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Editorial

Modeling disturbance and succession in forest landscapes using LANDIS: introduction

Modeling forest landscape change is challenging because it involves the interaction of a variety of factors and processes, such as climate, succession, disturbance, and management. These processes occur at various spatial and temporal scales, and the interactions can be complex on heterogeneous landscapes. Because controlled field experiments designed to investigate such broad-scale interactions are typically not possible, landscape models are among the few tools available to evaluate the processes underlying forest landscape response to alternative management and human-modified disturbance regimes.

The LANDIS model (from LANDscape DIsturbance and Succession) simulates spatial forest dynamics including forest succession, seed dispersal, species establishment, various disturbances, and their interactions. The purpose of LANDIS is to simulate the reciprocal effects between disturbance and successional processes on forest tree species across large (10^4–10^6 ha) landscapes and long time scales (50–1000 years). LANDIS and its descendents are becoming widely used to answer research and management questions in a diversity of ecosystems around the world. These ecosystems include various temperate deciduous systems of the Midwestern United States (e.g., He and Mladenoff, 1999; Gustafson et al., 2000, 2004; Sturtevant et al., 2004) and China (Xu et al., 2004), boreal ecosystems of North America (Mehta et al., 2004; Pennanen et al., 2004) and Finland (Pennanen and Kuuluvainen, 2002), coastal chaparral of Southern California, USA (Franklin et al., 2001), and high elevation coniferous forests of Switzerland (Schumacher et al., 2004). LANDIS research questions range from the evaluation of forest successional pathways (Franklin et al., 2001) to interactions between disturbance regimes and fire risk (Gustafson et al., 2004; Sturtevant et al., 2004), and the effect of landscape change on population viability of wildlife (Akçakaya, 2001). This diversity of landscape-scale research also has spurred numerous LANDIS developments in recent years.

The recent surge of scientific activity using LANDIS suggested a need to comprehensively document and review the lessons learned through the development and application of the model. To this end, Eric Gustafson, David Mladenoff and Hong He organized a special session at the 16th Annual Symposium of the US Chapter of the International Association for Landscape Ecology, which was held in Banff, Alberta, Canada in April 2003. The special session brought together researchers from around the Northern Hemisphere who are using LANDIS to study a wide range of ecosystems and ecological questions. The purpose of the symposium was to study and debate the strengths and weaknesses, opportunities and limitations of the modeling approach embodied in LANDIS. Fourteen papers were presented

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in the special session, of which eleven are presented here in this special issue, and two more papers (Mehta et al., 2004; Xu et al., 2004) were invited. We have organized the papers into five sections: (1) the historical roots of LANDIS, (2) model sensitivity and assumptions, (3) research and management applications, (4) new developments that follow the age-list and ordinal-ranking paradigm of the original model, and (5) new developments that provide additional mechanistic detail of succession within individual cells.

The first section contains a single paper that documents the history and impetus for the initial development of LANDIS. Mladenoff, 2004 reviews the key modeling and ecological advances, as well as the expanding broad-scale questions asked by researchers and managers alike, that led to the design choices in the original LANDIS model. Despite the exponential increase in computer capacity, physical and scientific constraints still result in a fundamental trade-off between mechanistic detail and modeling scope. Hence the design choices made a decade ago remain relevant today, perhaps explaining the endurance of LANDIS as a research tool, and its increasing role in guiding management decisions.

The second section explores the sensitivity of the model to spatial detail, input data uncertainty, and spatial model assumptions. Syphard and Franklin, 2004 examined the effects of spatial aggregation of input data (cell size) on modeled species composition and fire disturbance. They found spatial aggregation resulted in less frequent, more unpredictable fires, and plant species distribution became more variable. They suggest modelers can detect ranges of resolutions for which appropriate levels of spatial generalization can be made.

Wimberly, 2004 applied the technique of structural analysis to explore the sensitivity of LANDIS v3.6 results to the spatial assumptions inherent in the formulation of the model. Structural analysis differs from traditional sensitivity analysis by manipulating model formulations rather than parameter values. He studied species response to a fire gradient in the Southeastern US as a function of three key spatially structured attributes: spatially varying species establishment probabilities, spatially varying disturbance regimes, and limitations to the dispersal of propagules. This paper illustrates a formalized method for evaluating guiding hypotheses underlying a model's design that could be applied to any ecological model.

Deriving the detailed species and age information required by LANDIS as input for each cell on a landscape is extremely problematic because such detailed information is seldom available for large areas. A commonly used method to generate LANDIS initial conditions involves the probabilistic assignment of species and age cohorts to cells based on a known statistical distribution for each land type or forest type. Xu et al., 2004 used a Monte Carlo technique to study the propagation of uncertainty through time of such an approach. They found that the uncertainty related to initial conditions was relatively low at the beginning of simulations, and increased gradually over simulation time, eventually reaching equilibrium. At the landscape level, species percent area and their spatial patterns were not substantially affected by the uncertainties of species age structure at the cell level.

