Journal of Environmental Management (2001) **63**, 281–292
doi:10.1006/jema.2001.0482, available online at http://www.idealibrary.com on IDEAL®

Using a GIS model to assess terrestrial salamander response to alternative forest management plans

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Received 19 February 2000; accepted 8 June 2001

A GIS model predicting the spatial distribution of terrestrial salamander abundance based on topography and forest age was developed using parameters derived from the literature. The model was tested by sampling salamander abundance across the full range of site conditions used in the model. A regression of the predictions of our GIS model against these sample data showed that the model has a modest but significant ability to predict both salamander abundance and mass per unit area. The model was used to assess the impacts of alternative management plans for the Hoosier National Forest (Indiana, USA) on salamanders. These plans differed in the spatial delineation of management areas where timber harvest was permitted, and the intensity of timber harvest within those management areas. The spatial pattern of forest openings produced by alternative forest management scenarios based on these plans was projected over 150 years using a timber-harvest simulator (HARVEST). We generated a predictive map of salamander abundance for each scenario over time, and summarized each map by calculating mean salamander abundance and the mean colonization distance (average distance from map cells with low predicted abundance to those with relatively high abundance). Projected salamander abundance was affected more by harvest rate (area harvested each decade) than by the management area boundaries. The alternatives had a varying effect on the mean distance salamanders would have to travel to colonize regenerating stands. Our GIS modeling approach is an example of a spatial analytical tool that could help resource management planners to evaluate the potential ecological impact of management alternatives.
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Keywords: spatial models, GIS, forest management, risk assessment, terrestrial salamanders, timber harvesting, fragmentation, biological diversity, landscape change, land use planning.

Introduction

The relationship between pattern and process is the focus of landscape ecology, but the practical application of landscape ecology principles by land managers has been difficult due to a lack of analytical and spatial tools. Evaluation of alternative management practices to provide multiple values and benefits requires both spatial and temporal information. For example, timber harvesting profoundly affects the composition and structure of forested landscapes in both time and space by modifying vegetation and habitat (Franklin and Forman, 1987). These patterns have ecological consequences for species and ecological communities. Evaluating the consequences of timber management is difficult without large-scale contextual (spatial) and long-term (temporal) information about the patterns expected under management alternatives.

Computer simulation offers a practical approach for generating patterns expected under specific management strategies (Li *et al.*, 1993; Gustafson

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and Crow, 1994; Spies *et al.*, 1994). These expected patterns can be evaluated using other models that predict the biological response of organisms to spatial patterns. To test this premise, we developed and tested a GIS model of the spatial distribution of terrestrial salamanders based on vegetation composition, forest age, and topography. The model can generate predictions over very large areas, and uses spatial data that are readily available for many managed forests. We studied salamanders because they represent physiologically sensitive species that are responsive to changes in microclimate and forest floor debris caused by timber management activities. We used a timber harvest simulation model (HARVEST; Gustafson and Crow, 1996; Gustafson, 1999) to generate stand-age maps of future forest landscapes under alternative management strategies developed for the Hoosier National Forest in southern Indiana (USA) (Figure 1). We then applied the salamander GIS model to these landscape patterns to assess the potential impacts of the management alternatives on terrestrial salamanders.

Situation

The National Forest Management Act of 1976 requires the US Department of Agriculture Forest Service to complete a plan for each National Forest that constitutes a comprehensive statement of management direction. The Hoosier National Forest (HNF) published its first Land and Resource Plan in 1985, and it included even-age management (mostly by clearcutting) over most of the Forest (USDA Forest Service, 1985). Because of strong public opposition, the 1985 Plan was replaced by a 1991 Forest Plan Amendment (USDA Forest Service, 1991) that placed greater emphasis on protecting and managing ecosystems, and on providing a visually pleasing landscape. In contrast to the 1985 Plan, the 1991 Amendment called for primarily uneven-age management using group selection (removal of small ($\leq 0{\cdot}4$ ha) patches of trees) over a much smaller portion of the land base. Gustafson and Crow (1996) used a timber harvest simulator (HARVEST) to compare the landscape structure resulting from these two alternative management strategies. Although realistic changes in landscape structure can be simulated using a harvest simulator such as HARVEST, interpreting the ecological consequences of these spatial patterns remains difficult. Habitat suitability for many species may be determined by multiple characteristics of vegetation and site conditions, and these may interact in complex ways to determine population abundance.

Amphibian species associated with forests are thought to be sensitive to forest management (Blaustein and Wake, 1990). In the case of terrestrial salamanders there is sufficient information available in the literature (e.g. Heatwole, 1962; Bennett *et al.*, 1980; Duellman and Trueb, 1986; Pough *et al.*, 1987; deMaynadier and Hunter, 1995) to construct spatially explicit hypotheses about abundance, although this information was developed from studies conducted outside Indiana. In this study, we used published data to formulate a hypothesis about how vegetation and topography interact to determine site moisture and thereby control terrestrial salamander abundance. We formalized this hypothesis mathematically in a GIS model that generates a map of the spatial distribution of predicted salamander abundance across a managed landscape. Concern has also

