CHAPTER

A Review of LANDIS and Other Forest Landscape Models for Integration with Wildlife Models

12

Hong S. He

The essential goal of wildlife management is to conserve wildlife populations. This goal is often evaluated with wildlife habitat models or population models. These wildlife models often assume that wildlife habitats remain static (Akçakaya 2001). Such an assumption can be problematic when models span long time periods and large spatial extents. Habitat abundance, quality, and distribution will change due to many natural and anthropogenic processes, including spatial and landscape processes. Forest landscape processes are a set of spatially contagious processes such as fire, wind, seed dispersal, insect and disease propagation, and forest harvest. They operate at large spatial (10^3–10^7 ha) and temporal scales (10^1–10^3 years), overlapping with the scales required to study habitat and population change. Forest landscape processes are key factors affecting forest landscape dynamics and consequently habitat, abundance, quality, and distribution for wildlife. Such processes can be addressed with forest landscape models. Integrating forest landscape modeling and wildlife modeling provides a viable tool to fully address forest wildlife habitats and population under various natural and anthropogenic regimes (Akçakaya et al. 2004, Wintle et al. 2005, Pichancourt et al. 2006, Shifley et al. 2006).

Over the past 15 years, there has been a rapid development in the field of forest landscape modeling, fueled by both technological and theoretical advances (Noon et al., this volume). From a technological perspective, forest landscape models have benefited greatly from increasing computing capacity and the development of GIS, remote sensing, and software engineering (Roloff et al., this volume). Incorporating ecological processes into forest landscape models and digitally representing these processes and their interactions can be facilitated through the use of well-designed computer software (He et al. 1999, He et al. 2002). The discipline of landscape ecology studies the interaction of spatial pattern and ecological processes under various spatiotemporal scales and theories of disturbance, equilibrium, and nonequilibrium approaches of vegetation and ecosystems. Landscape ecology provides a strong theoretical and conceptual basis for forest landscape modeling. The general background of forest landscape model development is reviewed by Sklar and Costanza (1990), Gardner et al. (1999), Mladenoff and Baker (1999), Mladenoff (2004), Scheller and Mladenoff (2007), and He (2008).

Forest landscape models share two common features: (1) They simulate forest vegetation response at large spatial and temporal scales; and (2) they simulate outcomes of repeated, stochastic landscape processes (e.g., seed dispersal, fire, wind, insects, diseases, harvests, and fuel treatments). Depending on the model purpose and design limitations, forest landscape models may differ in the key ecological processes incorporated, the extent to which mechanistic details are simulated for each process, and the type and scope of applications. These differences render certain forest landscape models more suitable for wildlife modeling than others.

I review approaches used to simulate site-level vegetation dynamics in forest landscape modeling because different approaches have different potentials and limitations for use with wildlife modeling. I use the LANDIS model to illustrate a general framework of integrating a forest landscape model with habitat suitability models or population models. I show that (1) habitat suitability can be evaluated under a combination of forest management and natural disturbance scenarios; (2) habitat suitability is dynamic, driven by succession, disturbance, and management; (3) habitat maps can be derived using relevant species and age class combinations targeted specifically to individual wildlife species; and (4) aggregations and disaggregations of vegetation classes using raster data simulated in the LANDIS model allow habitats to be mapped at multiple scales. Finally, I discuss limitations of the LANDIS model in this coupled modeling framework.

FOREST LANDSCAPE MODELS AND THEIR POTENTIALS IN WILDLIFE MODELING

A forest landscape model simulates spatiotemporal characteristics (distribution, shape, abundance, etc.) of at least one recurrent landscape process in a spatial context. Under this definition, a forest landscape model (1) is a simulation model where the model objects of time t are derived from the model objects of time t–1; (2) simulates recurrence of one or more landscape processes; and (3) operates at a large spatial and temporal extent that is adequate to simulate the landscape process (He 2008).

Forest landscape models have been developed using diverse approaches largely driven by research or application. Two features that are keys to integrating forest landscape models with wildlife models are the number and types of landscape processes simulated and the type of vegetation data tracked by each model entity (i.e., basic modeling unit such as pixel or polygon).

Most forest landscape models employ simplified approaches to simulate site-level vegetation dynamics, under the premise that fine-scale, site-level dynamics can be aggregated, whereas modeled landscape-scale objects are relatively less affected (Rastetter et al. 1992). Three approaches are generally used to simulate site-level vegetation dynamics, each approach having its own potentials and limitations for wildlife modeling.

Landscape Process Models

Landscape process models do not explicitly simulate site-level vegetation dynamics; rather, variables representing simulated landscape processes are used as surrogates for site-level succession dynamics (He 2008). For example, the variable time since last fire is used to represent stand age in DISPATCH (Baker et al. 1991) and ONFIRE (Li et al. 1997), time since last treatment is used to represent the amount of fuel accumulated in FIRESCAPE (Cary 1998), and time since last harvest is used to represent stand age in HARVEST (Gustafson and Crow 1996), while the actual site-level vegetation or succession is not simulated. These models are either highly theoretical or tend to work in the systems where dominant landscape processes may override site-level succession dynamics. For example, in boreal forests in Canada (Li et al. 1997), western coniferous forests in the United States (Romme and Despain 1989), chaparral shrub lands in southern California (Franklin et al. 2005), and Eucalypt forests in Australia (Gott 2005), fires tend to be stand replacing, and once they occur, they can reset succession to the initial stage.

For this group of models, inferences about vegetation are usually derived using empirical relationships based on the variables representing the landscape process such as time since last disturbance or harvest recorded at each site (pixel or polygon). The inferred vegetation information is usually general, such as stand development stage (e.g., young or old forests) or seral stages such as early, mid, or late successional vegetation. The inferred vegetation characteristics and these simulated spatial patterns can then be used to model wildlife habitats or populations. For example, HARVEST is a timber harvest allocation model developed by Gustafson and Crow (1994). It does not track actual timber or vegetation for each site and therefore does not simulate site-level dynamics. Rather, it allows the input of specific rules of clearcutting to generate landscape patterns that reflect the “look and feel” of managed landscape. The output of HARVEST can be used to determine the effect of variation in harvest size, rotation, and total harvest area on the spatial pattern of a forested landscape. The simulated spatial patterns were further assessed for a generalized neotropical migrant forest bird using a GIS model (Gustafson and Crow 1994).

