Evaluating the Impact of Invasive Species in Forest Landscapes: The Southern Pine Beetle and the Hemlock Woolly Adelgid

John D. Waldron, Robert N. Coulson, David M. Cairns, Charles W. Lafon, Maria D. Tchakerian, Weimin Xi, Kier Klepzig, and Andrew Birt

John D. Waldron, Department of Environmental Studies, University of West Florida, Pensacola, FL 32514; **Robert N. Coulson**, Knowledge Engineering Laboratory, Texas A&M University, College Station, TX 77845; **David M. Cairns** and **Charles W. Lafon**, Department of Geography, Texas A&M University, College Station, TX 77845; **Maria D. Tchakerian** and **Weimin Xi**, Knowledge Engineering Laboratory, Texas A&M University, College Station, TX 77845; **Kier Klepzig**, USDA Forest Service Southern Research Station, Forest Insect Research, Pine-ville, LA 71360; and **Andrew Birt**, Knowledge Engineering Laboratory, Texas A&M University, College Station, TX 77845.

Abstract

The southern pine beetle, *Dendroctonus frontalis* (Zimmerman) (Coleoptera: Curculionidae: Scolytinae) (SPB), is an indigenous invasive species that infests and causes mortality to pines (*Pinus* spp.) throughout the Southern United States. The hemlock woolly adelgid, *Adelges tsugae* (Annand) (Homoptera: Adelgidae) (HWA), is a nonindigenous invasive species that infests and causes mortality to Eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*T. caroliniana* Engelm.) throughout their range in Eastern North America. Both of these insect species occur in the Southern Appalachians, and both have recently caused tree mortality exceeding historical records. Herbivory by both species is of concern to forest managers, but for different reasons. In the case of the SPB, emphasis centers on forest restoration strategies, and in the case of the HWA, the concern is on predicting the impact of removing hemlock from the forest environment. Both of these issues can be investigated using a landscape simulation modeling approach. LANDIS is a simulation modeling environment developed to predict forest landscape change over time. It is a spatially explicit, landscape-scale ecological simulation model that incorporates disturbance by fire, wind, biological disturbance (insects and pathogens) and harvesting. Herein, we present a case study using LANDIS to evaluate the impact of herbivory by the SPB and HWA on forest landscapes in the Southern Appalachians.

Keywords: Invasive species, LANDIS, modeling, Southern Appalachians.

Introduction

In 2003, five general areas were identified as concerns to healthy forests in the United States—wildfires, nonnative invasive insects and pathogens, invasive plant species, outbreaks of native insects, and changing ecological processes (USDA-FS 2003). Eastern forests in the United States have been subject to unprecedented threat due to invasion by forest pests (Brockerhoff and others 2006, Liebhold and others 1995, Lovett and others 2006) that threaten extinction of host species, engineer fragmented landscapes, and add to fuel loads, which increase risk of wildland fires. Disturbances exert a strong influence on forest structure, composition, and diversity (Connell 1978, Huston 1994, White 1979). However, different types of disturbance have different consequences for vegetation. Surface fires, for example, primarily kill small trees and spare the larger individuals (Abrams 2003, Frelich 2002), often slowing the rate of successional replacement. Canopy disturbances such as insect outbreaks primarily damage larger trees and may accelerate the process of succession (Abrams and Scott 1989, Frelich 2002, Lafon and Kutac 2003, Veblen and others 1989).

Stohlgran and Schnase (2006) suggested that risk analysis techniques, including simulation modeling, that are often used in the assessment of health risks and other hazards, are not only applicable to invasive species, but are needed. Forest managers have been increasingly integrating stand-level forecasting tools, such as the Forest Vegetation Simulator (FVS), in the forest decisionmaking process (Dixon 2002). More recently, landscape models that operate at a scale of 100s to 1000s of km^2 have begun to be evaluated for use in forest management (e.g., Shifley and others 2000).

LANDIS (Mladenoff and He 1999) is a simulation modeling environment developed to predict forest landscape change over time. It is a spatially explicit landscape-scale ecological simulation model that incorporates both natural (fire, wind, and biological disturbance) and anthropogenic disturbance (harvesting). LANDIS has been adapted for use in a variety of forest management applications. Examples of applications relevant to this study include He and others (2002b) (forest harvesting and fire disturbance), Akcakaya (2001) (risk assessment and landscape habitat models), Schifley and others (2000), Mehtaa and others (2004) (landscape change and management practices), and Gustafson and others (2000) (forest succession and harvesting).

Landscape models offer the unique ability to assess forest process and pattern over broad spatial and temporal scales. Forest managers increasingly need to implement management strategies that incorporate forest sustainability, ecological restoration, wildlife habitat viability, recreational opportunities, and scenic value. Many of these concerns involve broad spatial and temporal scales. The objective of this study is to demonstrate the effectiveness of using LANDIS for forest threat assessment and restoration. To illustrate this, we examine one nonnative invasive insect, hemlock woolly adelgid (HWA) (*Aldelges tsugae* Annand [Homoptera: Adelgidae]) and one indigenous invasive insect, southern pine beetle (SPB) (*Dendroctonus frontalis* Zimmermann [Coleoptera: Curculionidae]). Both insects currently threaten tree species within the Southern Appalachian Mountains of Eastern North America. In this analysis, we present initial results from our work with LANDIS 4.0 and present a framework for using LANDIS II, which will help evaluate the potential impacts of existing and future multiple interacting forest threats in eastern forests.

Background

The SPB and the HWA are two very different forest-damaging insects that inhabit host tree species that exploit opposite ends of the moisture gradient found in the Southern Appalachian Mountains (Figure 1), although they occasionally occur together at either end of their natural range. We chose these insects to illustrate the utility of LANDIS in investigating forest insect threats because they represent the extreme cases of an indigenous pest that has the potential to cause great damage (SPB) and an invasive pest that has the potential to remove an entire host plant species from eastern forests (HWA).