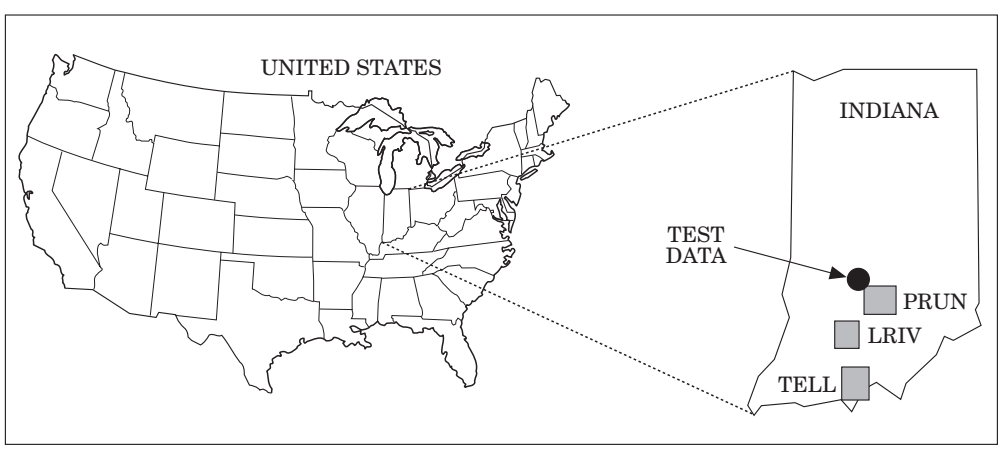

Figure 1. Map showing location of the study areas within the Hoosier National Forest, and the area where salamanders were sampled to test the GIS model. LRIV, PRUN, and TELL are study areas.

been raised about the limited ability of salamanders to recolonize sites disturbed by clearcutting (Blaustein *et al*., 1994; Petranka, 1994). Our model output can also be used to assess the average distance colonizers must travel to reach young, disturbed sites as they mature.

The HNF consists primarily of the central hardwood forest type dominated by maple (*Acer saccharum*), beech (*Fagus grandifolia*), oak (*Quercus* spp) and hickory (*Carya* spp) with embedded pine (*Pinus*) plantations. Pine occurs only in plantations. This area is an unglaciated, dendritic network of hills and ravines (Schneider, 1966), forming two major ecological subsections, the Brown County Hills and the Crawford Uplands. Ravines are typically about 60 meters deep.

Objectives

Our objectives in this study were to (1) construct a GIS model to predict salamander abundance on the HNF, (2) test the model by sampling salamander abundance across the full range of site conditions used in the model, and (3) use the model to compare the predicted responses of terrestrial salamanders to different timber management strategies on the HNF, as simulated by the HARVEST model.

Methods

Predicting salamander abundance

Predictive model

We constructed a theoretical GIS model predicting salamander abundance from site conditions important for terrestrial salamanders, related primarily to physiographic features and stand management history. These features are commonly represented within a GIS as digital elevation models and stand age maps. Salamanders require moisture to maintain respiration, as do most amphibians, and they are easily desiccated (Duellman and Trueb, 1986). The risk of desiccation limits the surface activity of salamanders and therefore their foraging opportunities. Areas with lower moisture levels should support lower densities of salamanders. Site moisture is therefore a critical factor to predict habitat suitability for salamanders. We assumed site moisture was linearly related to slope position (see below) (J. Van Kley, 1993, pers. comm.). Site moisture is further affected by slope aspect, and the relationship between aspect and moisture varies with physiographic province (Van Kley, 1993). We assumed that site moisture was 40% less on southwest-facing slopes, and 20% less on Crawford Upland sites, than on northeast-facing slopes on Brown County Hills sites (J. Van Kley, 1993, pers. comm.).

Slope position was defined relative to the bottom (=1) and the top (=100) of the slope and was derived from a 30-m digital elevation model as follows. We developed GIS functions to identify ridge tops and valley bottoms that were then stored as separate GIS layers. Using a proximity function, we created layers representing the distance of each pixel from the nearest ridge (r) or valley bottom (b), respectively. Slope position (s) for each pixel was then calculated by

$$s=[b/(r+b)]^{*}100.$$

We applied a cosine transformation of aspect (a) so that $a=0{\cdot}0$ for northeast slopes (azimuth=45°) and $a=2{\cdot}0$ for southwest slopes (Beers *et al*., 1966). Predicted relative (range=1−100) site moisture (m) for each pixel is

$$m=|s-101|-(a^{*}p)$$

where $p=20$ on Brown County Hills sites and $p=10$ on Crawford Upland sites.

Site disturbance by clearcutting has also been shown to affect salamander abundance in eastern forests (Pough *et al*., 1987; Petranka *et al*., 1993), and we included the effects of stand age on salamander abundance in our model. We related stand age (x) to salamander numbers (y) by fitting a third order polynomial (Figure 2) to data on mean

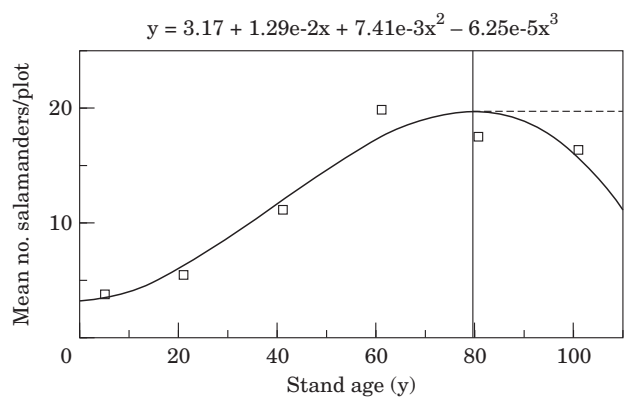

Figure 2. Polynomial used to relate salamander abundance to stand age. Data points were derived from Figure 3 of Petranka *et al*., 1993. Stands aged>80 yr were assumed to have the salamander abundance represented by the dashed line.

number of salamanders (all species) in western North Carolina study plots published by Petranka *et al*. (1993).

$$y=3{\cdot}17+0{\cdot}0129x+0{\cdot}0074x^2-0{\cdot}00006x^3$$

These data are also consistent with the results obtained by Pough *et al*. (1987) in central New York. However, we constrained the function so that stands aged >80 yr (Figure 2) were calculated as 80-yr-old stands because these studies suggest that the observed decline in abundance in stands >80 yr is probably due to sampling variation, and not biologically significant.