These models usually simulate one landscape process, either fire or harvest, because simulating multiple landscape processes generally requires simulating site-level succession. Thus, application of these models is limited primarily to situations in which there is interest in the effects of one dominant landscape process, such as fire or timber harvest, but not both.

Succession Pathway Models

Succession pathway models track vegetation types for each model unit (pixel or polygon) and use state-and-transition models to represent succession by linking vegetation types or development stages to the transition time. Succession proceeds along pathways until it reaches a climax or stable vegetation type. Succession pathways are deterministic, but stochastic characteristics such as transition time and transition probability can be built in using Markov modeling (e.g., Gardner et al. 1999, Hargrove et al. 2000). Landscape processes interact with the pathway by forwarding or rewinding succession stages. It is possible to incorporate a landscape process of different forms (e.g., fire with different intensities) or multiple landscape processes (e.g., fire, insect, disease, and harvesting) into succession pathways.

Succession pathway models are highly empirical; the transition time and direction are often quantified from empirical knowledge through field observation. Succession pathways can be as simple as vegetation development stages (e.g. seedling, sapling, young forest, and old forest) or as specific as major vegetation types of different seral stages such as those developed by Keane et al. (2004) for mountain pine beetle.

Single pathway models are usually associated with one landscape process, such as fire in the model by EMBYR (Gardner et al. 1999, Hargrove et al. 2000). In EMBYR, vegetation is interpreted as fuel types and updated per iteration via a predefined transition probability. Multiple pathway models are associated with multiple landscape processes or one model object with multiple forms; examples are LANDSUM (Keane et al. 2002), SIMPPLLE (Chew et al. 2004), and LADS (Wimberly et al. 2000). In LANDSUM and LADS, fire can have multiple forms in terms of intensity, such as stand replacement fire (high severity) and nonlethal surface fire (low severity). Vegetation can have multiple predefined pathways under these fire severities.

The potential to integrate succession pathway models with wildlife models varies depending on the succession pathways defined. The advantage of succession pathway models is that when empirical knowledge is available, succession pathway approaches have the flexibility to incorporate multiple landscape processes. Multiple succession pathways may provide alternatives of disturbance and management, under which more realistic examination of wildlife response can be achieved. A limitation of integrating succession pathway models with wildlife models is the predefined pathways. Since succession pathways are predefined in these models, wildlife habitat types are also predefined. Thus, succession pathway models may be of limited value for studying wildlife habitats that are not included in the predefined succession pathways, which are driven by disturbance and succession stages.

Vital Attribute Models

Vital attribute models use vital attributes defined as a set of autecological characteristics necessary to predict plant species' behavior in environments of recurrent disturbance (Nobel and Slatyer 1980). The vital attributes generally reflect plant species succession (longevity, sexual maturity, sprouting), competition (shade tolerance), dispersal, and their tolerance to disturbance. They can be defined either for individual species or functional groups of species (Roberts and Betz 1999). Vegetation dynamics on an individual site are simulated as competitive processes driven by species' longevity, maturity, seeding and resprouting capability, and environmental suitability, defined by species' vital attributes. Without disturbance, more shade-tolerant species will outcompete less shade-tolerant species to reach climax or a stable state. Species' vital attributes can also interact with disturbances through species' tolerance to disturbance. Postdisturbance response is driven by a combination of species' longevity, maturity, seeding capability, sprouting capability, and environmental adaptability. Roberts (1996) first implemented the vital attribute approach in LANDSIM, a polygon-based model, and this approach is used by the LANDIS models (Mladenoff 2004).

Vital attribute approaches are more mechanistic, less deterministic, and more flexible in deriving vegetation or habitat types than succession pathway approaches because vegetation types are not predefined. Vital attribute approaches generally have a greater potential for integration with wildlife models than do landscape process or successional pathway models. The reason is that vegetation type is an emergent property determined by the interactions of plant species, environment, disturbance, and/or management. Thus, wildlife habitat requirements can be defined specifically based on a focal plant species or a group of plant species, and habitats can be generated from model outputs such as plant species and age class.

THE LANDIS MODEL

Overall Model Design and Structure

LANDIS is a vital-attribute, raster-based forest landscape model (Mladenoff et al. 1996, Mladenoff and He 1999) (Fig. 12-1). Each raster unit or cell tracks (1) the presence or absence of 1- to 10-year age cohorts of individual species; (2) fuel accumulation level; (3) the time since last disturbance (e.g., fire, wind, insects, and disease) and the time since last management (e.g., harvest and fuel treatment); and (4) species establishment ability in particular land types. For each cell, species birth, growth, death, regeneration, random mortality, and vegetative reproduction are simulated at 1- to 10-year time steps. At landscape scales, seed dispersal, disturbances, and management are simulated each iteration. To simulate heterogeneous landscapes, one uses land types derived from other