The third section describes specific applications of LANDIS to address research and management questions. Mehta et al., 2004 used LANDIS v3.6 to compare several forest management scenarios and their long-term effects (>100 years) in Northern Minnesota, USA. The management scenarios included no harvesting, varied rotation ages and clearcut sizes, clustered clearcuts, and landowner-coordinated harvesting. They were able to evaluate the effects of these management scenarios by comparing the resulting spatial pattern and age structure.

Shang et al., 2004 used LANDIS v3.7 to study three alternative fire management scenarios in the Missouri Ozarks, USA. They used the recently developed fuel module (He et al., 2004, described below) to simulate two fuel reduction treatments for comparison with a no-treatment scenario. They were able to predict potential fire probability and intensity for each forest stand through time under each scenario.

Landscape change models are now being used to provide dynamic input for subsequent process models (e.g., Akçakaya, 2001). Larson et al., 2004 used landscape output from LANDIS to drive a population viability model for ovenbirds (*Seiurus aurocapillus*). They used a habitat suitability model to translate the LANDIS output into different levels of habitat quality based on tree species composition, age structure, and distance to edges created through simulated harvesting. Mapped habitat suitability was then imported into a metapopu-

lation model (RAMAS-GIS: Akçakaya, 1998) to determine population viability under different harvest scenarios.

The fourth section contains three papers that describe new LANDIS developments that are consistent with its original age-list and rank-ordered attribute architecture. Each of these changes will be incorporated into a new version of LANDIS (v4.0). This new model version has been designed as a set of interacting dynamic linked libraries (dll) that can be turned on or off, depending on the research question at hand. Yang et al., 2004 addressed a previous limitation to the fire algorithms in LANDIS that restricted the range of possible fire regimes that could be simulated. A second assumption driving fire dynamics in LANDIS v3.7 and earlier was that fuel conditions could be approximated by a simple function of the time since the last fire disturbance (He and Mladenoff, 1999). This assumption limited the ability to investigate interactions of multiple disturbance regimes and their cumulative effect on fire risk. He et al., 2004 resolved this issue by designing a new fuel module, where fuel may be modified by any disturbance. The new module still classifies fuels into categories, but the categories have been expanded to define fine dead, coarse dead, and live fuel types. The fuel module allows the explicit interaction between species composition, each of the disturbance types (fire, wind, harvesting, and biological), and the dynamics of fire.

Last in this section, insects and disease cause significant mortality of some tree species in many forest ecosystems. This mortality can dramatically alter successional trajectories, and may result in high fuel loads that can lead to severe fire risk. Sturtevant et al., 2004 describe a new LANDIS module with flexible parameters to allow the simulation of disturbances by a wide variety of 'biological disturbance agents' (BDAs), including insects and disease. They use Eastern spruce budworm as a test case, illustrating the application of the BDA module to "neutral" landscape (*sensu* Gardner et al., 1987) patterns of budworm host.

The final section contains three papers that explore alternative modeling strategies to provide additional mechanistic detail at the cell level, with the intent of improving successional dynamics within the model. In each case, the authors simulated the relative abundance of each species cohort and attached the new quantitative information as attributes to the species age-list, an idea originally proposed by He et al. (1999). Schumacher et al., 2004 presented an approach that integrates a simple tree succession sub-model within the framework of LANDIS. They incorporated quantitative descriptions of forest structure, and included physical routines incorporating climate variables such as temperature and precipitation (drought) in stand-scale ecological processes. Their work provides a framework for studying possible transitions from weakly to strongly disturbed forest landscapes under climatic change scenarios and modified management regimes.

Pennanen et al., 2004 developed and calibrated the Q-LAND model for a boreal forest landscape in Quebec, Canada, based upon the LANDIS and FIN-LANDIS models. In Q-LAND, a density variable is added to describe each age cohort. Other important added features of Q-LAND include the detailed handling of seed dispersal including seed mass and natural regeneration.

Finally, Scheller and Mladenoff, 2004 describe a new biomass module for LANDIS that simulates the dynamics of live and dead biomass within each cell on the landscape. Biomass of each individual species cohort is simulated through a linkage with the forest ecosystem model PNET-II (Aber et al., 1995). Unlike other developments to LANDIS, biomass becomes a new "currency," which the model uses to simulate successional dynamics within cells. The new biomass currency will eventually be integrated with all LANDIS modules in a forthcoming model, LANDIS-II.

LANDIS is a powerful tool for studying the very complex interactions between forest succession and disturbances at large scales over long time periods. The ability to understand interacting phenomena is critical as we seek to manage forests for multiple uses and to mitigate the negative consequences of natural disturbances such as fire, wind and insect outbreaks. Much of the recent development in LANDIS is in response to the urgent need to understand how these interacting phenomena relate to wildfire risk. For example, recent massive fires in Southern California could not be contained because of a prior bark beetle outbreak and dense vegetation that was the legacy of previous management practices. It is precisely these types of interactions that LANDIS v4.0 is designed to simulate. Other modifications to LANDIS have been driven by the realization that not all successional dynamics can be captured using the presence/absence paradigm

in the original LANDIS design (e.g., Q-LAND, LANDIS-II).