Field surveys on the HNF have documented a paucity of all amphibians in pine stands (Ewert, M. A., J. N. Barron, C. R. Etchberger, C. L. Grimes, E. Levri, M. J. Lodato, B. Nelson and C. E. Nelson unpublished report), which is consistent with other studies (Bennett *et al*., 1980; Pough *et al*., 1987; deMaynadier and Hunter, 1995). Pine stands tend to be drier and have less understory vegetation than deciduous areas (Van Kley *et al*., 1995). Based on this information, we assumed that pine stands support only 15% of the salamander abundance predicted for 80-yr-old deciduous stands (Figure 2). Finally, we related salamander abundance to moisture (m) by assuming that relative salamander abundance increased linearly as site wetness increased. The slope and intercept of this relationship were estimated using data on salamander abundance in California and Oregon (Welsh and Lind, 1988). The model predicts relative salamander abundance (sa) using values derived from stand age (y) and the digital elevation model (m):

$$sa=y^*(0{\cdot}983+0{\cdot}017m).$$

sa was normalized to range between 1 and 100, and output to a GIS layer. These relationships are shown graphically in Figure 3. The model considered only forested habitat, so non-forest habitats were assigned zero. The model was implemented using PC-ERDAS (v.7·5).

Predictive model testing

To verify the predictive ability of the model for the HNF we collected empirical data on terrestrial salamander abundance and compared them to the predictions of the model. We sampled terrestrial salamander abundance and mass in April of 1997 and 1998 in the Pleasant Run Unit of the HNF (Figure 1). Four species of salamanders were captured in the study area (*Plethodon cinereus*, *P. dorsalis*, *P. glutinosus* and *Eurycea longicauda*), and all were captured at least once. *E. longicauda* is a stream salamander that ventures a little further from streams than other stream salamanders in the study area. We did not study the pond-breeding salamanders because the *Ambystoma* spp. live in burrows that could not be sampled, and the terrestrial stage of *Notopthalmus viridescens* was uncommon in the study area. Sampling occurred along transects within randomly selected forested stands. Transects were stratified by slope position (top, middle, bottom), aspect (north (316–45 degrees azimuth), east (46–135 degrees), south (136–225 degrees), west (226–315 degrees)), and stand type. Stand types included pine plantations and three deciduous types–young (15–25 yr after clear cutting), intermediate (26–60 yr since cutting), and mature (>60 yr since cutting). Transects were 100 m long and followed topographical contour lines. This transect length was sufficient to disperse the plots and sample the range of conditions, but short enough to stay within a stand type. Transects were located randomly within an area having a given slope position and aspect. Twenty randomly spaced 2-m^2 plots (i.e. 1·4 m × 1·4 m) were sampled along each transect. In 1997, 460 plots were sampled on 23 transects, and in 1998, 661 plots were sampled on 27 different transects, giving a total of 1121 plots (2242 m^2 of forest).

In each plot, cover objects were overturned to expose salamanders. Next, all litter within the plot

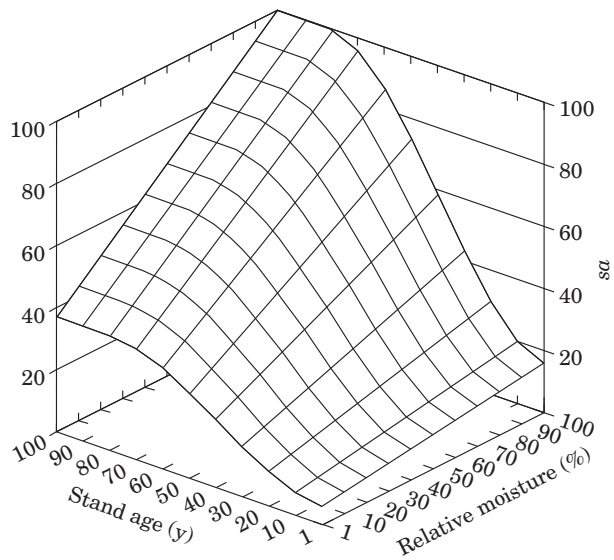

Figure 3. Relationship between relative salamander abundance (*sa*) and relative site moisture (*m*) and stand age (*x*), as formulated in the salamander model.

was scraped down to the mineral soil and piled in the middle of the plot. The pile of litter was then sifted to collect all salamanders. Salamanders were identified to species, and weighed using an Ohaus spring scale (±0·1 g). All salamanders were released immediately and litter and cover objects were replaced.

Abundance was quantified as the mean number of individuals and the mean salamander mass per plot for each transect ($N = 20$ plots). We compared the results of these surveys to the model by plotting the abundance measures against the model prediction at the center point of the transect. Because our test data did not use the same units as the model predictions (numbers and mass vs. relative abundance), we could not test for an expected slope between empirical and model results (e.g. slope = 1·0). Instead, after verifying the Gaussian nature of the variables, we fitted a regression line to these plots and tested the null hypothesis that the slope = 0.