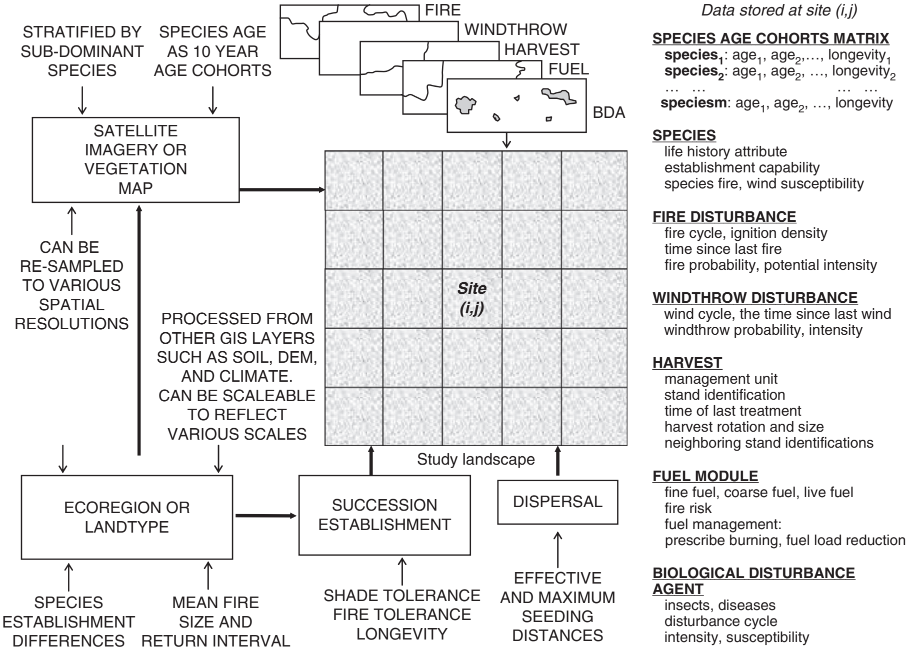

FIG. 12-1

LANDIS model structure (duplicated from Figure 1 in He et al. 2005). In LANDIS, a landscape is divided into equal-sized individual cells or sites. Each *site* (*i, j*) resides on a certain land type and includes a unique list of species present and their associated age cohorts. The species/age cohort information varies via establishment, succession, and seed dispersal, and interacts with disturbances. For disturbance heterogeneity (except for wind and biological disturbances), LANDIS stratifies the heterogeneous disturbance regimes using disturbance regime maps. Within-regime heterogeneity is further simulated by the stochastic process of each disturbance regime, and pixel-level heterogeneity is simulated through the interaction of disturbance and vegetation in the particular pixel.

climate and soil GIS data layers to stratify the landscape into smaller homogenous land units. At a given focal resolution such as within each ecoregion, physical conditions are assumed homogeneous, as are some characteristics such as fuel accumulation and decomposition rates, and species establishment (He et al. 1999, Mladenoff and He 1999). LANDIS simulates succession as a nonspatial process and seed dispersal, fire, wind, insect and disease, timber harvesting, and fuel treatment as spatial processes (He et al. 2005).

Succession

Succession is a result of birth establishment, growth, death, and vegetative reproduction of individual species and competition among species. Species' competitive ability is determined based on simple logical rules by the combination of life history attributes and land type suitability (Mladenoff and He 1999). Shade-intolerant species (species with lower shade-tolerance class) cannot establish on a site where more shade-tolerant and mature species are present. On the other hand, the most shade-tolerant species are delayed in establishment on an open site until specified years of shade creation are met. A shade-checking algorithm defines shade by the most shade-tolerant species cohort present that is also sexually mature. Species cohorts younger than the minimum seed-producing age are ignored in this shade-checking algorithm. This approach was implemented as a surrogate for crown closure. Without disturbance, shade-tolerant species will tend to dominate the landscape if other attributes are not highly limiting and land types (reflected as species establishment coefficients) are generally suitable.

In LANDIS, vegetation heterogeneity is modeled at multiple hierarchical levels from the landscape to the pixel. Land type captures the highest level (coarse grain) of spatial vegetation-heterogeneity caused by various environmental controls. A somewhat uniform suite of ecological conditions that results in similar species establishment patterns is assumed for each land type. Within a land type, stochastic processes such as seed dispersal can result in intermediate-level heterogeneity of a species distribution. At an individual site or pixel level, succession, competition, and probabilistic establishment may result in heterogeneity of species presence and age cohorts even among pixels that were initially identical.

Natural Disturbance

To simulate different types of disturbances and their effects on tree species composition and landscape pattern is central to the design of LANDIS. LANDIS can simulate three different types of natural disturbances (fire, wind, and biological), which can be applied in any combination. While each disturbance module follows its own set of rules, there are some basic designs common to all disturbance modules that are described here.

A disturbance event can be simplified into three steps: (1) selecting sites to be disturbed; (2) determining disturbance intensity; and (3) removing susceptible and intolerable species-age cohorts (e.g., disturbance-caused mortality or effects). Disturbance site selection involves both the starting site (e.g., ignition) and spread algorithms that vary by disturbance types. For example, a wind or fire event spreads across a subset of sites forming disturbance patches. In each case, stochastic (e.g., ignition and some components in spread) and deterministic processes (mortality) determine the final shape and form of the disturbance event.

Disturbance intensity classes in LANDIS approximate the relative strength of the simulated disturbance event, and their specific calculation varies by disturbance type. Vulnerability of species and/or age cohorts to a given disturbance type can vary; in LANDIS, tolerance class defines the relative vulnerability of a species to a given disturbance type and intensity, and susceptibility class defines the relative vulnerability of a species age group to a given disturbance type and intensity (He and Mladenoff 1999). For example, fire is simulated, in general, as a bottom-up disturbance, in which the youngest age cohorts are most susceptible to mortality. However, a low intensity fire may not kill species of high fire tolerance class even if its age cohorts are young. Removal of intolerant species and susceptible age classes is resultant from the interaction of disturbance intensity and species tolerance and susceptibility at each site and calculated for each species age cohort present on that site to determine which species age cohorts are removed by the disturbance.

Timber Harvest and Fuel Treatment

The LANDIS harvest and fuel treatment modules use a hierarchical approach that reflects the typical decisions made and execution of timber harvest and fuel treatment activities in managed forests. In both modules, a landscape is divided into forest management areas that represent spatial zones to which specific management goals are assigned. Within each management area, the landscape is divided into stands of various forest types. Stands are basic implementation units where harvest prescriptions are implemented. Each stand contains a group of grid cells, and each cell is populated with a specific combination of species and age cohorts. Management practices are the combination of temporal, spatial, and species components (Gustafson et al. 2000) and specify (1) when or how often to harvest or treat fuel for a stand; (2) how to allocate harvest and fuel treatment based on stand ranking, which in turn is based on user-specified criteria such as economic value or fuel loading; and (3) how to harvest a species age cohort (shelterwood, selection, and clear-cutting) or conduct a particular fuel treatment (prescribed burn or coarse woody debris reduction). The combination of these three components covers most forest management practices currently being used across a wide spectrum of ownership (Gustafson et al. 2000; He et al. 2004; Shang et al. 2004, 2007).