Southern Pine Beetle Case

In the Southern Appalachian Mountains, xeric slopes and ridges have historically been dominated by yellow pines (*Pinus* spp.). Because altered disturbance regimes have begun to change the appearance of the landscapes, understanding the dynamics of these systems is important to forest managers in implementing management strategies on public lands. On these landscapes, fire and SPB are the two most influential natural disturbance agents. SPB has caused extensive damage to pine forests throughout the Southeastern United States (Coulson 1980, Coulson and others 2004). On Southern Appalachian xeric ridges, SPB colonizes a variety of pine species including pitch pine (*Pinus rigida* Mill.), Virginia pine (*Pinus virginiana* P. Mill.), Table Mountain pine (*Pinus pungens* Lamb.), and occasionally eastern white pine (*Pinus strobus* L.) (Payne 1980). Interactions between available soil moisture and resin flow, the primary tree defense against SPB (Tisdale and others 2003, among others), have long been noted (Hodges and Lorio 1975, Hodges and others 1979) and are likely affected by such landscape characteristics.

Fire and SPB are thought to drive the regeneration of yellow pine forests on xeric ridges in the Southern Appalachians (Harmon 1980, Harrod and others 1998, Williams 1998). Williams (1998) conjectured that SPB and other non-fire disturbances in xeric pine-oak forests will lead toward hardwood domination in the absence of fire. It has further been hypothesized that these communities are maintained in a drought-beetle-fire cycle (Barden and Woods 1976, Smith 1991, White 1987, Williams 1998). Understanding the relationship between fire, SPB, and mesoscale forest

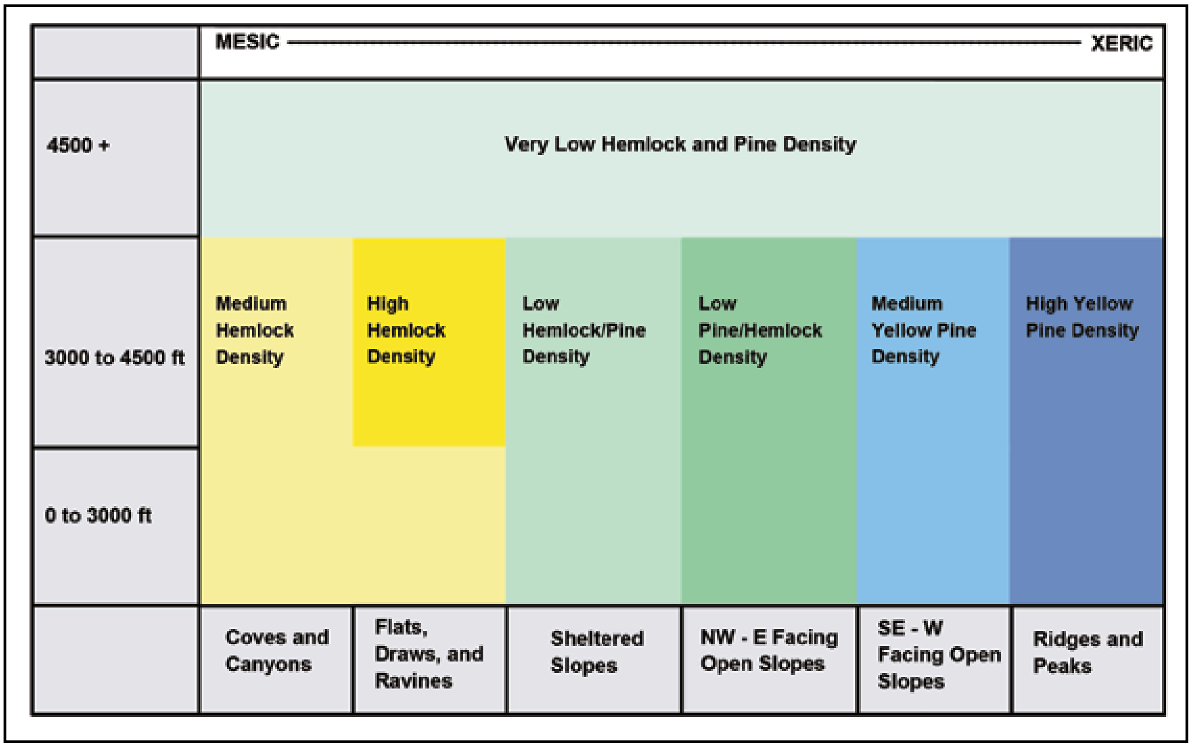

Figure 1—Density of yellow pine and hemlock in the Southern Appalachian Mountains. This illustration depicts the distribution of hemlock and pine density in the southern Appalachian Mountains. The highest densities of hemlocks are found in flats, draws, and ravines at an elevation of 3,000 to 4,500 feet, whereas the highest densities of yellow pines are found on ridges and peaks between elevations of 0 and 4,500 ft (Based on Whittaker 1956).

dynamics can provide direction for forest planners and managers in maintaining and restoring this unique environment.

Hemlock Wooly Adelgid Case

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) and Carolina hemlock (*Tsuga caroliniana* Engelm.) appear in mesic flats, draws, ravines, coves, and canyons of the Southern Appalachian Mountains (Whittaker 1956). Although once more abundant in the forest, hemlock populations declined dramatically approximately 5,500 years ago because of a climatic shift that resulted in summer droughts. These droughts weakened the hemlocks and left them vulnerable to a subsequent widespread insect outbreak (Allison and others 1986, Davis 1981, Haas and McAndrews 2000). In its northern range, canopy gaps were filled by *Acer*, *Betula*, *Fagus*, *Pinus*, *Quercus*, and *Ulmus* (Fuller 1998). Although hemlock did reestablish itself, its recovery may have taken up to 2,000 years and, in many sites, is still not as prominent as it was before the decline (Fuller 1998, Haas and McAndrews 2000). Now, hemlocks are at risk from the invasive exotic insect pest HWA.