Simulating alternative timber harvest strategies

Timber harvest simulation model

HARVEST is a timber harvest simulator, linked to a GIS, that simulates the allocation of stands for timber harvest in a spatially explicit manner through time (Gustafson and Crow, 1996; Gustafson, 1999). The model allows flexible simulation of harvest activity using parameters commonly found in National Forest Plan standards and guidelines. Only four input maps are required: stand age, forest type, management area boundaries (spatial zones with specific management objectives), and stand identifier value (for model bookkeeping purposes). It produces landscape patterns that have spatial attributes resulting from the initial landscape conditions and the planned management actions. The model does not attempt to optimize timber production or quality, and it ignores many of the site attributes considered by forest planners, such as visual objectives and road access. Instead, it stochastically mimics the allocation of stands for harvest by forest planners, using the parameters of the broad management strategies. Modeling this process allows us to link harvest activities with landscape patterns. In our study, we considered only harvests that produce openings >0·1 ha within the forest (clearcutting, shelterwood and group selection). The effect of single-tree selection on salamander abundance appears to depend on the species (Pough *et al.*, 1987; Pais *et al.*, 1988), and we assumed that single-tree selection would produce little change in the abundance of salamanders as a group (N. Murphy, pers. observ.).

HARVEST allows control of the size distribution of harvests, the total area of forest to be harvested, the rotation length (by specifying the minimum age on the input stand map where harvests may be allocated), and the width of buffers left around harvest openings. Group selection is implemented on the HNF such that one-sixth of a stand is cut on each entry, and entries occur every 20–30 yr (USDA Forest Service, 1991; T. Thake, pers. comm.). The model selects stands for group selection from those stands with an age greater than the prescribed rotation length; it then tracks stands managed by group selection, ensuring re-entry at 30-yr intervals, and prevents other treatments in those stands. Within group-selected stands, openings are placed randomly, with at least 30 m (1 pixel) between openings. HARVEST is described in detail in Gustafson and Crow (1996) and Gustafson (1999), and is available on the Internet (http://www.ncrs.fs.fed.us/harvest/harvhome.htm).

Simulation study areas

Study areas were selected in three of the four administrative units of the HNF [Pleasant Run (PRUN) study area (34 053 ha), Lost River (LRIV, 38 822 ha), and Tell City (TELL, 49 515 ha)] (Figure 1). Stand age maps of National Forest land within the three study areas were digitized from paper-based and mylar planning maps and gridded to 30 m cells, and ages were calculated as of 1988. We used the management area (MA) boundaries of the two published management plans. Each MA has a specific management objective, and the MA boundaries encompass tracts to be managed to meet that objective. Several disjunct polygons of a particular MA may be designated within an administrative unit. The objectives of each MA and the arbitrary decimal designations (e.g. 3·1, see Table 1) are used consistently among all National Forests. The MA boundaries within each study area were manually transferred to 1:100 000 US Geological Survey maps, digitized, and gridded to 30-m cells. Land use on non-Forest Service land was derived from Landsat Thematic Mapper (TM) imagery collected in 1988, as described in Gustafson and Crow (1994). Classes distinguished were forest, grazed pasture/young winter

Table 1. Harvest intensities as derived from the 1985 Hoosier National Forest Plan and the 1991 Forest Plan Amendment

Model parameter	1985 MA[1]					1991 MA[1]
	2·1	3·1	3·2	6·1	Total	2·8
Mean clearcut opening size (ha)	–	7·0	4·9	4·0	–	2·8
Mean group opening size (ha)	0·4	–	–	–	–	0·2
Maximum opening size (ha)	0·7	10·8	7·2	5·4	–	4·0
Total harvested/decade[2] (ha)	96·0	2360·6	2890·0	363·0	5709·6	2504·8
Harvest rate/decade[3] (%)	5·4	11·5	7·8	7·5	9·5	6·4
Timber yield/decade[2] (Mbf)	180	4928	6006	767	11 881	4120
Rotation length (years)	80	80	120	120	–	80
Buffer width[4] (m)	30	30	30	30	–	30

[1]Forest Plan management areas. The (arbitrary) decimal designation is that used by the Forest Service.
[2]Represents harvest activity by management area across the entire Forest.
[3]Represents percent of forest within the management area that is harvested each decade.
[4]The width of buffers left between harvest allocations and other harvests, streams, and openings.

wheat, meadow/hay fields, row crops, water, and road/developed.

Simulation experiments

We simulated five specific management alternatives on each study area: (1) the 1985 Forest Plan (USDA Forest Service, 1985), (2) the 1991 Forest Plan Amendment (USDA Forest Service, 1991), (3) the management area (MA) boundaries of the 1985 Plan with the harvest intensity of the 1991 Amended Plan (85 Intensity-91 Map), (4) the MA boundaries of the 1991 Plan Amendment with the harvest intensity of the 1985 Plan (91 Map-85 Intensity), and (5) no harvest (i.e. no openings produced or maintained on National Forest land). The 91 Map-85 intensity scenario used the parameters of MA 3·1, the most intense of the 1985 Plan harvest scenarios (Table 1), to provide the greatest contrast with the 1991 plan harvest intensity (MA 2·8). We simulated 150 yr of management under each alternative; given the low variability of the spatial patterns produced by the simulations (see Results), three replicates were adequate to ensure robust results. Wildlife openings were maintained throughout the simulations except in the no-harvest scenario, where conversion to forest was simulated and closed canopy forest was reached in two decades. All harvested stands regenerated to forest, and pine stands harvested were assumed to convert to hardwood, as proposed in both management plans. We did not simulate harvest activity on privately owned inholdings to avoid confounding our assessment of the effects of public land management strategies. The existing pattern of forest openings on private land was derived from the TM imagery, and these conditions were maintained throughout the simulations.