Operational Design of LANDIS

LANDIS has been continually updated and improved (Mladenoff and He 1999, He et al. 2005, Scheller and Mladenoff 2007). LANDIS uses a component-based approach to conduct simulation, which breaks the monolithic program into multiple small, standalone, and functionally more specific components (He et al. 2002, Scheller and Mladenoff 2007). The model is complex in terms of algorithms, interactions, and parameters. However, due to the modular design (He et al. 1999, 2002), LANDIS is relatively easy to use because users need to parameterize only the components of interests while turning off all modules not of interest.

Operationally, the model is a free-standing program. Implemented processes such as wind, fire, insect and disease, harvest, and fuel management have their

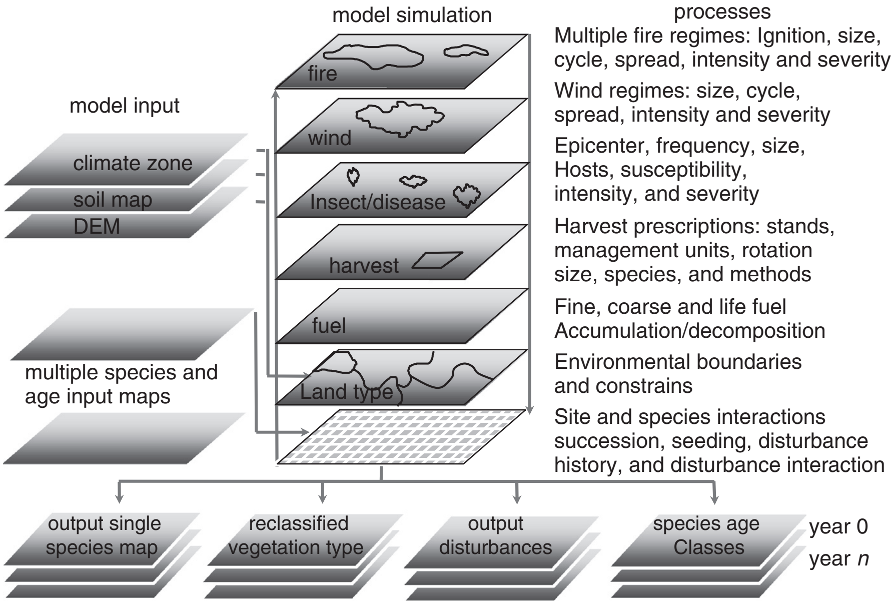

FIG. 12-2

The LANDIS model is a free-standing program that operates on a raster GIS format. Implemented processes such as harvest, fuel management, and disturbance can have their own respective input maps. The model can output maps of individual species, individual species age cohorts, forest type, and various disturbance and management history maps.

own respective input maps. The model can output maps of individual species, individual species age cohorts, forest type, and various disturbance and management history maps (Fig. 12-2).

GENERAL FRAMEWORK FOR INTEGRATING WILDLIFE MODELS AND LANDIS

One approach to integrating a wildlife model with LANDIS is to conduct scenario analysis. The lack of management experience at landscape scales and the limited feasibility of conducting landscape-scale experiments have resulted in the increasing use of scenario modeling to analyze the effects of different management actions on focal forests or wildlife species. Model scenarios are created by altering input parameters to reflect changes in climate, disturbance, and/or fuel or harvest alternatives, whereas the built-in model relationships remain unchanged. Comparing results from different model scenarios provides relative measurements regarding the direction and magnitude of changes within the simulated landscape.

Multiple simulation scenarios are derived by using the same set of spatial input and varied nonspatial input representing different simulation scenarios. Spatial input includes species composition and age classes representing the initial or current vegetation conditions, land type or ecoregion map that reflects the environmental heterogeneity, disturbance regimes maps, stand map, and management unit map for harvesting and fuel treatment. Nonspatial input includes parameters of each disturbance regime and management alternative as well as species vital attributes driving vegetation succession dynamics. Each scenario is independently simulated, and the output for each scenario contains time series maps of individual species, age classes, vegetation types, and disturbance and management effects (Fig. 12-3).