In its native Japan, HWA populations are maintained at low densities on hemlocks (*Tsuga diversifolia* (Maxim.) Mast. and *T. sieboldii* Carr.) by a combination of host resistance and natural enemies (McClure 1992, 1995a, 1995b; McClure and others 2000). The first report of HWA in North America was in the Pacific Northwest in the 1920s; however, western hemlocks were resistant to the adelgid. In the Eastern United States, the first reports of HWA were in 1951 in Richmond, Virginia (Gouger 1971; McClure 1989, 1991). With no natural resistance or natural predators, HWA slowly made its way northeast and has subsequently been moving southwest along the eastern side of the Appalachian Mountains. Little is known about stand-level characteristics that influence HWA susceptibility in the Southeastern United States. However, studies on HWA infestation levels in the northeastern range of this insect noted only latitudinal effects on infestation severity (Orwig and Foster 1998, Orwig and others 2002). This would seem to suggest that all hemlock stands have the potential of being infested and killed, regardless of site and stand factors.

Methods

Study Area

This study uses a simulated landscape drawn from data approximating the communities and conditions within Great Smoky Mountains National Park. Great Smoky Mountains National Park is a 2110 km^2 World Heritage Site and International Biosphere Reserve straddling the border between western North Carolina and eastern Tennessee. Great Smoky Mountains National Park serves as an ideal model for this study as most major ecosystems of the Southern Appalachians are represented, and the general topographic distribution of communities and tree species has previously been described (Whittaker 1956).

The Southern Appalachian Mountains, although not representative of all eastern forests, are unique because they represent one of the most biologically diverse regions of the world (SAMAB 1996). A complex system of physiography, environmental site conditions, adaptive life history characteristics, and disturbance history has created a distinctive vegetation structure (Elliott and others 1999). Due to this complexity, Southern Appalachian landscapes contain a variety of community types ranging from mesophytic hemlock-hardwood forests on moist valley floors to yellow pine woodlands on xeric ridges and from low-elevation temperate deciduous forests to high-elevation spruce-fir forests (Whittaker 1956, Stephenson and others 1993). Such high biodiversity areas have been thought by some to act as potential barriers to invasion because of increased competition and by others as at risk of invasion due to the higher potential for suitable habitat niches (Brown 2002, Brown and Peet 2003, Elton 1958, Kennedy and others 2002, Levine and D'Antonio 1999).

Model Description

LANDIS is a spatially explicit computer model designed to simulate forest succession and disturbance across broad spatial and temporal scales (He and Mladenoff 1999a 1999b; He and others 1996, 1999a, 1999b; Mladenoff and He 1999). Whereas LANDIS was originally developed to simulate disturbance and succession on glacial plains in the Upper Midwest (Mladenoff 2004), it has been successfully adapted for use in mountainous areas (He and others 2002a; Shifley and others 1998, 2000; Waldron and others 2007; Xu and others 2004).

LANDIS is raster-based, with tree species (max 30) simulated as the presence or absence of 10-year-age cohorts on each cell. At the site (cell) scale, LANDIS manages species life history data at 10-year time steps. Succession is individualistic and is based on dispersal, shade tolerance, and land type suitability. Disturbances that can be modeled include fire, wind, harvesting, and biological agents (insects, disease) (Sturtevant and others 2004a).

Fire in LANDIS is a hierarchical stochastic processes based on ignition, initiation, and spread (Yang and others 2004). Mortality from fire is a bottom-up process whereby low-intensity fires kill young, fire-intolerant species, whereas fires of higher intensity can kill larger trees and more fire-tolerant species (He and Mladenoff 1999a).

Biological disturbances in LANDIS 4.0 are modeled using the Biological Disturbance Agent (BDA) module. Biological disturbances are probabilistic at the site (cell) level. Each site is assigned a Site Vulnerability (SV) probability value that is checked against a uniform random number to determine if that site has been infected. Site vulnerability can be directly equated with the Site Resource Dominance (SRD) value that ranges from 0 to 1 and is based on species and species age. This value can also be modified by three variables to determine the impact on a given site—Modified Site Resource Dominance (SRDm), Neighborhood Resource Dominance (NRD), and the temporal scale of outbreaks. The functioning of these variables and of the BDA in general is described in detail in Sturtevant and others (2004b).

Simulation Methods

We used LANDIS 4.0 to simulate forest dynamics on a 120-ha idealized landscape. The landscape was a 100 by 120 cell grid with a cell size of 10 m by 10 m, the smallest cell size recommended for use with LANDIS. Using this small cell size allowed us to operate at approximately the scale of the individual canopy tree, following the logic of gap models. The landscape was divided into 18 individual land types arranged according to the mosaic chart used by Whittaker (1956) to depict the elevation and moisture gradients on the Great Smoky Mountains landscape. The land types are arranged in three rows and six columns. The rows represent (from bottom to top) low (400–915 m)-, middle (916–1370 m)-, and high (1371–2025 m)-elevation zones. The columns represent different topographic moisture classes. Moisture availability decreases from left to right, as follows: (1) coves and canyons; (2) flats, draws, and ravines; (3) sheltered slopes; (4) east- to northwest-facing slopes; (5) southeast- to west-facing slopes; and (6) ridges and peaks. Elevation also influences moisture availability. For example, a low-elevation ridgetop would have drier conditions than a mid-elevation ridgetop. Although the simulated landscape incorporates the full range of environments in the Great Smoky Mountains, our interest in this paper is only on the successional patterns for those land types under the greatest threat by SPB and HWA (Figure 1). We present results for mid-elevation ridges and peaks (SPB) and mid-elevation flats, draws, and ravines (HWA) to illustrate the utility of the model in assessing insect threats.