Quantification of experimental results

We applied the predictive salamander model to each of the modified stand age maps produced for each management alternative using HARVEST, producing a map showing predicted salamander abundance for each. These maps were quantified by calculating the mean predicted abundance value of all forest (non-zero) pixels, and the model predictions were plotted as a function of time. To establish the pre-simulation trend, the 1988 stand age maps were successively recoded by decrementing by 10 the age value (A) at time t for each pixel j to produce the stand age map of the previous decade (i.e. $A_{j(t-10)}=A_{j(t)}-10$). We repeated this process to establish the pattern of forest openings since 1948. Stands that reached an age of zero during this process were assumed to have been mature forest (>80 yr) at the time they were cut.

To assess the fragmenting effect of timber harvest on salamander habitat quality, we calculated the average distance between cells where salamander abundance was reduced by timber harvest ($sa \leq 50\%$), and those likely to contain potential colonizers ($sa > 50\%$); sa is a relative value, and we arbitrarily chose the 50% threshold. Some of the cells with low sa values were pine plantations, but these remained constant among alternatives. We used the GIS to calculate the distance from pixels representing low salamander abundance ($sa \leq 50\%$) to the nearest pixel of relatively high salamander abundance ($sa > 50\%$). We then calculated the mean distance value of these pixels.

Statistical analysis

To evaluate the relative effects of harvest intensity and the zonation of harvest activity (restricted spatially by MA boundaries) on salamander abundance and colonization distance, we used a repeated measures ANOVA to test for treatment effects reflecting harvest intensities (INTENSITY), management area boundaries (MAP), and time (DECADE). The time-periods were included in the analysis to account for potential autocorrelation among spatial pattern measures across successive decades.

Results

Predictive model testing

Over 500 salamanders were captured during sampling over a 2 year period (243 *P. cinereus*, 245 *P. dorsalis*, 24 *P. glutinosus* and 4 *E. longicauda*). The regression of the predictions of our GIS model against these sample data showed that the model has a modest, but significant ability to predict both salamander abundance ($F=12{\cdot}2546$, $\Pr>F=0{\cdot}0010$) and mass per unit area ($F=9{\cdot}2424$, $\Pr>F=0{\cdot}0038$) (Figure 4). The analysis of variance indicated that the model explained about 20% of the total variance for salamander abundance, and about 16% for salamander mass (Table 2). The null hypothesis that the model provides no predictive ability (i.e. slope=0) was rejected for both salamander abundance ($T=3{\cdot}5$, $\Pr>T=0{\cdot}001$) and salamander mass ($T=3{\cdot}04$, $\Pr>T=0{\cdot}004$).

Simulation experiments

The replications of the simulations for each scenario produced little variability in mean salamander abundance. Harvest levels in all MAs were high enough that most stands > rotation age were harvested each decade. Consequently, the opportunity for stochastic variation in the spatial pattern of harvest openings was limited. Even the 1991 Plan had a high number of stands harvested because the reliance on group selection required harvest in many stands to achieve the specified timber production. Although harvest intensity was high within MA 2·8 (1991 Plan), much less of the land base was dedicated to timber production (MA 2·8) than under the 1985 Plan. Alternatives with lower harvest intensities within MAs would result in greater spatial pattern variability. The variability in our results was too low to show clearly with error bars on line graphs, so error bars are not shown. The standard deviation from the mean salamander abundance never exceeded 0·02.

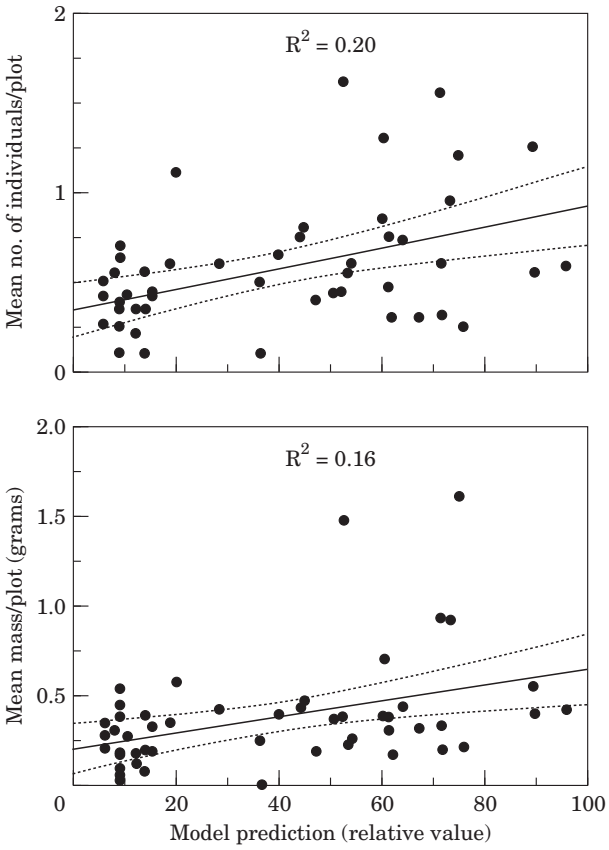

Figure 4. Plot of empirical test data against model predictions. The solid is a regression line fit to the data, and the dotted line represents the 95% confidence interval for the slope of the regression line. Relative abundance (x-axis) is scaled as a percent of the maximum possible abundance prediction.

Table 2. Analysis of variance comparing empirical measures of salamander abundance and the relative abundance predictions of the salamander model

Source	df	SS	F	Prob>F	R^2
NUMBER OF SALAMANDERS					
Salamander model	1	1·263	12·28	0·001	
Error	48	4·936			
Total	49	6·199			0·204
SALAMANDER MASS (G)					
Salamander model	1	0·738	9·21	0·004	
Error	48	3·848			
Total	49	4·586			0·161

Mean salamander abundance was affected more by harvest intensity than by the management area boundaries in our simulations. Examination of the sums of squares of the main effects shows that harvest intensity (INTENS) accounted for 68–76% of the variability in predicted mean salamander abundance, while management area boundaries (MAP) accounted for only 4–16% of the variability and DECADE accounted for only 3–17% (Table 3). The only factor affecting salamander abundance that varied among simulations was stand age. The total area harvested each decade determined the frequency distribution of stand age classes, and the spatial distribution of age classes across the landscape was determined by the management area boundaries.

