	300	40	5	1	100	200	0	0.1	0
Betula alleghaniensis	300	40	4	2	100	400	0	0.25	0
B. papyrifera	**120**	**30**	**2**	**2**	**200**	**5000**	**0.05**	**0.5**	**0.05**
Fraxinus nigra	150	20	2	1	100	200	0	0.05	0.05
Larix larix	**180**	**15**	**1**	**1**	**50**	**200**	**0**	**0.05**	**0.25**
Picea glauca	**200**	**10**	**3**	**2**	**30**	**200**	**0.25**	**0.05**	**0**
P. mariana	**200**	**30**	**3**	**3**	**80**	**200**	**0.25**	**0.05**	**0.25**
Pinus banksiana	**70**	**15**	**1**	**2**	**50**	**250**	**0.75**	**0.05**	**0**
P. resinosa	250	35	2	4	12	275	0.50	0.05	0
P. strobus	400	15	3	3	100	250	0.50	0.1	0
Populus balsamifera	**150**	**10**	**1**	**2**	**200**	**5000**	**0**	**0.5**	**0**
P. tremuloides	**90**	**15**	**1**	**2**	**500**	**5000**	**0.05**	**0.75**	**0**
Prunus penssylvanica	**30**	**10**	**1**	**1**	**30**	**3000**	**0.05**	**0.5**	**0**
Quercus rubra	250	25	3	3	30	3000	0	0.25	0
Thuja occidentalis	350	30	4	1	45	60	0	0.25	0.05
Tilia Americana	250	15	4	2	30	120	0	0.1	0

Species in bold were used in both boreal and subboreal scenarios, all others were used exclusively in subboreal scenarios. Vital attribute parameters were adapted from Burns and Honkala (1990), and species establishment coefficients were estimated from Kotar and Burger (2000). See Section 2.2.

[a] Parameter abbreviations: Lng = longevity; Mat = Maturity; Shd = shade tolerance, Fire = fire tolerance, EffD = effective seeding distance, MaxD = maximum seeding distance.

Table 3
Initial conditions used for LANDIS simulations

Communities	**Ab**[a]	**Bp**	**Ll**	**Pg**	**Pm**	**Pb**	**Pbal**[b]	**Pt**	**Pp**	Ar	As	Ba	Fn	Pr	Ps	Qr	To	Ta
Xeric																		
Early-com						**20**								20				
Early-rare		**10**						**10**	**10**						10			
Mid-com	**10**			**20**	**20**	**50**				20				50				
Mid-rare	**10**	**70**		**20**				**70**		20					70			
Late-com	**60**			**60**						80				120				
Late-rare	**80**				**100**										150			
Mesic																		
Early-com		**10**					**10**	**10**					10					
Early-rare						**20**			**20**									
Mid-com	**10**	**70**		**20**			**70**	**70**		30	10	10	70			50		10
Mid-rare	**10**					**50**								10	10		10	
Late-com	**60**			**60**						100	60				100			60
Late-rare	**80**			**100**							80	100				120	100	
Hydric																		
Early-com			**20**															
Early-rare		**20**	**20**															
Mid-com			**70**		**30**													
Mid-rare		**70**	**70**		**30**												10	
Late-com					**100**													
Late-rare	**50**				**100**												50	

Each of the three common (Com) community types were populated on 30% of the land type, and each of the three rare community types were populated on 3.3% of the land type. Species in bold were simulated in both boreal and subboreal scenarios, species in plain text were only simulated in subboreal scenarios. Initial conditions were based on current distributions in North Central Minnesota, USA (Kotar and Burger, 2000).

[a] First letter of genus and species shown in Table 2.

[b] *Populus balsamifera*.

of available sites, and the three rare communities were randomly assigned in equal proportions to the remaining 10% of sites.

The following response variables were used to evaluate the behavior of the BDA module: (1) total landscape-wide disturbance; (2) land type-level disturbance; and (3) the degree of spatial aggregation in budworm disturbance patterns. The clumpiness index from Fragstats (v 3.3) was used to describe aggregation on a continuous scale from −1 to 1, where −1 = uniform pattern, 0 = a random pattern, and 1 = a maximally aggregated pattern. The clumpiness index equals the proportional deviation of the proportion of like adjacencies from that expected under a spatially random distribution (McGarigal et al., 2002). The temporal patterns of tree species abundance were also evaluated to determine whether the simulation results were compatible with successional pathways published in the literature.

