Linking population viability, habitat suitability, and landscape simulation models for conservation planning

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Abstract

Methods for habitat modeling based on landscape simulations and population viability modeling based on habitat quality are well developed, but no published study of which we are aware has effectively joined them in a single, comprehensive analysis. We demonstrate the application of a population viability model for ovenbirds (*Seiurus aurocapillus*) that is linked to realistic landscape simulations using a GIS-based habitat suitability index (HSI) model. We simulated potential future characteristics of a hardwood forest in southern Missouri under two tree harvest scenarios using LANDIS. We applied three different versions of the HSI model (lower, best, and upper estimates) to output from the landscape simulations and used RAMAS GIS to link estimates of temporally dynamic habitat suitability, through fecundity and carrying capacity, to ovenbird population viability. Abundances and viability differed more between the upper and lower HSI estimates than between the two forest management scenarios. The viability model was as sensitive to the relationship between reproductive success and habitat suitability as it was to rates of first-year survival and reproductive success itself. Habitat-based viability models and the wildlife studies they support, therefore, would benefit greatly from improving the accuracy and precision of habitat suitability estimates.

Combining landscape, habitat, and viability models in a single analysis provides benefits beyond those of the individual modeling stages. A comprehensive modeling approach encompasses all components and processes of interest, allows direct comparison of the relative levels of uncertainty in each stage of modeling, and allows analysis of the economic benefits and costs of different land use plans, which may be affected by landscape management, habitat manipulation, and wildlife conservation efforts. Using population viability, habitat suitability, and landscape simulation models in an integrated analysis for conservation

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planning is an important advancement because habitat quality is a critical link between human land use decisions and wildlife population viability.

1. Introduction

Including wildlife priorities in landscape management decisions is a common goal for commercial and noncommercial private landowners and public agencies. Developments toward that goal have followed two somewhat distinct paths. One effort has involved incorporating landscape simulations into management planning and assessing wildlife habitat quality using a geographic information system (GIS). The other has involved incorporating habitat quality into models of wildlife population viability. To date, the two paths have not joined together completely in a single analysis combining landscape, habitat, and viability models. A comprehensive approach such as this allows for an evaluation of uncertainty as it propagates through different models, and therefore it is perhaps best used to make relative comparisons among management alternatives rather than to estimate specific future conditions (McCarthy et al., 2003).

Simulation is an effective tool for projecting the structure and composition of landscapes and the potential effects of alternative management activities on wildlife populations. Models that simulate vegetation dynamics are especially useful for forest planning. Some of them, such as LANDIS (He et al., 1999, 2003; Mladenoff and He, 1999) and LMS (McCarter, 1997; McCarter et al., 1998), simulate the establishment, growth, and disturbance of trees in a spatially explicit, relatively high resolution (e.g., 30 m) GIS framework. Such models are becoming widely used for forest planning purposes (Klenner et al., 2000; Shifley et al., 2000). Marzluff et al. (2002) applied existing habitat suitability index (HSI) models (USFWS, 1980, 1981) to output from LMS to evaluate the effects of alternative forest management scenarios on the quality and quantity of habitat for 3 nongame wildlife species. Other HSI models have been revised or newly developed for application in a raster-based GIS (Gustafson et al., 2001; Larson et al., 2003), which facilitates the comparison of the quality, quantity, and spatial structure of wildlife habitat among landscape simulations.

The ultimate goal of wildlife management is often to maintain or increase population viability, rather than habitat quality. Managers of National Forests are mandated to consider viability in their forest planning processes [16 USC 1604; 36 CFR 217, 219 (2000)]. The theory and techniques for spatially structured population viability analysis (PVA) are well developed (Beissinger and Westphal, 1998). Some PVA models link demographic parameters to habitat quality, an approach that is especially useful if habitat quality is allowed to change over time. For example, Akçakaya and Raphael (1998) used RAMAS GIS (Akçakaya, 1998) to incorporate estimates of habitat availability into a PVA of northern spotted owls (*Strix occidentalis caurina*). Nickelson (1998) developed functions relating demographic parameters of coho salmon (*Oncorhynchus kisutch*) to specific habitat features, and the functions were used in a PVA (Nickelson and Lawson, 1998). In both examples, however, habitat changes were modeled as a proportional decrease in the quantity or quality of habitat over time rather than being based upon landscape or habitat simulations.