Mean salamander abundance was consistently higher for scenarios using the 1991 Plan harvest intensities than those using the 1985 Plan intensities (Figure 5) because less area in young age classes was produced by the 1991 Plan. The 1985 Plan did not reduce salamander abundance below levels observed between 1948 and 1988 on the PRUN and LRIV study areas, and it reduced salamander abundance only slightly below pre-simulation levels on the TELL study area. The early (1988–98) decline of the no-harvest scenario was due to the closure of wildlife openings, a change from non-forest to young forest, which initially decreased the mean age of all forest. Differences among study areas were generally caused by differences in the frequency distribution of age classes on the study areas (Gustafson and Crow, 1996), because the distributions of slope aspects and slope positions were similar among study areas.

Areas of relatively high salamander abundance were highly interconnected on all study areas (Figure 6). Increases in mean colonization distances (Figure 7) were related to increased area of

Table 3. Analysis of variance comparing the effects of harvest intensity (INTENSITY), the zonation of harvest activity by management area boundaries (MAP), and the time period simulated (DECADE) on relative salamander abundance across the landscape. Analysis includes three replicates of simulations conducted for 15 decades on the three study areas within the HNF

Source	Salamander abundance (*sa*)				
	df	SS	*F*	Prob > *F*	R^2
LRIV[1]					
MAP	1	41·6931	218·09	0·0001	
INTENSITY	1	332·3570	1738·51	0·0001	
DECADE	14	31·0209	11·59	0·0001	
Error	163	31·1613			
Total	179	436·2324			0·93
PRUN[1]					
MAP	1	160·7256	296·54	0·0001	
INTENSITY	1	766·2807	1413·80	0·0001	
DECADE	14	2·5934	0·34	0·9873	
Error	163	88·3463			
Total	179	1017·9460			0·91
TELL[1]					
MAP	1	96·2332	159·97	0·0001	
INTENSITY	1	861·7963	1432·58	0·0001	
DECADE	14	211·3267	25·09	0·0001	
Error	163	98·0555			
Total	179	1267·4118			0·92

[1]LRIV, PRUN, and TELL are study areas.

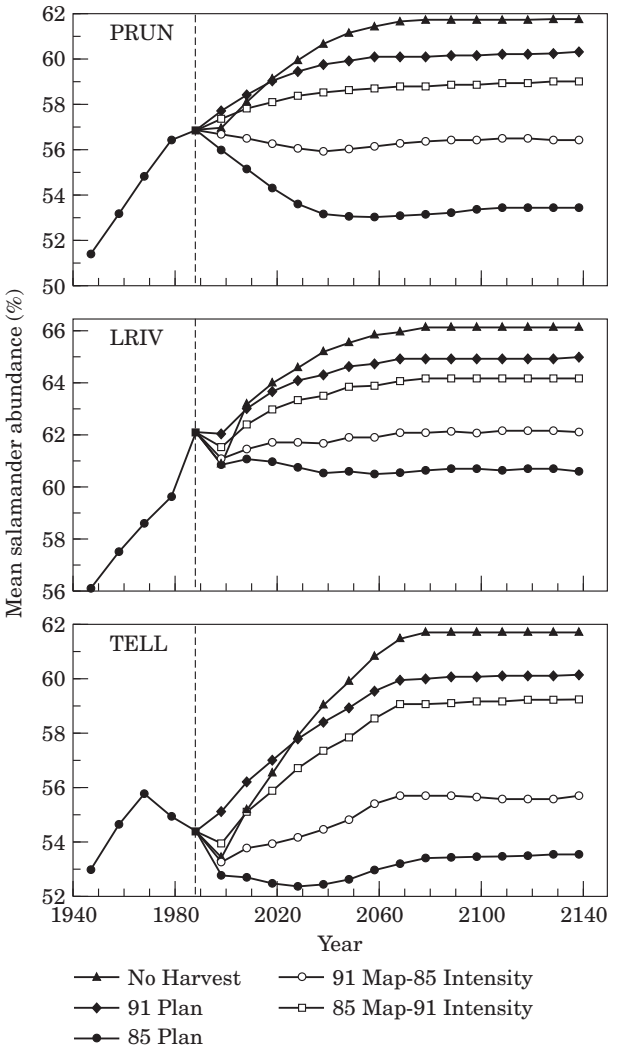

Figure 5. Change in the predicted mean relative abundance of salamanders over time resulting from simulation of management strategies. Relative abundance is scaled as a percent of the maximum possible abundance prediction. Simulations began using 1988 stand data. PRUN, LRIV, and TELL are study areas.