New modifications to LANDIS and its descendents have effectively expanded the modeling domain where LANDIS may be applied. These new developments parallel recent scientific advances in forest and landscape ecology, as well as technological advances in raw computing power and the capability to measure increasingly detailed forest attributes across large landscapes via remote sensing. However, the challenge before us is not what processes *can* be modeled, but rather what processes are *required* to capture the essential dynamics for the question at hand. Hence new design changes also include the ability to turn non-essential processes off, and the flexibility to modify individual modules without fear of errors propagating through the rest of the program. Such design changes are critical to insure the adaptability of LANDIS to new systems and research questions, both basic and applied.

The research reported in these pages highlights the power and utility of LANDIS to effectively answer questions across a broad domain of ecological processes and a wide variety of forested ecosystems. It also has its limitations. For example, its probabilistic design is not well suited for making tactical decisions about the management of specific stands or locations, nor is LANDIS well suited for research or management questions focused at short time scales (i.e., less than a century time horizon). We hope that the papers contained in this special issue will encourage both researchers and managers alike think more broadly about the processes affecting forest landscape change. Landscape models such as LANDIS can also serve as effective communication tools between scientists and land planners to design and test new management strategies that may prevent the development of unintended and potentially dangerous landscape patterns. As evidenced by the recent catastrophic fire events witnessed in several regions of North America, long-term guidance for the management of forested landscapes is desperately needed.

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References

Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, J.M., Lathrop Jr., R.G., 1995. Predicting the effects of climate change on water yield and forest production in the Northeastern United States. Clim. Res. 5, 207–222.

Akçakaya, H.R., 1998. RAMAS GIS: linking landscape data with population viability analysis (version 3.0). Appl. Biomath., Setauket, NY.

Akçakaya, H.R., 2001. Linking population-level risk assessment with landscape and habitat models. Sci. Total Environ. 274, 283–291.

Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P., Deutschman, D., O'Leary, J.F., 2001. Simulating the effects of different fire regimes on plant functional groups in Southern California. Ecol. Model. 142, 261–283.

Gardner, R.H., Milne, B.T., Turner, M.G., O'Neill, R.V., 1987. Neutral models for the analysis of broad-scale pattern. Landscape Ecol. 1, 19–28.

Gustafson, E.J., Zollner, P.A., Sturtevant, B.R., He, H.S., Mladenoff, D.J., 2004. Influence of forest management alternatives and landtype on susceptibility to fire in northern Wisconsin, USA. Landscape Ecol., in press.

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

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

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

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

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

Mehta, S., Frelich, L.E., Jones, M.T., Manolis, J., 2004. Examining the effects of alternative management strategies on landscape-scale forest patterns in Northeastern Minnesota using LANDIS. Ecol. Model. 180, 73–87.

Mladenoff, D.J., 2004. LANDIS and forest landscape models. Ecol. Model. 180, 7–19.

Pennanen, J., Greene, D.F., Fortin, M.-J., Messier, C., 2004. Spatially-explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes. Ecol. Model. 180, 195–209.

Pennanen, J., Kuuluvainen, T., 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. Forest Ecol. Manage. 164, 157–175.

Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol. Model. 180, 211–229.

Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially-explicit landscape model. Ecol. Model. 180, 175–194.

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

Sturtevant, B.R., Gustafson, E.J., Li, W., He, H.S., 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecol. Model. 180, 153–174.

Sturtevant, B.R., Zollner, P.A., Gustafson, E.J., Cleland, D.T., 2004. Human influence on fuel connectivity and the risk of catastrophic fire in mixed forests of northern Wisconsin. Landscape Ecol. In press.

Syphard, A.D., Franklin, J., 2004. Spatial aggregation effects on the simulation of landscape pattern and ecological processes in Southern California plant communities. Ecol. Model. 180, 21–40.

Wimberly, W.C., 2004. Fire and forest landscapes in the Georgia Piedmont: an assessment of alternative spatial modeling assumptions. Ecol. Model. 180, 41–56.

Xu, C., He, H.S., Hu, Y., Chang, Y., Larsen, D.R., Li, X., Bu, R., 2004. Assessing the effect of cell-level uncertainty on a forest landscape model simulation in Northeastern China. Ecol. Model. 180, 57–72.

Yang, J., He, H.S., Gustafson, E.J., 2004. A hierarchical fire frequency model to simulate temporal patterns of fire regimes in LANDIS. Ecol. Model. 180, 119–133.

Brian R. Sturtevant*
Eric J. Gustafson
Forestry Sciences Laboratory, North Central Research Station, USDA Forest Service, 5985 Highway K, Rhinelander, WI 54501, USA

Hong S. He
School of Natural Resources, 203m Anheuser-Busch Natural Resources Building, University of Missouri Columbia, MO 65211, USA

*Corresponding author. Tel.: +1 715 362 1105
fax: +1 715 362 1166
E-mail address: bsturtevant@fs.fed.us
(B.R. Sturtevant)