When sufficient empirical data exist, PVAs for landscape and wildlife management planning can be linked directly to habitat quality, which, in turn, can be linked directly to anticipated changes in the environment (e.g., landscape structure and composition). Liu et al. (1995) used a model that simulated forest dynamics and wildlife demography to conduct a PVA for Bachman's sparrows (*Aimophila aestivalis*). Their model linked three distinct levels of fecundity (0, 1, and 3 offspring per pair) directly to forest structure [i.e., the presence and age of pine (*Pinus* spp.) stands], but it lacked the realistic representation of habitat quality and a continuous functional relationship with fecundity. Providing any link between viability and habitat, however, is beneficial. Analysis of the relationship between a population and the habitat upon which it depends is critical

to understanding the impacts of human land use on wildlife.

Methods for habitat modeling based on landscape simulations and PVA modeling based on habitat quality are well developed, but no published study of which we are aware has effectively joined them in a single, comprehensive analysis. We completed the merging of the two development paths by incorporating all three desired elements of a habitat-based PVA for land management planning: landscape simulation, quantifying wildlife habitat quality, and population viability analysis. Inclusion of large-scale habitat models is essential because landscape patterns such as edge effects and area sensitivity are known to affect wildlife populations (Paton, 1994). We demonstrate the application of a population viability model for ovenbirds (*Seiurus aurocapillus*) that is linked to realistic landscape simulations using a GIS-based habitat suitability model.

2. Methods

2.1. Study area

We modeled forest management, ovenbird habitat suitability, and ovenbird demography in a 71,142-ha tract of the Mark Twain National Forest in the Ozark region of southern Missouri, USA. The study area was located in a 1.8 million-ha region that contained contiguous (92%) forest. The dominant forest cover was a mixture of the oak–hickory (*Quercus* spp., *Carya* spp.), oak–pine, and shortleaf pine (*P. echinata* Mill.) forest types.

2.2. Landscape simulation

We projected future forest conditions (i.e., age, species composition, and location of forest cover) using LANDIS, which models growth and reproduction of trees and simulates disturbances due to wind, fire, and tree harvest. LANDIS has been tested and applied with numerous species in a variety of ecological settings (e.g., Shifley et al., 1997, 2000a,b; He and Mladenoff, 1999a,b; Mladenoff and He, 1999; Gustafson et al., 2000; Franklin et al., 2001; He et al., 2002; Pennanen and Kuuluvainen, 2002; Akçakaya et al., 2004; Sturtevant et al., this volume).

In LANDIS, a landscape is organized as a mapped grid of cells (or sites), with vegetation information stored as attributes for each cell. Within each cell LANDIS represents the forest vegetation as a matrix showing the presence or absence of tree species (or species groups) by 10-year age classes. LANDIS simulates four spatial processes that affect the species composition and age structure of individual cells and, in aggregate, of the landscape as a whole. These spatial processes are fire, windthrow, harvesting, and seed dispersal (He et al., 2003). LANDIS and its various modules are described elsewhere in greater detail (He and Mladenoff, 1999a,b; He et al., 1999; Mladenoff and He, 1999; Gustafson et al., 2000).

LANDIS was previously calibrated and applied to landscapes in the Missouri Ozarks (Shifley et al., 1997, 2000a,b), and for this study we used that calibration to simulate changes in vegetation for our study area. We employed a 30 m × 30 m cell size in LANDIS, a compromise that permitted identification of canopy gaps as small as 0.09 ha, yet kept the computational requirements for our large landscape within the capacity of a dedicated workstation. This data structure allows LANDIS to accommodate large landscapes and is compatible with the types of data typically available to define current landscape conditions.