Results and Discussion

SPB

Our first goal in this study was to investigate the role of fire and SPB in xeric Southern Appalachian landscapes. The modeling projections presented here suggest that the regime of multiple interacting disturbances has important implications for the successional dynamics and vegetation characteristics in yellow pine woodlands of the Southern Appalachian Mountains. When acting alone, fire was projected to create conditions favoring pine presence at levels higher than input, although SPB disturbance acting alone resulted in the removal of yellow pines. Additionally, our model projections suggest that a combination of fire and SPB disturbance creates sustainable yellow pine communities over the long term. This conclusion is consistent with the hypothesis that fire and SPB are part of a disturbance regime that maintains yellow pine woodlands (Harrod and others 1998, 2000; Lafon and Kutac 2003; White 1987; Williams 1998) (Figure 2).

The results of this study yield several conclusions that are important to forest managers when undertaking restoration efforts. First, our projections suggest that Table Mountain pine (*Pinus pungens*), more than any other species, thrives when in a disturbance regime combining SPB and fire on xeric sites. Because Table Mountain pine is a Southern Appalachian endemic, it is also important for biodiversity conservation (Zobel 1969). These factors suggest that Table Mountain pine could be a species of particular interest for restoration efforts on mid-elevation ridges and peaks in the Southern Appalachians. Our results apply to the restoration of such stands and suggest that periodic burning will be required to maintain the compositional and structural integrity of stands affected by SPB. This conclusion is substantiated by empirical analogue (e.g., Harrod and others 1998, 2000; Lafon and Kutac 2003).

Hemlock Wooly Adelgid

Our second goal was to investigate the impacts of HWA on species composition in the Southern Appalachian Mountains. The results from this study are preliminary, but do show a reduction in hemlock and subsequent replacement by hardwoods (Figure 3). In particular, we see replacement of hemlocks with basswood (*Tilia* spp.), sugar maple (*Acer saccharum* Marsh.), yellow buckeye (*Aesculus octandra* Marsh.), yellow birch (*Betula alleghaniensis* Britton) and northern red oak (*Quercus rubra* L.). These results may not be ecologically correct, as we would anticipate rhododendron (*Rhododendron* spp.) already present in the understory or several potential nonnative invasive species filling many of the gaps created by hemlock removal (Figure 4). Rhododendron and thick shrub cover, in general, have been shown to neutralize tree regeneration in canopy gaps (Beckage and others 2000). Riparian areas in the Southern Appalachians, where we find most hemlocks, have also been shown to contain high exotic species cover and diversity (Brown and Peet 2003). The discrepancies in the landscape approach can be corrected easily by incorporating finer resolution gap models.