Responses to the three independent variables and their interactions were evaluated using analysis of variance (ANOVA) at the last outbreak, using a 3 × 2 × 2 factorial design. Three replicate landscapes with 512 by 512 one-hectare cells (total landscape size ≈262,000 ha) were generated for each of three land type patterns (random, multifractal H = 0.1, multifractal H = 0.6; Gardner, 1999). Neighborhood effects were evaluated using "no neighborhood" and 1000 m neighborhood radius scenarios. Species richness was evaluated using the boreal and subboreal scenarios. Simulations were each run for 25 time steps (250 simulation years).

3. Results

Each of the three factors examined (land type pattern, tree species diversity, and neighborhood influ-

Table 4
Analysis of variance of the response of the number of sites disturbed at simulation year 220 to the main effects, R^2 =1.0

Source of variation	df	Type III SS	*F*	Prob > *F*
Land type pattern (*ltp*)	2	61268883	117.94	<0.0001
Neighborhood (*n*)	1	128890609	496.2	<0.0001
Species richness (*r*)	1	2889134167	11122.6	<0.0001
ltp × *n*	2	18325192	70.55	<0.0001
ltp × *r*	2	1950382	7.51	0.003
n × *r*	1	12952801	49.87	<0.0001
lta × *n* × *r*	2	757731	2.92	0.073
Error (*e*)	24	6234082		
Total	35	3140547152		

ence) had significant effects on the behavior of the simulated budworm disturbance. Tree species richness had the strongest influence on the number of sites disturbed, as indicated by the ANOVA applied to simulation results for simulation year 220 (Table 4). At the land type-level, tree species richness had the most consistent influence over disturbance within xeric and mesic land types, where species-poor boreal scenarios experienced higher disturbance than species-rich subboreal scenarios (Fig. 4). Since the species richness of the hydric land type was similar between boreal and suboreal scenarios (Table 3), that variable had less influence on probability of disturbance in hydric land types (Fig. 4).

Neighborhood influence had the next strongest effect on the number of sites disturbed (Table 4). As expected, the application of the neighborhood reduced the percentage of sites disturbed in all land types at the first outbreak (simulation year 20) when tree species distributions were similar (Fig. 4). However, the neighborhood influence on the percentage of sites disturbed in subsequent outbreaks was less consistent. For example, a neighborhood influence caused wide oscillations in the percentage of sites disturbed within hydric land types, particularly within maps with aggregated land type patterns (Fig. 4f and i). While ANOVA indicated that land type pattern itself also had a significant influence on the percentage of sites disturbed at year 220, the response was much smaller than for the other two variables (Table 4). This resulted partly because the proportion of sites disturbed by a BDA could only be directly affected by spatial pattern of hosts when a neighborhood effect was applied. This fact explains why the temporal behavior of the budworm disturbance was so similar between different land type patterns when neighborhoods were not applied (Fig. 4).

Landscape-scale host response to disturbance was highly dependent on the mixture of species present, which was a function of both the land type and the forest ecosystem (boreal or subboreal) (Fig. 5). Budworm disturbance promoted diversity of host species in the xeric and mesic land types of boreal scenarios, and the dominance of balsam fir in these same land types in the subboreal scenarios. Disturbances in subboreal landscapes were both less common and less severe, allowing greater survival of balsam fir. This result was due to our assumption that the average (as opposed to maximum) host preference of species present on a given site best reflects host resources on that site. Hence the increased number of non-hosts simulated in the subboreal scenarios decreased the landscape vulnerability to spruce budworm. Competition between non-hosts and hosts also affected the relative abundance of host species. For example sugar maple, a highly shade-tolerant tree species, excluded all budworm hosts except balsam fir within mesic land types of subboreal scenarios (Fig. 5h and k).

Neighborhood influence on budworm disturbance had a subtle positive influence on primary hosts in xeric land types (Fig. 5d and j) and boreal mesic land types (Fig. 5e). In contrast, neighborhood influence had a negative influence on black spruce in hydric land types (Fig. 5f and l). This negative influence is likely due to a "spill-over" effect, where the host composition of adjacent land types increased the probability of disturbance in this otherwise budworm resistant land type.