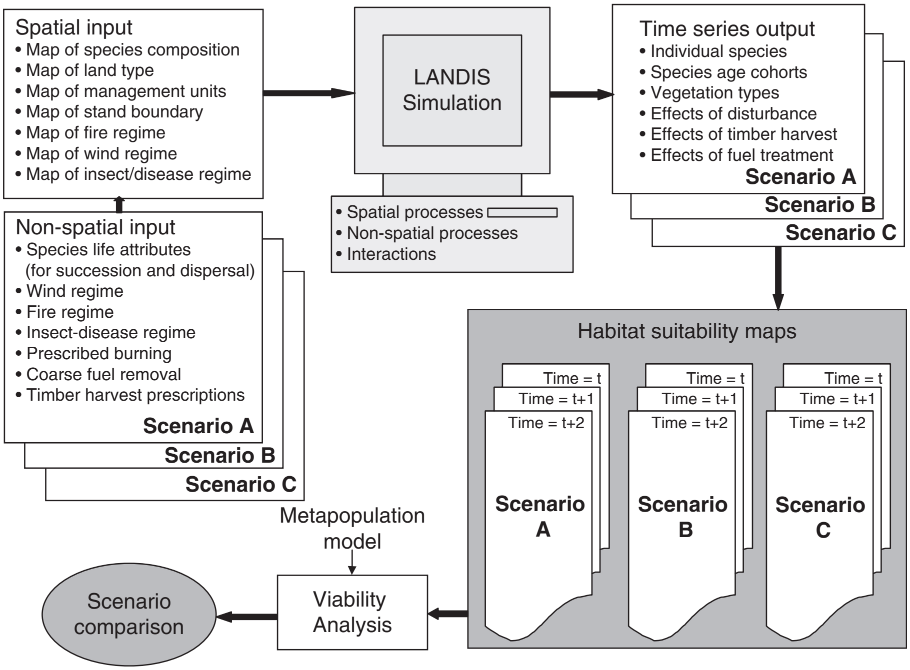

FIG. 12-3

Wildlife models can be integrated with multiple scenarios representing different management and disturbance alternatives that were simulated in LANDIS. The output for each scenario from LANDIS contains time series maps of individual species, age classes, vegetation types, and disturbance and management effects. Habitat suitability index (HSI) models can be used to create a time series of habitat (patch) maps from the LANDIS outputs, and population models can be used to assess viability. The habitat abundance, quality, and spatial structure over time via an HSI model and species viability via a metapopulation model can be compared among scenarios to evaluate the effects of disturbance and management alternatives on wildlife focal species or a suite of species.

For each scenario, LANDIS generates a time series of output maps of individual tree species and their age classes (Fig. 12-2). These output maps, along with other GIS layers, can be used as inputs for wildlife models, such as habitat suitability (HSI) models. This is an independent, post-LANDIS simulation process that is often performed in a GIS environment (Larsen et al. 2003) or with standalone software (Dijak et al. 2007; Dijak and Rittenhouse, this volume). This process often involves moving or sliding window GIS techniques, and within each window, HSI score, a measure of the quality of the habitat, is calculated based on plant species composition and age classes. Window sizes usually reflect the biological requirement of the focal species (e.g., home range or minimum territory requirement). The habitat abundance, quality, and spatial structure over time can be compared among scenarios to evaluate the effects of disturbance and management alternatives on wildlife habitat for a focal or a suite of species (Shifley et al. 2006).

Wildlife habitat models provide an assessment of habitat quality, but they do not provide specific information on populations. Population models can be applied to the time series of outputs from LANDIS, or habitat maps produced from these, to simulate population trajectories and viability. Thus, the effects of modeled scenarios of disturbance and management on wildlife population can be more specifically compared and evaluated (Akçakaya et al. 2004; Wintle et al. 2005; Akçakaya and Brook, this volume; Bekessy et al., this volume). Linking population models with LANDIS is first based on habitats delineated from habitat modeling (Fig. 12-3). The habitat quality (e.g., HSI score) of each pixel can be further used to derive habitat patches and their maximum carrying capacity (Akçakaya et al. 2005). This often provides the initialization of wildlife population for each pixel at the beginning of the LANDIS simulation year. Other demographic factors such as sex ratio, reproduction rate, fecundity, and survival rate are either measured directly in the field or parameterized from published sources to support the subsequent demographic modeling, and can also be linked to habitat quality. Typical results of demographic modeling coupled with LANDIS include species abundance and viability under various simulated disturbance and management regimes (Akçakaya et al. 2004, 2005). The coupling of LANDIS and a wildlife model can be loose or seamless. In the former case, LANDIS is run independently, and the simulated results are separately analyzed with wildlife habitat or population models (Larson et al. 2004, Shifley et al. 2006). Seamless simulations using LANDIS and the population model RAMAS can be run with the RAMAS-LANDIS model (Akçakaya et al. 2004; Bekessy et al., this volume).

Akçakaya et al. (2004) demonstrated the use of RAMAS-LANDIS in assessing the effects of forest management scenarios on sharp-tailed grouse (*Tympanuchus phasianellus*) in the northern Wisconsin Pine Barrens. The region has been severely altered since human settlement, resulting in relatively old red pine (*Pinus resinosa*) and lack of jack pine (*Pinus banksiana*) forests that affect sharp-tailed grouse, which persisted in fire-generated openings of presettlement times (Radeloff et al. 2006). In this work, Akçakaya et al. (2004) simulated eight management scenarios using LANDIS. These scenarios contained silvicultural parameters ranging from small to large clearcut sizes of jack pine, as well as several clearcut sizes and minimum cutting age combinations under red pine management (Radeloff et al. 2006). They showed that different timber harvest scenarios result in different amounts of available habitat, measured by the total carrying capacity of all habitat patches. Scenarios with the largest amount of habitat, however, were the worst scenarios in terms of population viability. Such results suggest that ranking management options only in terms of the habitat they provide for threatened or declining species, while ignoring the demography of species, may be misleading. Also, approaches that ignore changes in landscape may overestimate viability and give results that are too optimistic compared with the more realistic simulations that incorporate landscape dynamics.

Wintle et al. (2005) also used the approach developed by Akçakaya et al. (2004) and examined the effects of eight management and disturbance scenarios on brown creeper (*Certhia americana*) in a managed, boreal landscape in north-central Ontario, Canada (see Bekessy et al., this volume). Disturbance scenarios include the current fire regime under fire suppression (long fire return interval, small mean fire size, and higher fire intensity) and natural fire regime (short fire return interval, large mean fire size, and lower fire intensity). The management scenarios ranged from no timber harvesting to natural disturbance-emulation harvesting to intensive harvesting with fire suppression and salvage logging in burned forests under altered fire regime. Compared with using the metapopulation model alone, results from the integrated model showed that trajectories for the brown creeper under alternative management scenarios differed from the base-model, with declines predicted as the intensity of disturbance increased, and under most scenarios the predicted minimum population size was not in direct proportion to the change of carry capacity over the simulation. Their results suggested that population processes, beyond simple habitat availability, influenced model results.