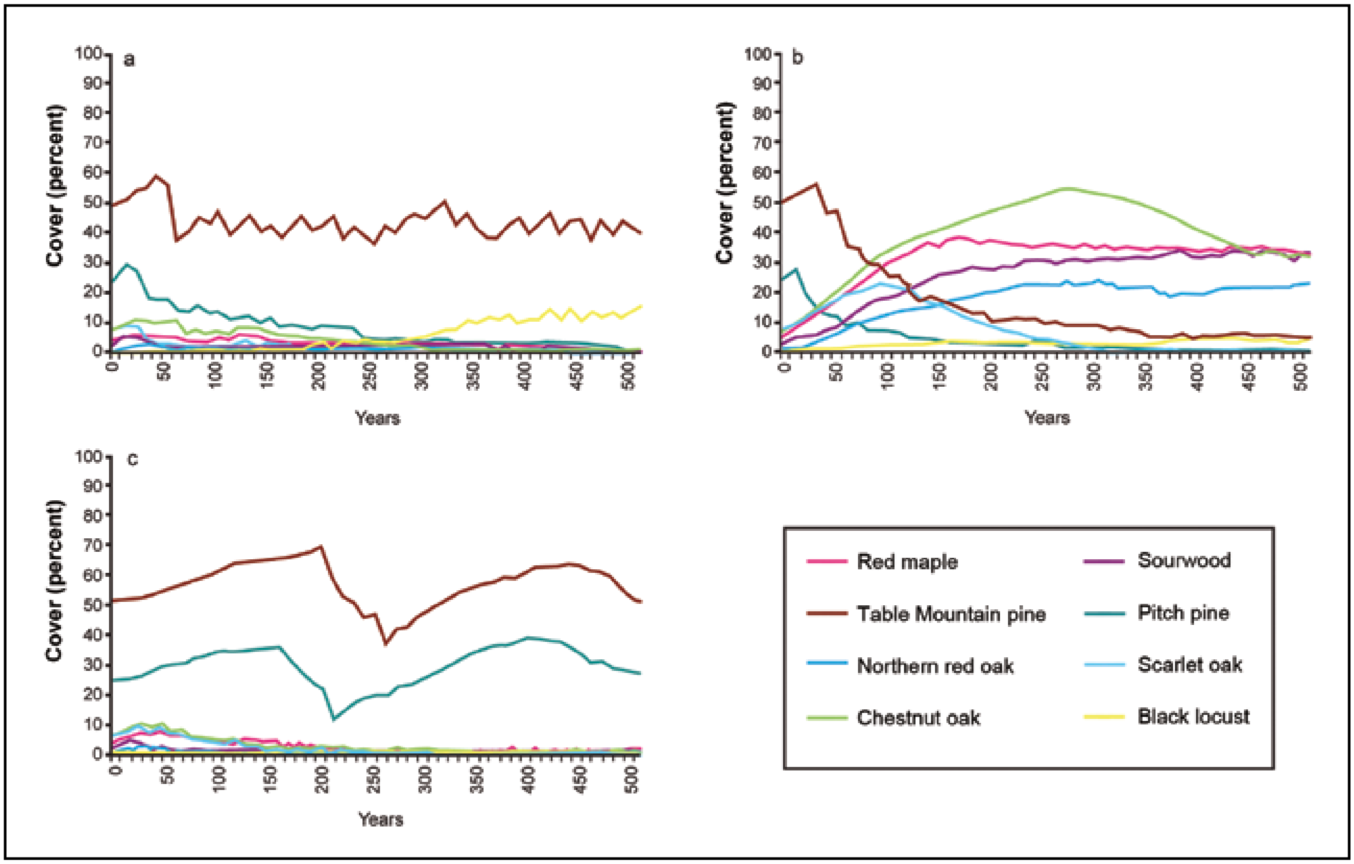

Figure 2—Successional trajectory of mid-elevation Ridges and Peaks. The following three graphs show the successional trajectory of mid-elevation ridges and peaks and represent percentage cover on the y-axis and model run year on the x-axis, which ends at year 500 for mid-elevation ridges and peaks. The fire and SPB scenario (a) show a continued dominance of Table Mountain pine but a reduction in pitch pine. The SPB-only scenario (b) shows a replacement of both pine species with hardwoods. The fire-only scenario (c) demonstrates a continuation of Table Mountain pine and pitch pine. Graphs reflect the percentage of cells occupied on the land type by each species.

Discussion

Through this study, we have demonstrated that different forest pests in different ecological regions, within the same geographic bounds, require different management strategies. If the desired outcome were the maintenance of Table Mountain pine-pitch pine communities, managers would be warranted in using prescribed burning or allowing for natural fires to burn without suppression along with SPB chemical control measures on xeric mid-elevation ridges and peaks. If the maintenance of pitch pine were not considered important, then burning alone would be an acceptable strategy. Although other silvicultural practices could recreate these conditions in the short run, burning is necessary to maintain these conditions as Table Mountain pine needs stand and site disturbance, light, and heat for successful regeneration (Della-Bianca 1990). On the other hand, there are no immediate controls for HWA. Whereas the imminent destruction of hemlocks by HWA evokes parallels to the chestnut blight fungus (*Cryphonectria parasitica*), which has decimated American chestnuts, there is a major difference. Chestnut blight can survive quite well on the deadwood of a variety of species, and, hence, it will always be present in the environment—therefore constraining the ability of any viable new American chestnut populations. Hemlock woolly adelgid, on the other hand, requires the presence of either eastern or Carolina hemlock to survive in Eastern North America (McClure 1987). One management strategy would simply be to save nursery stocks of hemlocks in a controlled environment for replanting once the HWA has destroyed all the naturally occurring hemlocks and then, itself, perished due to a lack of viable hosts.