The clumpiness index of disturbed sites ranged from approximately zero (random) to a maximum of approximately 0.2, indicating some aggregation. ANOVA applied to the clumpiness index indicated highly significant main effects and interactions at simulation

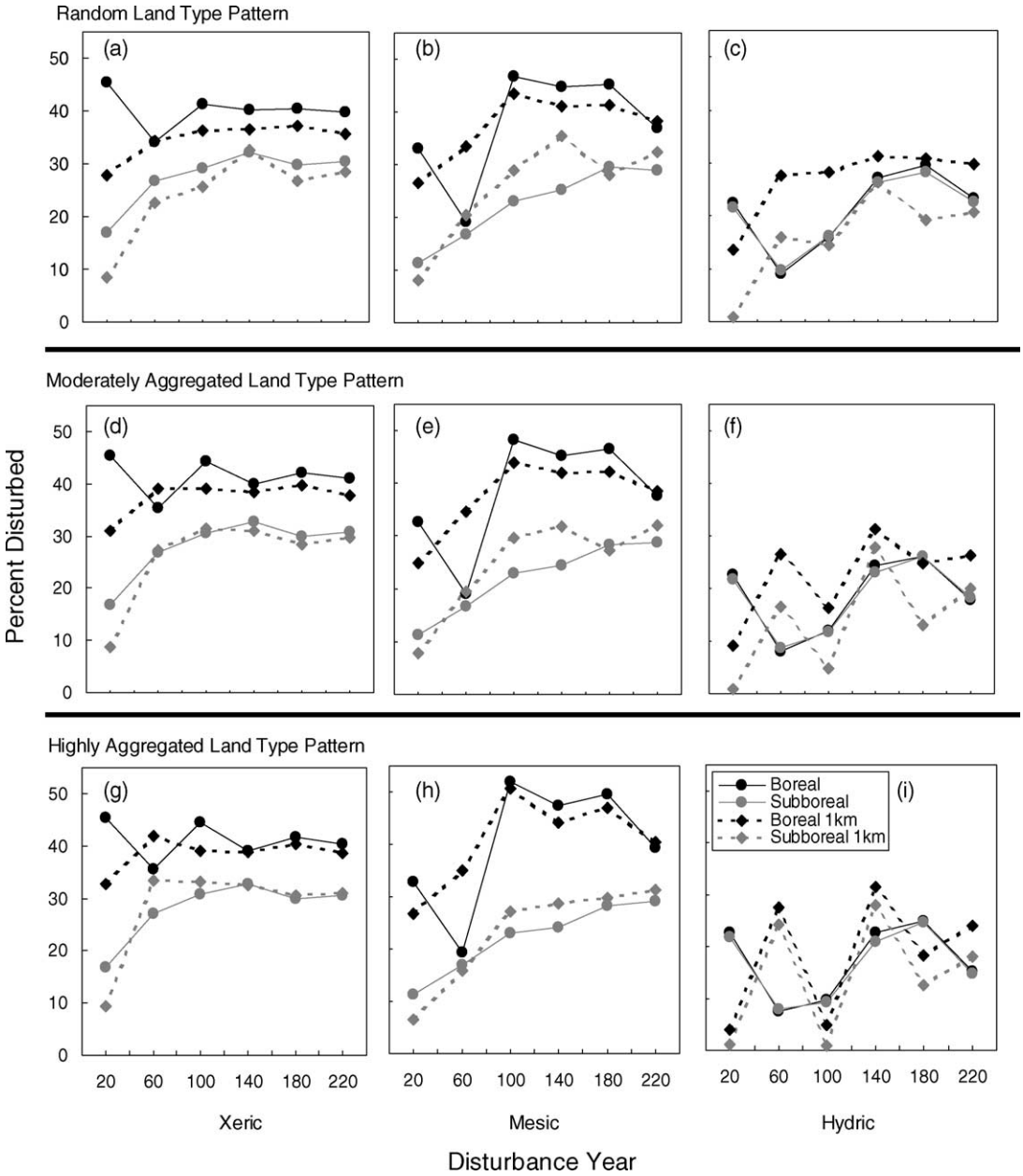

Fig. 4. Temporal disturbance patterns in different land types within land types with increasing aggregation in the land type pattern. Points represent disturbance events, whereas lines only indicate trends in disturbance events through time. Error bars representing one standard deviation of the mean of three replicates were too small to display.