We represented forest cover using four species groups that encompass nearly 80% of the basal area in the study region: the white oak group (*Q. alba* L., *Q. stellata* Wangenh., *Q. muehlenbergii* Engelm.), the black oak group (*Q. velutina* Lam., *Q. coccinea* Muenchh., *Q. rubra* L.), the shortleaf pine group (*P. echinata* Mill. and *Juniperus virginiana* L.), and the maple group (*Acer rubrum* L. and *A. saccharum* Marsh). Hickories comprise the majority of the remaining basal area, but they typically occur as isolated individuals in association with the species listed above. Ecological land types (based on Miller, 1981), stand maps, initial forest cover type, and initial forest age classes for the landscape were derived from inventory data and GIS layers provided by the Mark Twain National Forest.

The frequency and size of simulated wildfire disturbances on the landscape were patterned after observations in the fire records maintained by the Mark Twain National Forest for the period 1970–1995. We assumed continuation of the current practice of active fire suppression and, thus, set the mean fire return interval in

LANDIS to the current rate of approximately 415 years. This corresponds to the frequency of fires likely to kill at least some overstory trees and create openings large enough to promote natural forest regeneration.

We based the rate of wind disturbance on the findings of Rebertus and Meier (2001), who inventoried windfall gaps along 105 km of transect through the Missouri Ozarks. Simulated windfall openings >0.09 ha in size affected 614 ha per decade under the no harvest scenario and 320 ha per decade under the even-aged management scenario.

The LANDIS harvest module (Gustafson et al., 2000) simulates forest-harvesting activities based upon management area and stand boundaries. We simulated two disturbance scenarios: (1) no harvest (i.e., forest growth and succession disturbed only by fire and windthrow) and (2) even-aged management on a 100-year rotation (i.e., forest growth and succession disturbed by fire, by windthrow, and by clearcutting 10% of the area each decade, always harvesting the oldest stands first). Wilderness areas, scenic river corridors, and other areas where timber harvest is administratively excluded were also excluded in our harvest scenarios. Following a simulated disturbance the sites reverted to natural reproduction and succession based on the algorithms in LANDIS as previously calibrated and applied to this ecoregion (Shifley et al., 1997, 2000a,b).

Initial landscape conditions were identical for the two simulated disturbance scenarios. Many processes in LANDIS are simulated stochastically—the specific outcome of an event is determined by a random draw from a probability distribution of possible outcomes. Consequently, repeated LANDIS runs of a given scenario based on a different sequence of random numbers generally result in differences in the exact timing and location of disturbance events, and, hence, in the associated forest conditions at a given place and time. We initially performed five LANDIS runs of each scenario using a different sequence of random numbers for each and compared the results. We discovered that although there were differences in the maps for projected future conditions, the differences in aggregate landscape statistics were small for repeated runs of the same scenario. The coefficient of variation among multiple runs of a single scenario was generally less than 5% for length of edge, area of forest by age class, area by species group, and core area of mature forest. Although inclusion of all iterations of the landscape

simulation would have provided a slightly more complete representation of environmental stochasticity, we applied the habitat suitability and population viability models described in subsequent sections to one set of paired simulations that used the same sequence of random numbers to govern stochastic elements of the LANDIS simulations.

2.3. Quantifying habitat quality

Although LANDIS allows >1 age class of >1 tree group to occur within a raster cell, in our habitat model we assumed forest characteristics were best represented by the oldest age class of the dominant tree group. It is reasonable to view information from LANDIS as a surrogate for forest type and size class, and we wanted to develop a habitat model that also could be applied to other sources of landscape data (e.g., from other forest simulators, remotely sensed images), many of which provide only information about cover types and tree size classes. Dominance was calculated in LANDIS as the age of the oldest trees present within a tree group divided by the longevity of that tree group (He et al., 2003). For example, 50-year-old pines with a longevity of 250 years were dominant to 60-year-old white oaks with a longevity of 400 years. Henceforth, we use 'tree species' and 'tree group' to mean the dominant tree species group in a cell and 'tree age' to mean the age of the oldest trees of the dominant species group in a cell.