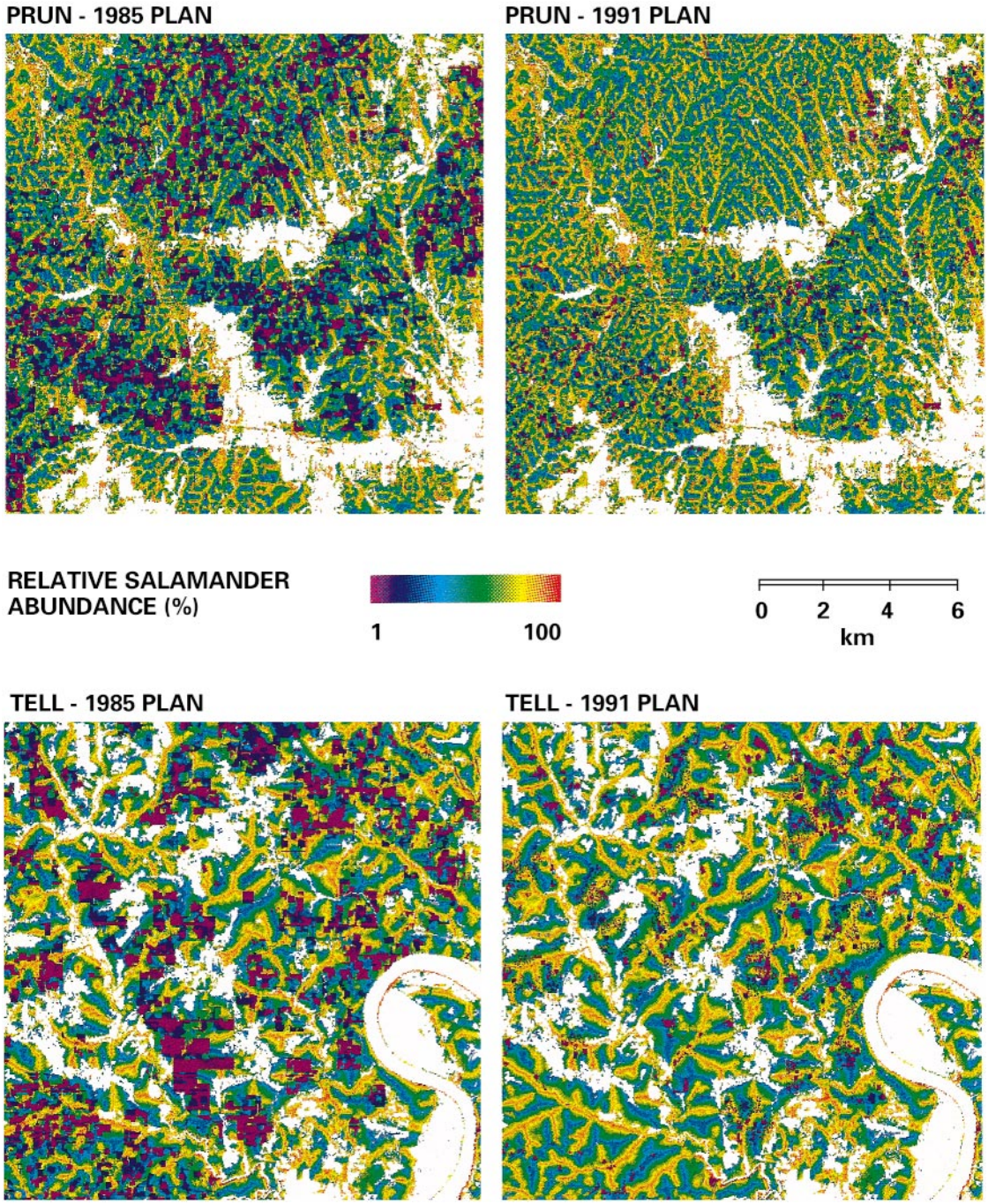

Figure 6. Maps of the spatial distribution of predicted mean relative salamander abundance at the end of simulation (150 yr) of the 1985 and 1991 Plans. Relative abundance is scaled as a percent of the maximum possible abundance prediction. PRUN and TELL are study areas. The LRIV study area is not shown.

young stands with relatively low salamander abundance (see Figure 5). These young stands often enlarged existing areas of low salamander abundance resulting in increased mean colonization distance. Declines before simulation were probably due to aging of young stands and a decrease in the average size of harvest treatments.

Discussion

Our salamander model provides predictive insight into the effect on salamander abundance of features that vary at a coarse scale across a landscape (i.e. topography and forest stand age). Our model predicts the expected salamander abundance as

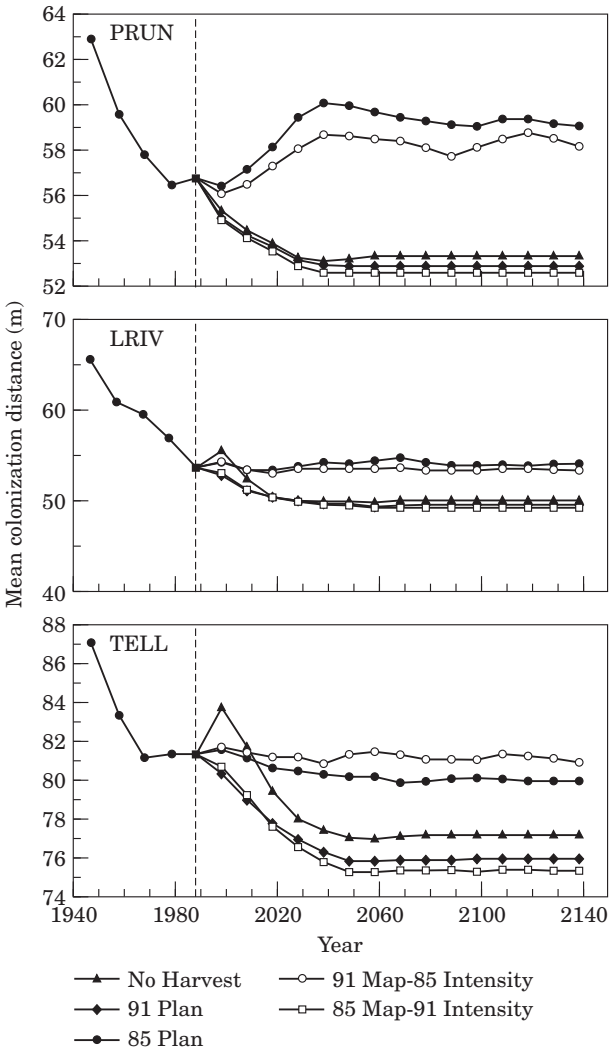

Figure 7. Change in the predicted mean colonization distance over time resulting from simulation of management strategies. This distance is the mean distance of pixels representing relatively poor salamander habitat ($sa \leq 50$) from the nearest pixel of relatively good salamander habitat ($sa \geq 50$). Simulations began using 1988 stand data. PRUN, LRIV, and TELL are study areas.