year 220 (Table 5). Interestingly, the pattern of disturbances in boreal and subboreal landscapes relative to random patterns was identical when no neighborhood was applied (Fig. 6), despite large differences in the numbers of sites disturbed in the different scenarios (Fig. 4). Random pattern of land types, and presumably hosts, created a disturbance pattern that was also approximately random (i.e., clumpiness in-

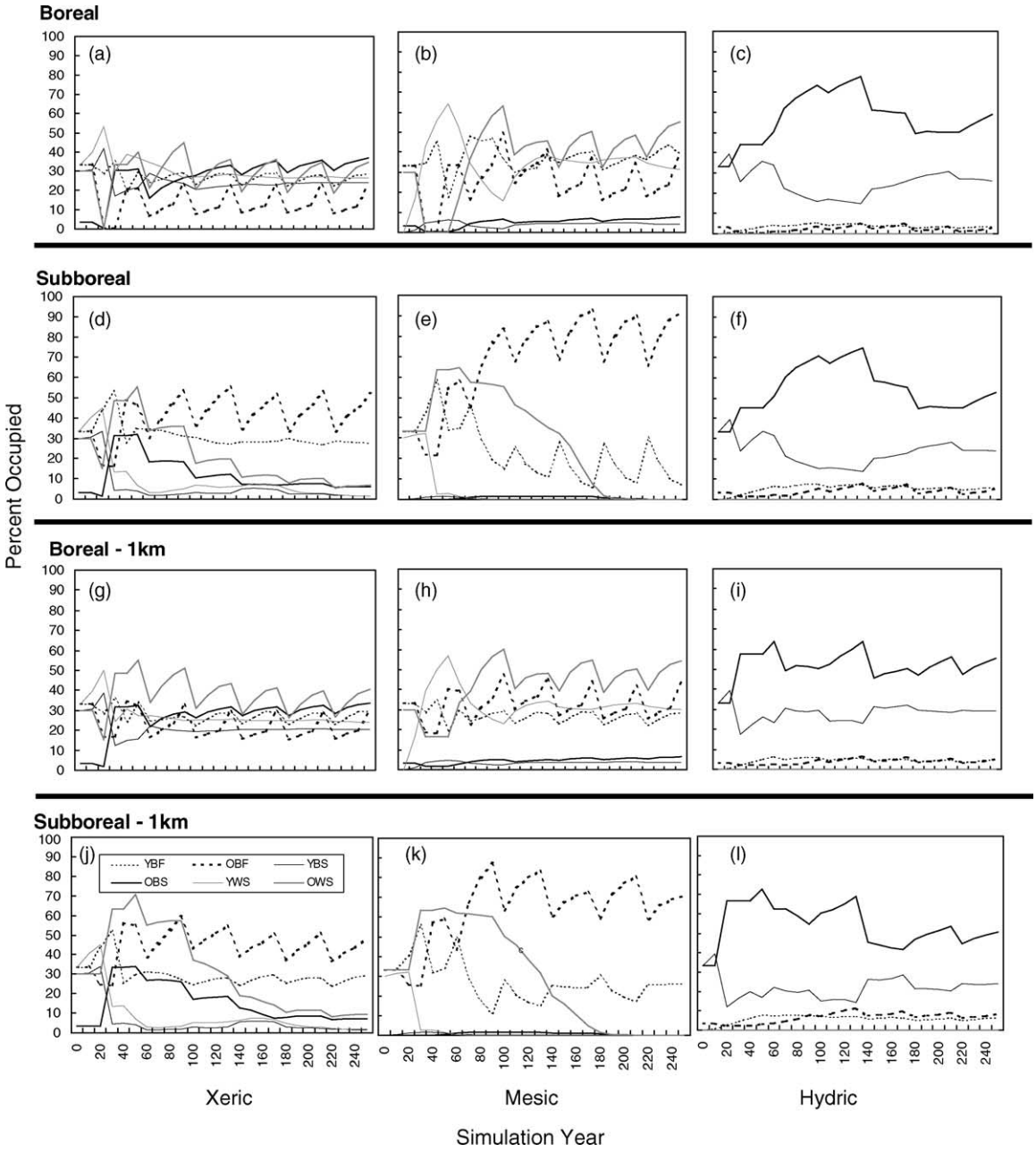

Fig. 5. Temporal patterns of host species in young (10–40) and old (50+) age-cohorts in boreal and subboreal scenarios with no neighborhood and a 1 km neighborhood applied. Only the moderately aggregated land type scenarios are shown, and non-host species are not displayed. YBF and OBF are young and old balsam fir, respectively (dashed lines); YBS and OBS are young and old black spruce, respectively (black solid); YWS and OWS are young and old white spruce, respectively (gray solid).