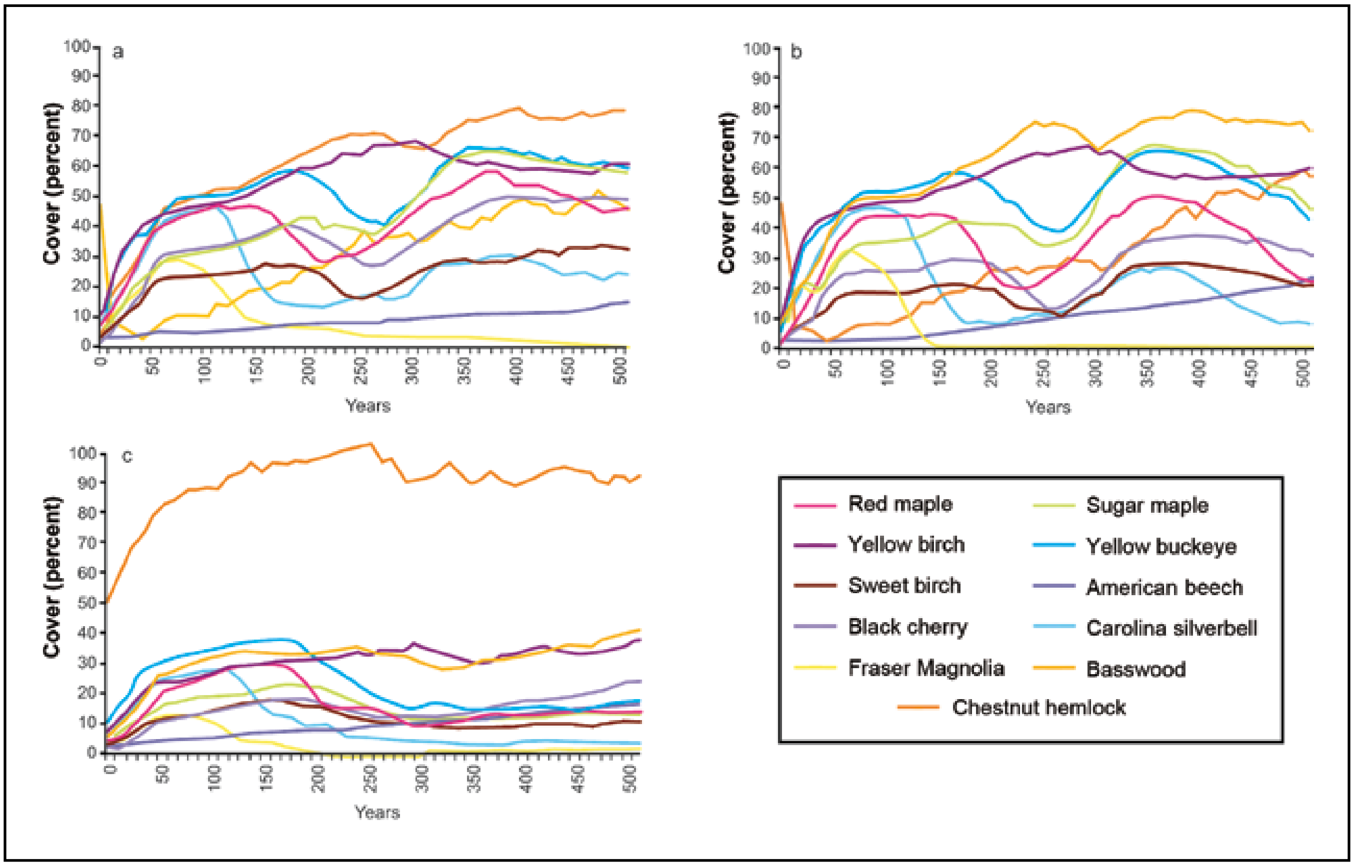

Figure 3—Successional trajectory of mid elevation Flats, Draws, and Ravines. The following three graphs represent percentage cover on the y-axis and model run year on the x-axis, which ends at year 500 for mid-elevation flats, draws, and ravines. In both the fire and HWA scenario (a) and the HWA-only scenario (b), eastern hemlock is replaced by hardwood species, particularly basswood, yellow buckeye, yellow birch, and sugar maple. In the fire-only scenario (c), hemlock maintains its dominance due to the very infrequent fire return on mesic sites. Graphs reflect the percentage of cells occupied on the land type by each species.

We set out to describe a modeling framework for assessing the impacts of SPB and HWA herbivory on forests. The advantage of using LANDIS is that all of these processes and outputs are described and captured in a simple, tractable, and transparent modeling environment. In the context of periodically abundant pests or invasive species, this transparency and simplicity are important because there is often a need for reactive and immediate research into potential impacts. One of the great strengths of LANDIS is that because a well-described and proven model framework already exists, parameterization and hence, model outputs, can be achieved relatively easily by drawing on published literature, expert knowledge, and practical experience. The adoption of a proven model also allows a truly comparative study between the assessments of the impact of different pests. For this initial study, we chose to illustrate the temporal dynamics of vegetation in response to insect outbreaks within the most vulnerable land types in the Southern Appalachians. The spatial dynamics of vegetation change and insect outbreaks across land types is another key feature of this real-world problem that affects the distribution of pests and the damage they cause and the successional dynamics of impacted vegetation leading to restructuring of the forest. Although the broader spatial patterns and processes were not within the scope of this study, we are currently using LANDIS to explore these issues.

Directions for Future Research

Recently, LANDIS II has been released. In a major change from LANDIS, the life history parameters have been updated to include both minimum and maximum age of resprouting as well as a postfire resprout function, which allows for serotiny or resprout. LANDIS II also allows for the calculation of aboveground live and dead biomass (as kg/ha) and tracks woody and leaf litter dead biomass. Biomass can also be used as an alternative to the original succession function using species age. Disturbances that can be modeled follow those of LANDIS. In LANDIS II, each ecological process operates on its own individual time step (units: year). For example, fire may operate at a 5-year time step, whereas SPB occurs at a 7-year time step and HWA at a 1-year time step. Also, while LANDIS was limited to 30 species, LANDIS II can have an unlimited number of plant species. Changing to LANDIS II will undoubtedly aid in sorting out some of the problems in the HWA case, as we will be able to incorporate species such as rhododendron and invasive species, as well as have the ability to model HWA annually rather than at 10-year increments.

The Harvesting module in LANDIS II allows for both tree removal and planting within user-defined management areas. There are several functions for species removal. Clearcut removes all species within a stand. Individual species can be removed either as all, a percentage of the species, the oldest cohort within the species, all cohorts except the oldest, the youngest cohort, and all cohorts except the youngest cohort. There are several other differences between the two-model versions. First, climate change scenarios are now possible as land type parameters can be altered according to temporal grouping. Second, the order of disturbances can be randomized so that within a series of runs you might, for example, have fire run either before or after the BDA is run. Finally, LANDIS II is modular. This modularity allows for the relatively easy incorporation of new modules (such as ice storm disturbance) as well as the alteration of existing modules to meet research needs.

Our goal for future research is to test the capacity of LANDIS II using a landscape modeling environment to evaluate changes in composition and structure of Eastern United States forests undergoing multiple interacting environmental threats. Specifically, we are adapting LANDIS II to model the combined effects of key invasive biological disturbance agents and nonnative invasive plant species on the composition and structure of Southern Appalachian forests. This will allow us to determine the effects of changes in forest structure and composition on fire regimes, biodiversity, and wildlife habitat, to investigate strategies for restoring key ecosystems that may be significantly impacted by multiple-threat interactions, and to test contemporary ecological theory, such as the relationship between biodiversity and invasibility. Also, by incorporating Gap models, we will be able to address additional questions beyond those for which LANDIS II is suitable.

Gap models simulate the establishment, growth, and death of individual trees on small plots (Perry and Enright 2006). Unlike LANDIS, they do not consider the influence of landscape structure on disturbance and succession. Their value lies in their ability to simulate interactions among individual plants in a detailed, mechanistic way. Such local-scale interactions between individual plants that vary in size, growth rate, shade-tolerance, moisture/nutrient requirements, and other attributes are thought to govern successional processes, including exotic species invasions (Huston 2004, Shea and Chesson 2002). Gap models also are capable of representing the interactions between different plant functional types, e.g., trees and shrubs. Although most commonly applied to problems of forest succession, gap models have been used to investigate the dynamics of herbaceous vegetation as well (e.g., Peters 2002). By employing a combined approach of gap and landscape modeling, we will be able to rectify the problems encountered in the HWA study and provide more detailed succession projections.

Literature Cited

Abrams, M.D.; Scott, M.L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. Forest Science. 35: 42–49.

Abrams, M.D. 2003. Where has all the white oak gone? Bioscience. 53: 927–939.

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

Allison, T.D.; Moeller, R.E.; Davis. M.B. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. Ecology. 67: 1101–1105.

Barden, L.S.; Woods, F.W. 1976. Effects of fire on pine and pine-hardwood forests in the Southern Appalachians. Forest Science. 22: 399–403.