We developed an HSI model for ovenbirds in our study area (Larson et al., 2003). Ovenbirds are small neotropical migrant songbirds that breed in Missouri. They are a forest-dwelling species that builds nests and forages for invertebrates on the ground (Van Horn and Donovan, 1994). We selected ovenbirds as a model species because they respond to landscape structure (i.e., patch size and edges with nonhabitat), they represent species whose habitat consists of late-successional hardwoods, and they are of some conservation concern as nongame birds.

The habitat model for ovenbirds related three primary variables to the suitability of nesting cover and foraging habitat on a 0–1 index scale. Suitability increased approximately linearly with tree age between approximately 10 and 50 years and was slightly greater on mesic ecological land types than xeric ecological land types containing trees of the same age. We based

ecological land type categories on a classification for the Mark Twain National Forest (Miller, 1981; Larson et al., 2003). The second variable identified cells dominated by pines as not suitable for ovenbirds. The third variable reduced habitat suitability by half within 30 m of an edge with nonhabitat defined by a value of 0 for the first variable (i.e., tree age by land type). This application of the third variable was likely to bias habitat suitability low around gaps in the forest canopy caused by small disturbances (e.g., tree mortality), but it is unknown how large a forest opening needs to be to reduce nesting or foraging success in ovenbirds. Habitat suitability was not reduced near edges with cells dominated by pines because edges between forest types have not been shown to affect habitat suitability for ovenbirds.

Each cell received a suitability index (SI) score on a 0–1 scale for each of the three variables. The HSI value of a cell was the product of the three SI scores because the second and third variables simply modified the suitability of appropriately-aged forest. Optimal habitat (i.e., HSI = 1) occurred on mesic forest sites that contained hardwoods ≥50 years old and that were >30 m from a nonhabitat edge.

We created upper and lower limits for ovenbird habitat suitability by simultaneously changing parameter values in the three variables of the HSI model, using a simplified application of the method described by Burgman et al. (2001). Assumptions for the lower limit were that tree age limits for a given SI value were 10 years greater than in the original model and the negative edge effect extended twice as far (60 m) from edges with nonhabitat. Assumptions for the upper limit were that tree age limits were 10 years less, pines and hardwoods provided equally good habitat, and the 30-m edge effect reduced habitat quality by 20% rather than 50%. We applied all three versions of the HSI model to the output from the forest management simulations.

2.4. Population viability

2.4.1. Model structure

We used RAMAS GIS to model ovenbird population trajectories under the two forest management scenarios. The modified Leslie matrix model was for females only, included two stages, and was based on a post-breeding census and annual time steps (Noon and Sauer, 1992). The first stage consisted of young of the year (hereafter referred to as juveniles) and was

not counted in population censuses to simulate survey methods for breeding birds, which generally do not count young of the year (usually nestlings at the time of surveys). The second stage consisted of "adult birds" ≥1-year-old. We parameterized the stage matrix based on published values for survival and fecundity, some of which were estimated on our study site. Annual adult survival was 0.62 (Donovan et al., 1995; DeSante et al., 1998; Porneluzi and Faaborg, 1999). We assumed that juvenile survival was half that of adults, an assumption commonly used in the absence of empirical values for juvenile migrant songbirds (Ricklefs, 1973; Greenberg, 1980; May and Robinson, 1985). We used a fertility rate of 1.4 female fledglings per female (Donovan et al., 1995; Porneluzi and Faaborg, 1999) for both stages because stage-specific fertility rates are not known for ovenbirds and likely do not vary greatly in migratory songbirds (Noon and Sauer, 1992). Because ovenbirds are a neotropical migratory bird, we linked reproductive success and density dependence to habitat conditions simulated on our study site (see Section 2.4.2). We assumed survival was not dependent on simulated habitat conditions, however, because adult survival is generally high during the breeding season (Sillett and Holmes, 2002) and individuals spend only about 4 months on the breeding grounds. We also assumed that the landscape was inhabited by a single population of ovenbirds, that all habitat was available to individuals (i.e., no dispersal barriers), and that there was no immigration or emigration from the population.