Larson et al. (2004) combined all three components of a habitat-based population viability analysis for land management planning, including landscape simulation using LANDIS, quantifying wildlife habitat quality using HSI models, and population viability analysis using RAMAS GIS. They demonstrated this application for ovenbirds (*Seiurus aurocapillus*) in two simulation scenarios: (1) no harvest, in which forest growth is only disturbed by fire and windthrow; and (2) even-aged management on a 100-year rotation, in which forest growth and succession are disturbed by fire, windthrow, and a clearcut of 10% of the area each decade. They found that ovenbird habitat quality in the study area differed between the no harvest and even-aged harvest scenarios during the first 100-year period, but was similar during the second 100-year period, since natural tree mortality and wind and fire disturbance in the later stage of the simulation increased. Their results further showed that the viability of ovenbird populations was noticeably lower under the even-aged management scenario. These results cannot be derived using habitat suitability models or population models alone. However, the trade-off of involving all three models is increased uncertainties, which are difficult to evaluate due to the complexity of models.

ADVANTAGES AND LIMITATIONS

The main advantages of linking wildlife models to landscape vital-attribute models such as LANDIS are (1) the rich data of individual tree species and age classes recorded for each pixel, and (2) the ability to simulate multiple landscape processes that impact landscapes and wildlife. Wildlife species have a wide range of habitat requirements that can be assessed using basic vegetation information such as vegetation type and age. For example, ovenbirds prefer late successional forest habitat, prairie warblers (*Dendroica discolor*) prefer early successional forest habitat, and hooded warblers (*Wilsonia citrina*) prefer forest gaps. The respective habitat for each species can be derived from the LANDIS tree age map by interpreting 0–20-year-old forest as gaps or patches of early successional forest and forest >40 years old as mature and late successional forest (Shifley et al. 2006). Pine warblers (*Dendroica pinus*), for example, prefer mature coniferous forest, so LANDIS tree age and tree species maps can be used to assess habitat suitability (Larson et al. 2003). Because LANDIS records vegetation information at individual species and age class levels, vegetation information from the same set of simulations can be used to evaluate habitat for multiple wildlife species. Such flexibility is difficult to obtain with succession pathway models that use predefined vegetation or habitat types.

LANDIS is one of the few comprehensive forest landscape models that explicitly simulates silvicultural level timber harvest and common fuel treatments such as prescribed burning and coarse woody debris removal, along with simulation of fire, windthrow, and insect and disease disturbance. The capacity of including multiple landscape processes makes it possible to evaluate the effects of multiple disturbances on wildlife habitat and population dynamics (Shifley et al. 2008). The most common processes used to integrate LANDIS and wildlife models are timber harvesting and fire disturbance (e.g., Akçakaya et al. 2004, Wintle et al. 2005), whereas Larson et al. (2004) and Shifley et al. (2006) simulated all above disturbances except insect and disease in their studies. Common scenario comparisons include fire scenarios such as natural, current, historic, or scenarios with suppression (e.g., Wimberly et al. 2000, Keane et al. 2002); timber management scenarios representing combinations of harvest rotation, size, and even and uneven age harvesting (e.g., Shifley et al. 2000, Zollner et al. 2005); fuel treatments representing combinations of prescribed burning and coarse woody debris removal at various intensities and rotations (e.g., Shang et al. 2007); and current climate versus warming climate scenarios (e.g., Scheller and Mladenoff 2005).

Advantages of integrating LANDIS with HSI models or demographic models also include the flexible spatial scales that LANDIS accommodates. Because LANDIS tracks only the presence-absence of species age cohorts, not individual trees, the essential information of presence-absence is relatively independent of cell size, and therefore LANDIS is capable of simulating forest succession at cell sizes ranging from 10 to 500 m (He et al. 1999). Tracking presence and absence of species age cohorts greatly reduces the computational loads and allows the model to simulate much larger landscapes than models that track biomass for each age cohort. Raster-based modeling approaches employed in LANDIS allow habitat patches to be aggregated and disaggregated depending on the requirement of the wildlife species being studied. The aggregation and disaggregation can reflect the appropriate scale of interests. Furthermore, raster models support more complicated computation tasks such as proximity to water and home range sizes, which are often required to derive the habitat map.

There are several limitations to applying wildlife models with LANDIS, many of which are due to the LANDIS data structure. LANDIS records dead biomass as fine and coarse woody debris classes and cannot differentiate standing dead trees from other dead biomass. The model does not record the vigor of live biomass such as cavity trees. Both standing dead and cavity trees are unique habitat requirements, which have to be derived separately. For example, Fan et al. (2003, 2004) developed a model of cavity tree abundance for LANDIS output. Another limitation related to LANDIS data structure is that LANDIS does not directly record forest density and thus does not directly simulate canopy closure, a common requirement for many wildlife species. Independent functions in habitat models, however, can be used to derive tree density based on tree species, age, and land type, which are mapped in LANDIS (Larson et al. 2003).

Early versions of LANDIS used 10-year time intervals to simulate succession, which generally suits studies of long-term effects (e.g., >150 years). However, forest management plans of National Forests are required to be revised at 10- to 15-year intervals, and most forest management prescriptions (fuel treatment, timber harvest, etc.) are processed annually. Thus, a 10-year time step poses a limitation of examining short-term effects (e.g. <20 years). A version of LANDIS with 1-year time steps has been developed and tested (Syphard et al. 2007) for fire and succession modules. Additional developments are underway for the 1-year time step model to work with harvest, fuel treatment, and insect and disease modules. The development of LANDIS II with variable time steps sheds light on addressing the coarse temporal interval issue (Scheller et al. 2007).

Error propagation and uncertainty are obvious in such integrated models because of the numerous parameters and procedures involved in such modeling frameworks. Moreover, there is a lack of formal procedures to analyze error propagation and uncertainties in forest landscape models. In general, uncertainties embedded in model parameters are subjective uncertainties that are often related to measurement, observation, and synthesis. Uncertainties associated with random algorithms built in the model are stochastic uncertainties.

Stochastic uncertainties larger than subjective uncertainties suggest that input model parameters play little role in model outcome (Xu et al. 2004, 2005).