Table 5
Analysis of variance of the response of disturbance clumpiness disturbed at simulation year 220 to the main effects, model $R^2 = 0.98$

Source of variation	df	Type III SS	F	Prob > F
Land type pattern (*ltp*)	2	0.0061	430.93	<0.0001
Neighborhood (*n*)	1	0.0009	132.18	<0.0001
Species richness (*r*)	1	0.0011	157.49	<0.0001
ltp × *n*	2	0.0006	42.75	<0.0001
ltp × *r*	2	0.0004	30.01	<0.0001
n × *r*	1	0.0012	151.27	<0.0001
lta × *n* × *r*	2	0.0002	17.00	<0.0001
Error (*e*)	24	0.0002		
Total	35	0.0107		

dex ≈0; Fig. 6a). Increasing land type aggregation increased the aggregation of disturbances, but the disturbance pattern also fluctuated with time. The most striking variation in disturbance aggregation was observed when a neighborhood was applied to a boreal landscape with highly aggregated land types (Fig. 6c, Fig. 7). Since there is a negative feedback between disturbance amount/severity and the survival of host, there was some oscillation that occurred in each of the land types, but most notably the hydric land type (Fig. 4i, Fig. 7). This oscillation was a combined response to the initial conditions (Table 3) and differing establishment coefficients in each of the land types that created host age class distributions that were not synchronized across the land types. Disturbances therefore became clustered in certain land types during different disturbance events (Fig. 7). The oscillation dampened with time as the dispersion of disturbances became closer to random.

4. Discussion

The BDA module was designed to simulate the essential spatio-temporal patterns of tree mortality caused by biological disturbance agents that include both insects and disease. Consistent with the design of LANDIS, the module trades mechanistic detail (i.e., the details of site-specific BDA population dynamics) for the ability to simulate pattern across broad areas and long periods of time (Mladenoff this issue). The application of the module to spruce budworm disturbance in subboreal and boreal systems was not intended to precisely match the specifics of the disturbance behavior of spruce budworm, but rather to evaluate the sensitivity of module behavior to different assumptions and ecological settings. The simulations presented in this paper demonstrate that the module is capable of producing realistic spatio-temporal patterns of spruce budworm disturbances on the landscape. We believe that this approach will have wide applicability to a diverse array of destructive forest pests, but also recognize that no one approach can model the rich diversity of biological disturbances in forested ecosystems.

The most important factor controlling the probability of disturbance in the simulations was the species and age composition in the landscape. This result is a direct consequence of the assumption that site resources are best approximated by the average host preference on a site. Mixed stands generally experience less damage than pure stands of host in forests disturbed by spruce budworm (MacLean, 1980), suggesting that the average host value of tree species in a given site is an appropriate method for quantifying the total value of the site to spruce budworm. In the boreal scenarios, budworm disturbance promoted species richness (Fig. 5a and b). Van der Kamp (1991) suggested that forest pathogens perform a similar role in many forest communities by preventing the dominance of shade-tolerant species. However, balsam fir still dominated the host composition of subboreal landscapes in land-types where it had high establishment (Fig. 5g and h). This result is consistent with the ubiquity of balsam fir in subboreal landscapes of Northern Minnesota (Kotar and Burger, 2000) despite repeated budworm outbreaks over the last 40 years. Ghent et al., (1957) found that the influence of budworm disturbance on stand composition was sensitive to the survival of fir regeneration following an outbreak. Previous simulations demon-