Beckage, B.; Clark, J.S.; Clinton, B.D.; Haines, B.L. 2000. A long-term study of tree seedling recruitment in Southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research. 30: 1617–1631.

Brockerhoff, E.G.; Liebhold, A.M.; Jactel, H. 2006. The ecology of forest insect invasions and advances in their management. Canadian Journal of Forest Research. 36: 263–268.

Brown, R.L. 2002. Biodiversity and exotic species invasion in Southern Appalachian riparian plant communities. Chapel Hill, NC: University of North Carolina. [Not paged]. Ph.D. dissertation.

Brown, R.L.; Peet, R.K. 2003. Diversity and invisibility of Southern Appalachian plant communities. Ecology. 84(1): 32–39.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science. 199: 1302–1310.

Coulson, R.N. 1980. Population dynamics. In: Thatcher, R.C.; Searcy, J.L.; Coster, J.E.; Hertel, G.D., eds. The southern pine beetle. Tech. Bull. 1631. Washington, DC: U.S. Department of Agriculture, Forest Service: 71–105.

Coulson, R.N.; Klepzig, K.D.; Nebeker, T.E. [and others], eds. 2004. The research, development, and applications agenda for a southern pine beetle integrated pest management program. Proceedings of a facilitated workshop. August 11–14, 2003. Mountain Lake, VA: Southern State Agricultural Experiment Stations; USDA Forest Service; USDA Cooperative State Research, Education, Extension Service; and the Southern State Forestry Agencies. 56 p.

Davis, M.B. 1981. Quaternary history and the stability of forest communities. In: West, D.C.; Shugart, H.H.; Botkin, B.D., eds. Forest succession: concepts and application. New York: Springer-Verlag: 132–153.

Della-Bianca, L. 1990. *Pinus pungens* Lamb., Table Mountain pine. In: Burns, R.M.; Honkala, B.H., eds. Silvics of North America, Vol. 1. Conifers. Agric. Handbk. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 425–432.

Dixon, G.E. 2002. Essential FVS: a user's guide to the Forest Vegetation Simulator. Internal Rep. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Management Service Center. [Not paged].

Elliot, K.J.; Vose, J.M.; Shank, W.T. 1999. Long-term patterns in vegetation-site relationships in a Southern Appalachian forest. Journal of the Torrey Botanical Society. 126(4): 320–334.

Elton, C.S. 1958. The ecology of invasions by plants and animals. London: Methuen & Co. [Not paged].

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge, MA: Cambridge University Press. [Not paged].

Fuller, J.L. 1998. Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. Ecology. 79: 2337–2351.

Gouger, R.J. 1971. Control of *Adelges tsugae* on hemlock in Pennsylvania. Scientific Tree Topics. 3(1): 1–9.

Gustafson, E.J.; Shifley, S.R.; Mladenoff, D.J. [and others]. 2000. Spatial simulation of forest succession and harvesting using LANDIS. Canadian Journal of Forest Research. 30: 32–43.

Haas, J.N.; McAndrews, J.H. 2000. The summer drought-related hemlock (*Tsuga canadensis*) decline in Eastern North America 5,700 to 5,100 years ago. In: McManus, K. [and others], eds. Proceedings of a symposium on sustainable management of hemlock ecosystems in Eastern North America. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 81–88.

Harmon, M.E. 1980. Influence of fire and site factors on vegetation pattern and process: a case study of the western portion of Great Smoky Mountains National Park. Knoxville, TN: University of Tennessee. [Not paged]. M.S. thesis.

Harrod, J.; White, P.S.; Harmon, M.E. 1998. Changes in xeric forests in western Great Smoky Mountains National Park, 1936–1995. Castanea. 63(3): 340–360.

Harrod, J.C.; Harmon, M.E.; White, P.S. 2000. Post-fire succession and 20th century reduction in fire frequency on xeric Southern Appalachian sites. Journal of Vegetation Science. 11(4): 465–472.

He, H.S.; Hao, Z.; Larsen, D.R.; [and others]. 2002a. A simulation study of landscape scale forest succession in northeastern China. Ecological Modelling. 156: 153–166.

He, H.S.; Mladenoff, D.J.; Gustafson, E.J. 2002b. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. Forest Ecology and Management. 155: 257–70.

He, H.S.; Mladenoff, D.J. 1999a. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology. 80: 81–90.

He, H.S.; Mladenoff, D.J. 1999b. The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems. 2: 308–319.

He, H.S.; Mladenoff, D.J.; Boeder, J. 1996. LANDIS, a spatially explicit model of forest landscape disturbance, management, and succession-LANDIS 2.0 users' guide. Madison, WI: Department of Forest Ecology and Management, University of Wisconsin.

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

He, H.S.; Mladenoff, D.J.; Crow, T.R. 1999b. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecological Modelling. 114: 213–233.

Hodges, J.D.; Elam, W.W.; Watson, W.F.; Nebeker, T.E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. The Canadian Entomologist. 111: 889–896.

Hodges, J.D.; Lorio, P.J., Jr. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. Forest Science. 21: 283–290.

Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge, MA: Cambridge University Press. 708 p.

Huston, M.A. 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions. 10: 167–178.

Kennedy, T.A.; Naeem, S.; Howe, K.M. [and others]. 2002. Biodiversity as a barrier to ecological invasion. Nature. 417(6889): 636–638.

Lafon, C.W.; Kutac, M.J. 2003. Effects of ice storms, southern pine beetle infestations, and fire on Table Mountain pine forests of southwestern Virginia. Physical Geography. 24(6): 502–519.

Levine, J.M.; D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invisibility. Oikos. 87: 15–26.

Liebhold, A.M.; Macdonald, W.L.; Bergdahl, D.; Mastro, V.C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monographs. 30. 49 p.

Lovett, G.M.; Canham, C.D.; Arthur, M.A. [and others]. 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. BioScience. 56(5): 395–405.