SUMMARY

The quality of wildlife habitat is often evaluated using habitat suitability index models or more sophisticated population viability models. An emerging approach for assessing long-term management effects or landscape changes on wildlife is to link landscape models with wildlife models. In this framework, habitat dynamics under various natural and anthropogenic disturbances are simulated with a landscape model while impacts on wildlife, such as habitat abundance, quality, structure, and population size or trend, are evaluated with habitat models or population models. Over the past 15 years there has been rapid development in forest landscape modeling, fueled by both technological and theoretical advances. Here, I reviewed and classified forest landscape models in three groups, discussed their suitability for integration with wildlife models, and then discussed in detail the model LANDIS. Vital attribute models are generally the most flexible in deriving habitat types from the output of species and age classes. They are more suitable for integration with wildlife models than successional pathway models and landscape process models that do not simulate vegetation dynamics. LANDIS is a raster-based, vital attribute model that has been used with wildlife models. Applying LANDIS to habitat mapping and wildlife population modeling has the following advantages: (1) Habitat suitability can be evaluated under a combination of forest management and natural disturbance scenarios that are study site specific; (2) habitat suitability is dynamic, driven by succession, disturbance, and management; (3) habitat maps can be derived using relevant species and age class combinations targeting specific wildlife species; and (4) aggregations and disaggregations of vegetation classes using raster data simulated in the LANDIS model allow habitat mapping to be accomplished at multiple scales. In this chapter I also discussed LANDIS model structure and examples of habitat suitability mapping using LANDIS as well as limitations of integrating LANDIS with wildlife models.

ACKNOWLEDGMENTS

This work was funded by the Missouri GIS Mission Enhancement Program and the U.S. Forest Service, Northern Research Station. LANDIS can be freely downloaded at www.missouri.edu/~landis. I thank Joshua Millspaugh, Frank Thompson, and an anonymous reviewer for their helpful comments that improved this manuscript.

LITERATURE CITED

Akçakaya, H. R. 2001. Linking population-level risk assessment with landscape and habitat models. *Science of the Total Environment* 274:283–291.

Akçakaya, H. R, J. Franklin, A. D. Syphard, and J. R. Stephenson. 2005. Viability of Bell's sage Sparrow (*Amphispiza Belli* spp. Belli): Altered fire regimes. *Ecological Applications* 15:521–531.

Akçakaya, H. R., V. C. Radeloff, D. J. Mladenoff, and H. S. He. 2004. Integrating landscape and metapopulation modeling approaches: Viability of the sharp-tailed grouse in a dynamic landscape. *Conservation Biology* 18:526–537.

Baker, W. L., S. L. Egbert, and G. F. Frazier. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. *Ecological Modelling* 56:109–125.

Cary, G. J. 1998. *Predicting fire regimes and their ecological effects in spatially complex landscapes*. Dissertation. The Australian National University, Canberra, Australia.

Chew, J. D., C. Stalling, and K. Moeller. 2004. Integrating knowledge for simulating vegetation change at landscape scales. *Western Journal of Applied Forestry* 19:102–108.

Dijak, W. D., C. D. Rittenhouse, M. A. Larson, F. R. Thompson, III, and J. J. Millspaugh. 2007. Landscape habitat suitability index software. *Journal of Wildlife Management* 71:668–670.

Fan, Z., D. R. Larsen, S. R. Shifley, and F. R. Thompson. 2003. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. *Forest Ecology and Management* 179:231–242.

Fan, Z., S. R. Shifley, F. R. Thompson, III, and D. R. Larsen. 2004. Simulated cavity tree dynamics under alternative timber harvest regimes. *Forest Ecology and Management* 193:399–412.

Franklin, J., A. D. Syphard, H. S. He, and D. J. Mladenoff. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8:885–898.

Gardner, R. H., W. H. Romme, and M. G. Turner. 1999. Predicting forest fire effects at landscape scales. Pages 163–185 *in* D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: Approaches and applications.* Cambridge University Press, Cambridge, United Kingdom.

Gott, B. 2005. Aboriginal fire management in south-eastern Australia: Aims and frequency. *Journal of Biogeography* 32:1203–1208.

Gustafson, E. J., and T. R. Crow. 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird brood parasitism. *Landscape Ecology* 9:237–248.

Gustafson, E. J., and T. R. Crow. 1996. Simulating the effects of alternative forest management strategies on landscape structure. *Journal of Environmental Management* 46:77–94.

Gustafson, E. J., S. R. Shifley, D. J. Mladenoff, K. K. Nimerfro, and H. S. He. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research* 30:32–43.

Hargrove, W. W., R. H. Gardner, M. G. Turner, W. H. Romme, and D. G. Despain. 2000. Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* 135:243–263.

He, H. S. 2008. Forest landscape models, definition, characterization, and classification. *Forest Ecology and Management.* 254:484–498.

He, H. S., D. R. Larsen, and D. J. Mladenoff. 2002. Exploring component-based approaches in forest landscape modeling. *Environmental Modelling and Software* 17:519–529.

He, H. S., W. Li, B. R. Sturtevant, J. Yang, Z. B. Shang, E. J. Gustafson, and D. J. Mladenoff. 2005. *LANDIS 4.0 users guide. LANDIS: A spatially explicit model of forest landscape disturbance, management, and succession*. U.S. Forest Service, North Central Research Station, General Technical Report NC-263, St. Paul, Minnesota, USA.

He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology* 80:81–99.

He, H. S., D. J. Mladenoff, and J. Boeder. 1999. An object-oriented forest landscape model and its representation of tree species. *Ecological Modelling* 119:1–19.

He, H. S., Z. B. Shang, T. R. Crow, E. J. Gustafson, and S. R. Shifley. 2004. Simulating forest fuel and fire risk dynamics across landscapes—LANDIS fuel module design. *Ecological Modelling* 180:135–151.

Keane, R. E., G. J. Cary, I. D. Davies, M. D. Flannigan, R. H. Gardner, S. Lavorel, J. M. Lenihan, C. Li, and T. S. Rupp. 2004. A classification of landscape fire succession models: Spatial simulations of fire and vegetation dynamics. *Ecological Modelling* 179:3–27.

Keane, R. E., R. A. Parsons, and P. F. Hessburg. 2002. Estimating historical range and variation of landscape patch dynamics: Limitations of simulation approach. *Ecological Modelling* 151:29–49.