The population viability model included both demographic and environmental (i.e., temporal) stochasticity in survival and fertility (i.e., the vital rates). Environmental stochasticity was incorporated by selecting the vital rates for each annual time step from a lognormal distribution defined by its mean and a measure of variation. We used a coefficient of variation ($CV_{temporal}$) of 0.15 for both survival rates (Chase et al., 1997; Sillett and Holmes, 2002) and assumed that environmental stochasticity was twice as great for fledging rates as it was for survival rates (i.e., $CV_{temporal}$ = 0.30). We ran 1000 iterations of the ovenbird population viability model for each of the three potential levels of habitat suitability (i.e., lower limit, best estimate, and upper limit) resulting from the two forest management scenarios.

We used a ceiling-type density dependence mechanism in the population viability model. Population

growth was unaffected by density at abundances below carrying capacity (K). If the abundance of adults increased above K, it was reduced to K. A ceiling-type mechanism was an appropriate function for a territorial songbird, and density dependence based on the logistic growth equation or true contest competition was not compatible with habitat-dependent reproduction in RAMAS GIS.

2.4.2. Habitat dependence

Carrying capacity, initial abundance (N at time = 0, or N_0), and reproductive success were dependent upon habitat suitability, which differed between the two forest management scenarios and across time within each scenario. We assumed K was one adult female/ha, or one breeding pair/ha, if habitat suitability was ideal (i.e., HSI = 1) and that K decreased linearly to 0 as a function of habitat suitability. One pair/ha is approximately three times the observed density in contiguous mature forest in southern Missouri (Thompson et al., 1992; Porneluzi and Faaborg, 1999) and near the upper limit of densities reported anywhere in the ovenbird's range (Van Horn and Donovan, 1994; Holmes and Sherry, 2001). To calculate K we divided the sum of all cell-specific HSI values in the study area by 10, the number of cells in approximately 1 ha. That calculation assumes that each pair requires a territory consisting of ≥ 1 habitat unit, which is the product of the HSI value and the area in hectares. We specified N_0 to be half of the initial K. We also included in the initial population the number of juveniles necessary for a stable age distribution, given the vital rate values.

Reproductive success was linked to habitat quality through fecundity—the product of annual survival and fertility. We assumed that mean fecundity described above occurred on moderately good habitat with an HSI value of 0.7, fecundity was 0 when the mean HSI value was 0, and there was a linear relationship between relative fecundity and the mean HSI value in the study area. The slope of that relationship was 1.43. Use of a mean HSI value in the relationship requires us to assume that ovenbird territories can be sufficiently large to encompass ≥ 1 habitat unit, even in areas with habitat that is isolated or of low quality.

Values for K and relative fecundity were calculated for each map of HSI values, which represented the 10-year time steps of the LANDIS model. Values for K and relative fecundity for years without HSI maps were in-terpolated assuming a linear change in the values during each decade.

2.4.3. Model sensitivity

We analyzed the sensitivity of viability results to values of the following input parameters: survival of adults and fledglings, fertility, CV of vital rates, N_0, K, and the HSI value at which relative fecundity = 1. The sensitivity analysis involved changing parameter values by 10% in the direction that reduced ovenbird viability, and the altered versions of the viability model were applied to the series of best HSI estimates (i.e., not the upper or lower bounds) for the forest management scenario with no tree harvest. Assumptions about fledgling survival, N_0, and the relationship between fecundity and habitat quality were not based on empirical data from our study area, so interpretation of the results should be limited to comparing relative outcomes among simulation scenarios rather than making inferences about the ovenbird population based on the actual value of the quantitative results.

3. Results

3.1. Quantifying habitat quality

Each of the two simulated forest management scenarios resulted in 21 maps representing the starting condition plus twenty 10-year time steps. The area and spatial distribution of tree age classes changed most during the first 100 years of the landscape simulation (S. Shifley et al., unpublished data). The percentage of the landscape dominated by trees in the sawlog age class (>50 years old) in the no harvest scenario increased from 50% to a maximum of 88% in year 40 then decreased to approximately 70% in years 120–200. The maximum composition of sawlog trees in the even-aged management scenario changed less, increasing to 60% in year 20 and decreasing back to approximately 50% for years 60–200 (S. Shifley et al., unpublished data). The percentage of the landscape dominated by pines decreased from 15% during both scenarios and was slightly but consistently greater in the no harvest scenario (Fig. 1).