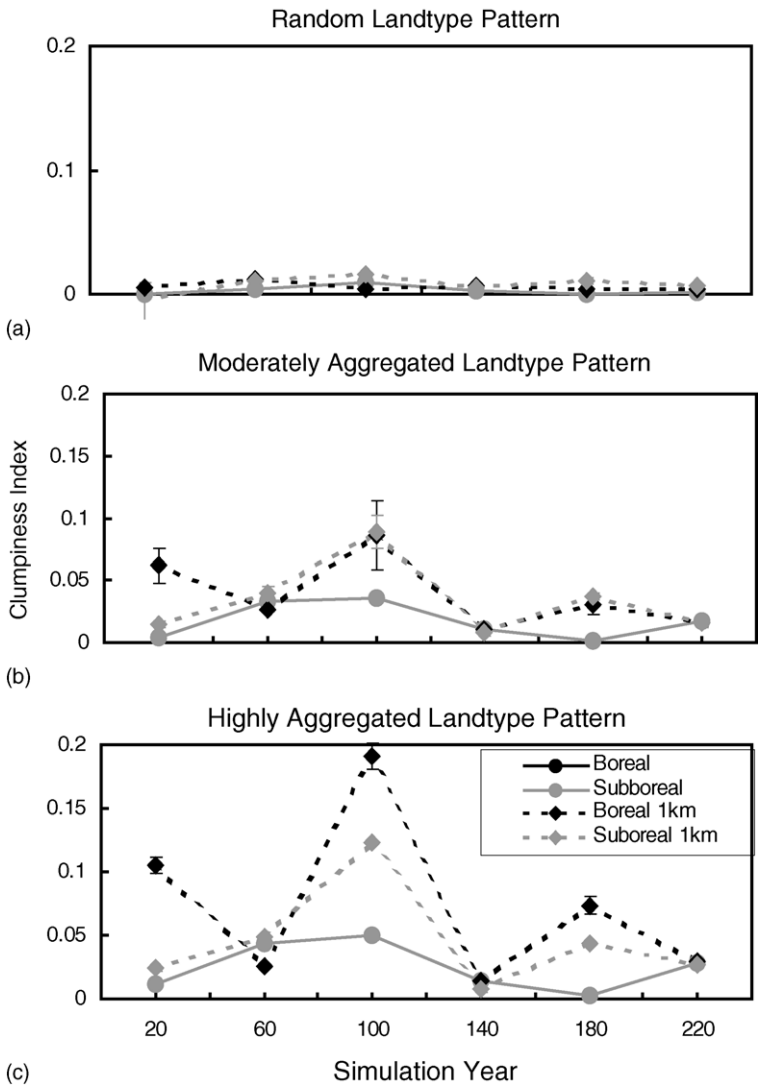

Fig. 6. "Clumpiness" of disturbed sites in landscapes with different land type patterns, where −1 = uniform pattern, 0 = a random pattern, and 1 = a maximally aggregated pattern (McGarigal et al., 2002). Clumpiness values for boreal scenarios were identical to subboreal scenarios, and are not shown. Points represent disturbance events, whereas lines only indicate trends in disturbance events through time. Error bars represent one standard deviation of the mean of three replicates. Note that the clumpiness index for boreal and subboreal without neighborhoods were nearly identical, therefore boreal no neighborhood symbols cannot be seen in any of the graphs.

strated that the relative amount of balsam fir that persisted in the landscape was sensitive to the vulnerability class of the youngest age cohort (Sturtevant, unpublished data). These results indicate that LANDIS is producing realistic succession dynamics in response to budworm disturbances. Combined fire and budworm disturbance regimes will be required to fully capture actual successional dynamics of most boreal and subboreal systems (Bergeron, 2000).

Neighborhood effects on stand vulnerability have only recently been quantified in budworm disturbances (Cappuccino et al., 1998; Radeloff et al., 2000). Simulations in this study suggest that neighborhood influence has some interesting implications for the spatio-