Larson, M. A., W. D. Dijak, F. R. Thompson, III, and J. J. Millspaugh. 2003. *Landscape-level habitat suitability models for twelve wildlife species in Southern Missouri*. U.S. Forest Service, North Central Research Station, General Technical Report NC-233, St. Paul, Minnesota, USA.

Larson, M. A., F. R. Thompson, III, J. J. Millspaugh, W. D. Dijak, and S. R. Shifley. 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling* 180:103–118.

Li, C., M. Ter-Mikaelian, and A. Perera. 1997. Temporal fire disturbance patterns on a forest landscape. *Ecological Modelling* 99:137–150.

Mladenoff, D. J. 2004. LANDIS and forest landscape models. *Ecological Modelling* 180:7–19.

Mladenoff, D. J., and W. L. Baker, editors. 1999. *Spatial modeling of forest landscape change: Approaches and applications.* Cambridge University Press, Cambridge, United Kingdom.

Mladenoff, D. J., and H. S. He. 1999. Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. Pages 125–162 *in* D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: Approaches and applications.* Cambridge University Press, Cambridge, United Kingdom.

Mladenoff, D. J., G. E. Host, J. Boeder, and T. R. Crow. 1996. LANDIS: A spatial model of forest landscape disturbance, succession, and management. Pages 175–180 *in* M. F. Goodchild, L. T. Steyaert, and B. O. Parks, editors. *GIS and environmental modeling: Progress and research issues.* GIS World Books, Fort Collins, Colorado, USA.

Nobel, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetation* 43:5–21.

Pichancourt, J.-B., F. Burel, and P. Auger. 2006. Assessing the effect of habitat fragmentation on population dynamics: An implicit modelling approach. *Ecological Modelling* 192:543–556.

Radeloff, V. C., D. J. Mladenoff, E. J. Gustafson, R. M. Scheller, P. A. Zollner, H. S. He, and R. H. Akçakaya. 2006. Modeling forest harvesting effects on landscape pattern in the Northwest Wisconsin Pine Barrens. *Forest Ecology and Management* 236:113–126.

Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neill, and J. E. Hobibie. 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications* 2:55–70.

Roberts, D. W. 1996. Landscape vegetation modelling with vital attributes and fuzzy systems theory. *Ecological Modelling* 90:175–184.

Roberts, D. W., and D. W. Betz. 1999. Simulating landscape vegetation dynamics of Bryce Canyon National Park with the vital attributes/fuzzy systems model VAFS/LANDSIM. Pages 99–124 *in* D. J. Mladenoff and W. L. Baker, editors. *Spatial modeling of forest landscape change: Approaches and applications.* Cambridge University Press, Cambridge, United Kingdom.

Romme, W. H., and D. G. Despain. 1989. The Yellowstone fires. *Scientific American* 261:37–46.

Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson, and D. J. Mladenoff. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201:409–419.

Scheller, R. M., and D. J. Mladenoff. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Global Change Biology* 11:307–321.

Scheller, R. M., and D. J. Mladenoff. 2007. An ecological classification of forest landscape simulation models: Tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology* 22:491–505.

Shang, Z. B., H. S. He, T. R. Crow, and S. R. Shifley. 2004. Fuel load reductions and fire risk in central hardwood forests of the United States: A spatial simulation study. *Ecological Modelling* 180:89–102.

Shang, Z. B., H. S. He, D. E. Lytle, S. R. Shifley, and T. C. Crow. 2007. Modeling the long-term effects of fire suppression on central hardwood forests in Missouri Ozarks, using LANDIS. *Forest Ecology and Management* 242:776–790.

Shifley, S. R., F. R. Thompson, III, W. D. Dijak, and Z. Fan. Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: A case study of issues, limitations, and opportunities. *Forest Ecology and Management: In press*.

Shifley, S. R., F. R. Thompson, III, W. D. Dijak, M. A. Larson, and J. J. Millspaugh. 2006. Simulated effects of forest management alternatives on landscape structure and habitat suitability in the Midwestern United States. *Forest Ecology and Management* 229:361–377.

Shifley, S. R., F. R. Thompson, III, D. R. Larsen, and W. D. Dijak. 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. *Computers and Electronics in Agriculture* 27:7–27.

Sklar, F. H., and R. Costanza. 1990. The development of dynamic spatial models for landscape ecology: A review and synthesis. Pages 239–288 *in* M. G. Turner and R. H. Gardner, editors. *Quantitative methods in landscape ecology.* Springer-Verlag, New York, New York, USA.

Syphard, A. D., J. Yang, J. Franklin, H. S. He, and J. E. Keeley. 2007. Calibrating a forest landscape model to simulate frequent fire in Mediterranean-type shrublands. *Environmental Modelling and Software* 22:1641–1653.

Wimberly, M. C., T. A. Spies, C. J. Long, and C. Whitlock. 2000. Simulating historical variability in the amount of old forests in the Oregon coast range. *Conservation Biology* 14:167–180.

Wintle, B. A., S. A. Bekessy, L. A. Venier, J. L. Pearce, and R. A. Chisholm. 2005. Utility of dynamic-landscape metapopulation models for sustainable forest management. *Conservation Biology* 19:1930–1943.

Xu, C., H. S. He, Y. Hu, Y. Chang, D. R. Larsen, X. Li, and R. Bu. 2004. Assessing the effect of cell level uncertainty on a forest landscape model simulation in northeastern China. *Ecological Modelling* 180:57–72.

Xu, C., H. S. He, Y. Hu, Y. Chang, X. Li, and R. Bu. 2005. Latin hypercube sampling and geostatistical modeling of spatial uncertainty in a spatially explicit forest landscape model simulation. *Ecological Modelling* 185:255–269.

Zollner, P. A., E. J. Gustafson, H. S. He, V. C. Radeloff, and D. J. Mladenoff. 2005. Modeling the influence of dynamic zoning of forest harvesting on ecological succession in a northern hardwoods forest. *Environmental Management* 35:410–425.