a function of topography (i.e. slope position and aspect) and forest age. It generates predictions over very large areas, and uses spatial data that are readily available for many managed forests. Although our model was constructed using data from sites in various parts of the United States, its ability to predict salamander abundance in Indiana suggests that the model incorporates some of the important features of salamander biology that make it broadly applicable. Microsite characteristics (e.g. abundance of coarse woody debris and litter depth) and weather (Crump, 1994) may be a source of much of the unexplained variation in our model (N. Murphy, unpublished data). Incorporating microclimate edge effects (e.g. Daolan and Chen, 2000) may result in improved prediction of spatial effects. For better site-specific prediction, additional information is required that may not be readily available from existing data sources. The model may also be relevant for other moisture sensitive species such as frogs. Conversely, it may also be useful for predicting habitat quality for species that favor dry habitats, such as reptiles. This modeling approach provides a feasible and cost-effective means to assess the potential impacts on terrestrial salamanders of forest management alternatives formulated during the strategic planning process. Predicting the impact of site-specific, tactical plans, or the effects of management on a specific salamander species may require more detailed models.

The two Forest Plans provided contrasting landscape patterns during 150 yr of simulated management. A strategy of using small, dispersed harvest units greatly increases fragmentation (Gustafson, 1998). However, the mean abundance of salamanders was affected more by harvest rates than by the spatial configuration of harvests because the scale at which salamanders perceive habitat is relatively small. Abundance was related to forest age, and lower harvest rates resulted in increased mean age of the forest. The size and proximity of harvests did not appear to exert a non-linear effect on mean salamander abundance as they do the existence of forest interior habitat (Gustafson and Crow, 1996), because no edge effects (affecting areas around the disturbance) were incorporated into our model of salamander abundance. The maximum difference in salamander abundance among alternatives was relatively low (5–10%, Figure 5). None of the alternatives may represent a threat to the long-term viability of salamander populations, although not enough is known about these populations to draw definitive conclusions. However, as minimum viable population guidelines are developed, these models will provide a useful tool to evaluate whether management alternatives will sustain those population levels, and how those populations will be distributed across the landscape.

Areas of relatively high salamander abundance were highly interconnected in all study areas (Figures 6, 7). Site moisture conditions are related to topography, and the more moist sites are found near bottoms and drainage, which are interconnected because of the stream patterns produced by geophysical erosion. Areas of good salamander habitat ($sa > 50$) almost always formed a matrix in each study area, with areas of poorer habitat (mostly caused by timber harvesting)

embedded within it (see Figures 6, 7). However, at some point (i.e. higher harvest intensity), this interconnected matrix would likely become fragmented.

Conclusions

The relationship between pattern and process has been the focus of landscape ecology, but the practical application of landscape ecology principles by land managers has been difficult due to a lack of analytical and spatial tools. Forest management has a profound effect on both terrestrial and aquatic habitats. Forest managers have long considered the impacts of management activities on mammals and birds, but recently have focused on overall biodiversity, including amphibians. The quality of terrestrial habitats is critical for maintaining amphibian populations (Marsh and Trenham, 2001). The modeling tools we have described provide a way to evaluate the ecological consequences of management alternatives on species whose habitat needs are determined primarily by site moisture. For example, a manager could ensure that good habitat will not become disconnected by a management strategy, or evaluate how various proportions of clearcut and group selection silviculture treatments impact salamander abundance. Furthermore, the long temporal scale of forest management effects can be appropriately considered by linking the two models.

We believe that the approach presented in this study could be adapted to investigate other management questions. Application of these models by planners and managers is feasible because the models use commonly available GIS data, and operate on commonly used computer platforms (e.g. Windows). The user can easily modify the salamander model to incorporate other important variables and new empirical data about the relationship between salamander abundance, stand age, and topography. We have demonstrated that the outputs from these models are themselves hypotheses that can be tested relatively quickly and easily, and they may be used to provide guidance and feedback to adaptive management practices.

Spatially explicit simulations models such as HARVEST are needed to evaluate management alternatives in both time and space, to aid in the design of landscapes for multiple benefits. We have illustrated the utility of combining a simulation model with a GIS predictive model based on the biology of a taxon, for risk assessment. Such analytical tools are needed to help resource planners develop management plans that will reliably conserve biological diversity and accommodate society's increasing demands for commodity resources.

Acknowledgments

We thank Monica Schwalbach, Ellen Jacquart, Libby Rice, Tom Thake, Mary Stafford, Steve Olsen and Deb Albright of the Hoosier National Forest for their assistance in providing data and information. We thank Kyle Forbes for digitizing maps and John Wright for GIS assistance. Bill Hargrove, Rick Howard, Patrick Zollner, Jim Petranka, Vicky Meretsky, Doug Karpa-Wilson, and three anonymous reviewers provided critical comments on earlier drafts of the manuscript. Lucy Burde gave editorial assistance.

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