McClure, M.S. 1987. Biology and control of hemlock woolly adelgid. Bulletin of the Connecticut Agricultural Experiment Station. 851 p.

McClure, M.S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). Annals of the Entomological Society of America. 82: 52–54.

McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomology. 20: 258–264.

McClure, M.S. 1992. Hemlock woolly adelgid. American Nurseryman. 175(6): 82–89.

McClure, M.S. 1995a. *Diapterobates humeralis* Oribatida: Ceratozetidae: an effective control agent of hemlock woolly adelgid (Homoptera: Adelgidae) in Japan. Environmental Entomology. 24: 1207–1215.

McClure, M.S. 1995b. Using natural enemies to control hemlock woolly adelgid. Frontiers of Plant Science. 47(2): 5–7.

McClure, M.S.; Cheah, C.A.S.J.; Tigner, T.C. 2000. Is *Pseudoscymnus tsugae* the solution to the hemlock woolly adelgid problem? An early perspective. In: McManus, K.A.; Shields, K.S.; Souto, D.R., eds. Proceedings of the symposium on sustainable management of hemlock ecosystems in Eastern North America. Gen. Tech. Rep. NE-267. Newton Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 89–96.

Mehtaa, S.L.E.; Frelicha, M.T.; Jones, J.M. 2004. Examining the effects of alternative management strategies on landscape-scale forest patterns in northeastern Minnesota using LANDIS. Ecological Modelling. 180: 73–87.

Mladenoff, D.J. 2004. Background, development, and diversification of LANDIS, a forest landscape change simulation model. Ecological Modelling. 180(1): 7–19.

Mladenoff, D.J.; He, H.S. 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J.; Baker, W.L., eds. Advances in spatial modeling of forest landscape change: approaches and applications. Cambridge, MA: Cambridge University Press: 125–162.

Orwig, D.A.; Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, U.S.A. Journal of the Torrey Botanical Society. 125(1): 60–73.

Orwig, D.A.; Foster, D.R.; Mausel, D.L. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography. 29: 1475–1487.

Payne, T.L. 1980. Life history and habits. In: Thatcher, R.C.; Searcy, J.L.; Coster, J.E.; Hertel, G.D., eds. The southern pine beetle. Tech. Bull. 1631. Pineville, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station: 7–28.

Perry, G.L.W.; Enright, N.J. 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. Progress in Physical Geography. 30: 47–72.

Peters, D.P.C. 2002. Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. Ecological Modelling. 152: 5–32.

Southern Appalachian Man and the Biosphere [SAMAB]. 1996. The Southern Appalachian assessment terrestrial technical report. Atlanta: U.S. Department of Agriculture, Forest Service, Southern Region. 288 p.

Shea, K.; Chesson, P. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution. 17: 170–176.

Shifley, S.R.; Thompson, F.R.; Larsen, D.R.; Dijak, W.D. 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Computers and Electronics in Agriculture. 27: 7–24.

Shifley, S.R.; Thompson, F.R.; Mladenoff, D.J.; Gustafson, E.J. 1998. Utilizing inventory information to calibrate a landscape simulation model. In: Proceedings of integrated tools for natural resources inventories in the 21st century. Gen. Tech. Rep. NC-212. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 549–561.

Smith, R.N. 1991. Species composition, stand structure, and woody detrital dynamics associated with pine mortality in the Southern Appalachians. Athens, GA: University of Georgia. [Not paged]. M.S. thesis.

Stephenson, S.L.; Ash, A.N.; Stauffer, D.F. 1993. Appalachian oak forest. In: Martin, W.H.; Boyce, S.G.; Echternacht, A.C., eds. Biodiversity of the Southeastern United States: upland terrestrial communities. New York: John Wiley: 255–304.

Stohlgren, T.J.; Schnase, J.L. 2006. Risk analysis for biological hazards: what we need to know about invasive species. Risk Analysis. 26(1): 163–173.

Sturtevant, B.R.; Gustafson, E.J.; He, H.S. 2004a. Modeling disturbance and succession in forest landscapes using LANDIS: introduction. Ecological Modelling. 180(1): 1–5.

Sturtevant, B.R.; Gustafson, E.J.; Lei, W.; He, H.S. 2004b. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecological Modelling. 180(1): 153–174.

Tisdale, R.A.; Nebeker, T.E.; Hodges, J.D. 2003. Role of oleoresin flow in initial colonization of loblolly pine by southern pine beetle (Coleoptera: Scolytidae). Journal of Entomological Science. 38: 576–582.

U.S. Department of Agriculture, Forest Service. 2003. America's forests: 2003 health update. AIB-776. Washington, DC: U.S. Department of Agriculture. 15 p.

Veblen, T.T.; Hadley, K.S.; Reid, M.S.; Rebertus, A.J. 1989. Blowdown and stand development in a Colorado subalpine forest. Canadian Journal of Forest Research. 19: 1218–1225.

Waldron, J.D.; Lafon, C.W.; Coulson, R.N. [and others]. 2007. Simulating the impacts of southern pine beetle and fire on the dynamics of xerophytic pine landscapes in the Southern Appalachians. Applied Vegetation Science. 10: 53–64.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review. 45: 229–299.

White, P.S. 1987. Natural disturbance, patch dynamics, and landscape pattern in natural areas. Natural Areas Journal. 7: 14–22.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs. 26: 1–80.

Williams, C.E. 1998. History and status of Table Mountain pine-pitch pine forests of the Southern Appalachian Mountains (U.S.A.). Natural Areas Journal. 18(1): 81–90.

Xu, C.; He, H.S.; Hu, Y. [and others]. 2004. Assessing the effect of cell-level uncertainty on a forest landscape model simulation in Northeastern China. Ecological Modelling. 180(1): 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. Ecological Modelling. 180: 119–133.

Zobel, D.B. 1969. Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. Ecological Monographs. 39(3): 303–333.

Continue