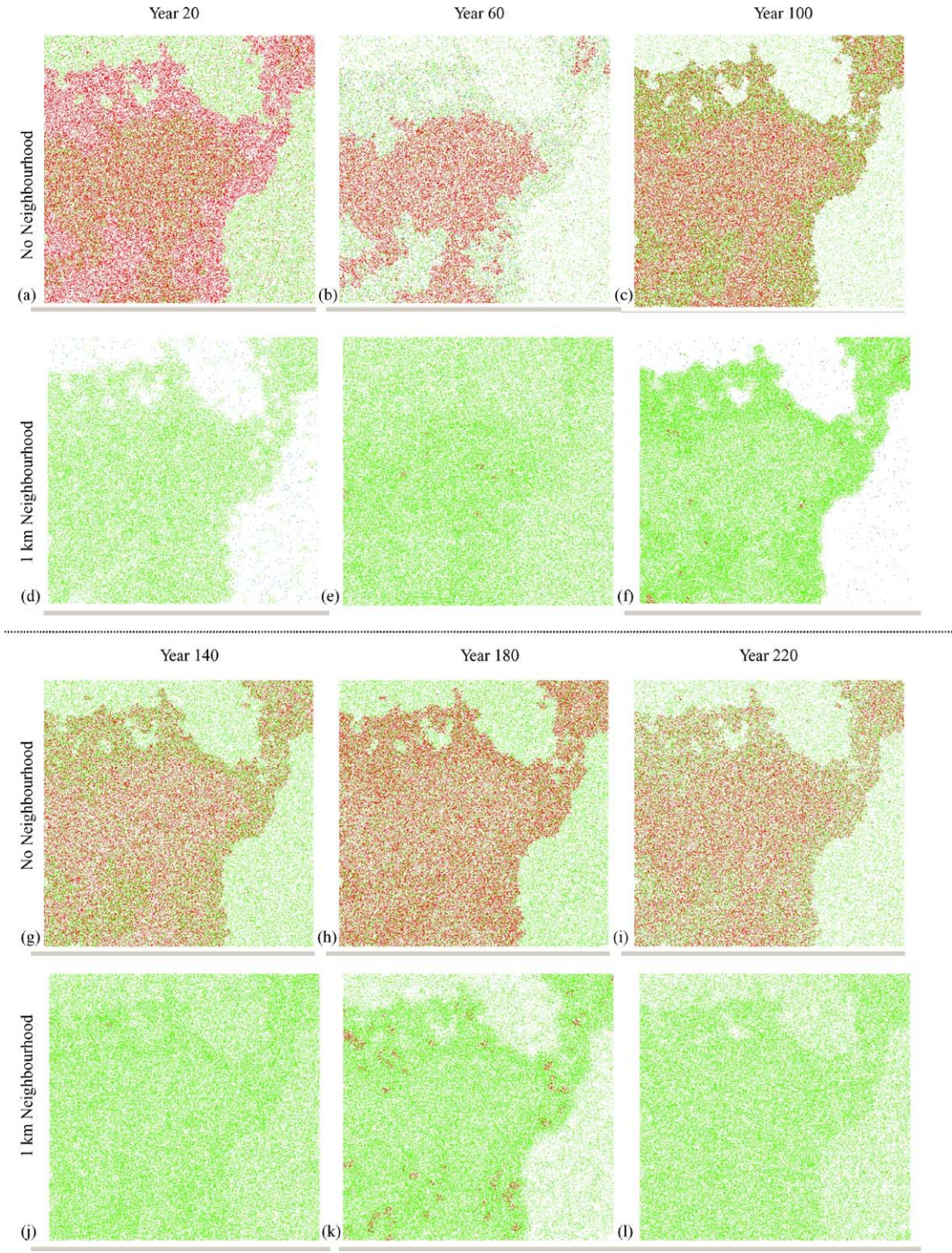

Fig. 7. Comparisons of the spatial patterns of disturbance severity for a landscape with a highly aggregated land type pattern when no neighborhood is applied (a–c, g–i) vs. a disturbance severity using a 1 km neighborhood (d–f, j–l). Red cells represent high severity disturbance, green cells represent moderate severity disturbance, and blue cells represent low severity disturbance.

temporal patterns of biological disturbances. First, the mean resource value of a landscape was reduced by the presence of non-host sites, particularly if the sites are highly interspersed (Fig. 2). This result is consistent with a long-standing but hotly debated "silvicultural hypothesis" of spruce budworm disturbance, which suggests that the homogenization of forests caused by logging practices has increased the amount and severity of budworm disturbance throughout much of boreal Canada (Miller and Rusnock, 1993). Other implications of the neighborhood are more subtle. For example, while reduced resource values resulted in lower landscape vulnerability to a given outbreak, lower disturbance rates enhanced the survival of host to be disturbed at the next outbreak (Fig. 4). Neighborhood influence typically homogenizes disturbance severity across heterogeneous landscapes (Fig. 7). Yet feedback between host survival and environmentally induced spatial patterns in host distribution can also create complex spatio-temporal patterns of mortality across the landscape (Figs. 4 and 7). While the silvicultural hypothesis is still unresolved (Miller and Rusnock, 1993), better understanding of the interactions between host pattern and disturbance at the landscape scale may help clarify the conditions under which forest management can affect landscape vulnerability to spruce budworm and other forest-pest species (Lewis and Lindgren, 2000).

In sharp contrast with fire disturbance ecology, characteristic spatial patterns of biological disturbances are not well-understood, particularly at large spatial scales (Hemstrom, 2001). In his review, MacLean (1980) noted a large degree of spatial heterogeneity in tree mortality following spruce budworm outbreaks, where "extremes of greatest and least mortality occurred within 50 m of one another, within what appeared to be a uniform stand." Such patterns indicate that at least some stochastic elements are affecting the fine-scale disturbance patterns caused by budworm. Kneeshaw and Bergeron (1998) investigated the gap structure of stands disturbed by budworm in Quebec, and found a high proportion of very small, tree-sized gaps. Disturbances simulated here generally approximated a random spatial distribution (Fig. 6). However, the resolution of the simulated sites was coarser than the scale of a typical tree gap. There are two alternative approaches that could be used to more realistically capture fine-scale disturbance caused by insects. The cell-size could be reduced to better approximate the size of a typical gap caused by a mature tree. This approach would likely result in a random pattern of tree mortality that might better represent reality, but the increased resolution would also drastically reduce the performance of the model and the ability to simulate large landscapes. Alternatively, we might implement "partial" mortality caused by budworm within a given cell. Future developments in LANDIS will allow such partial disturbances through the use of the new biomass module (Scheller and Mladenoff, this volume). At broader spatial scales, the spatial structure of host did cause some spatial aggregation in disturbance patterns, and this aggregation was enhanced when a neighborhood was used to calculate the resource dominance of the site (Fig. 6). However, strong spatial aggregation in disturbances will likely require spatial constraints on the behavior of the BDA, such as dispersal limitation.

Biological disturbance agents with limited dispersal ability will require simulation of dispersal to correctly simulate their spatial dynamics. These dispersal-limited BDAs include many important forest pathogens such as Armillaria root disease (*Armillaria* spp.) (Lundquist, 1993) and parasites such as mistletoe (Lavorel et al., 1999). Dispersal of insects or disease may be modeled as a percolation process within a rasterized map with different habitat types (Turner et al., 1989), or as focus expansion models (Zadoks and van den Bosch, 1994). Development of generalized spread algorithms is underway for the BDA module, but beyond the scope of this paper.

The regional outbreak functions used in this BDA module are gross simplifications of population dynamics. However, there are data sources available that can parameterize such simple functions. Examples for spruce budworm include dendrochronology studies (Blais, 1983; Swetnam and Lynch, 1993; Bergeron, 2000) and long-term aerial monitoring efforts (Erickson and Hastings, 1978; MacLean and MacKinnon, 1996). While the two temporal functions currently used in the module can be parameterized to simulate a wide array of historic disturbance patterns (e.g., Fig. 3), the categorical design of the regional outbreak status may potentially introduce unexpected model behavior that could be avoided with a continuous outbreak function. Nonetheless, given that the current LANDIS design is restricted to 10-year time steps, a continuous function will likely exceed the level of precision we can simulate with any confi-

dence. Future work in the module will investigate different population-based alternatives to the simplified temporal functions described here.

Another limitation in our design is that disturbances events are partially uncoupled from the host resource. For example, while disturbances occur in proportion to the availability of host, the host condition of the landscape has no influence over the temporal frequency or regularity of the disturbance events. Some forest pests, such as bark beetles, exhibit threshold population dynamics where some minimum levels of susceptibility must be met before an epidemic can take place (Rykiel et al., 1988). The BDA module will likely require modification before it can adequately simulate such disturbances. Still, our approach does have value because we can investigate the implications of a given biological disturbance regime on the spatio-temporal patterns of forest succession at large temporal and spatial scales.

In fire ecology, a wide range of approaches has been used to simulate interactions between fire and forests, where the selection of the modeling approach is dependent on the relevant spatial and temporal scales investigated (Gardner et al., 1999). Similarly, this paper demonstrates that the BDA module is useful for investigating the landscape-scale spatio-temporal dynamics of a regionally synchronized defoliator, whose outbreaks are relatively cyclical. The module design is flexible enough to accommodate a wide array of BDA life history traits, but its utility for simulating other BDA types remains to be seen. While future work might combine explicit population modeling with a pattern-based approach to simulating disturbances caused by insects and disease, the resulting models are likely to be cumbersome and far less general. Alternatively, detailed nonspatial models can complement simpler but spatially explicit models by characterizing the temporal dynamics of the "mean field" system without the complications of space. Relatively simple but spatially explicit models can then evaluate the implications of those temporal dynamics in heterogeneous landscapes.

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