The spatial distribution of habitat differed by forest management scenario whether the mean HSI values in the landscapes were different (e.g., year 50, Fig. 2) or
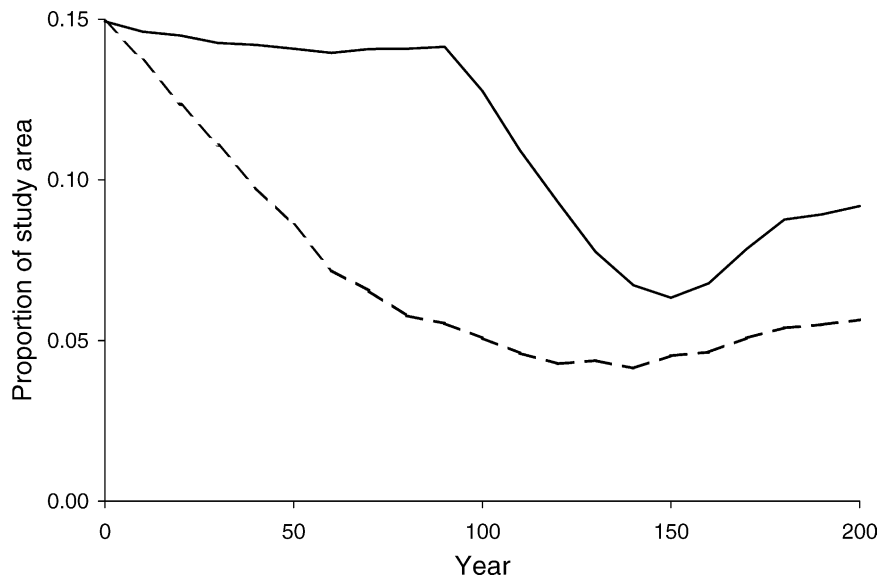
Fig. 1. Temporal trends in the proportion of the southern Missouri study area dominated by pines in the simulated no harvest (solid line) and even-aged (dashed line) forest management scenarios.

similar (e.g., year 100, Fig. 3). Trends in the mean HSI value for the entire landscape, which includes zeros for nonhabitat, were similar to those in the mean HSI value of habitat in the landscape (Fig. 4a) because the proportions of habitat and nonhabitat in the landscape were relatively constant over time (Fig. 4b). In the no harvest scenario, the temporal trend in mean HSI values

was similar to the trend in the area dominated by trees >50 years old.

3.2. Population viability

The stage matrix of the population viability model (i.e., without effects due to stochasticity, habitat

Table 1
Sensitivity of ovenbird population viability modeling results to a 10% change in parameter values using the 'no harvest' forest management scenario

Parameter changed	Parameter value		Abundance (N) in year 200		Median quasi-extinction threshold (N)[a]
	Original	Changed	Mean	S.D.	
None			25146	14843	8887
Adult survival[b]	0.62	0.558	496	1797	70
First-year survival[b]	0.31	0.279	3480	5724	874
Fertility[b]	1.4	1.26	3431	5852	898
HSI threshold[c]	0.7	0.77	3754	6430	884
CV of fertility	0.30	0.33	23431	14786	7704
CV of survival[d]	0.15	0.165	24950	15224	8010
Carrying capacity	45361[e]	40825[e]	22153	13224	8012
Initial abundance	22680	20412	26632	14686	9463

[a] Abundance below which 50% of simulated populations fell during the 200-year interval.

[b] Although the CV remained the same, changes in mean vital rates resulted in changes in their standard deviations.

[c] Habitat suitability index (HSI) value at which relative fecundity was 1.

[d] The change in CV was made to both adult and first-year survival.

[e] Carrying capacity was decreased at all time steps. Parameter values in this table represent year 0.
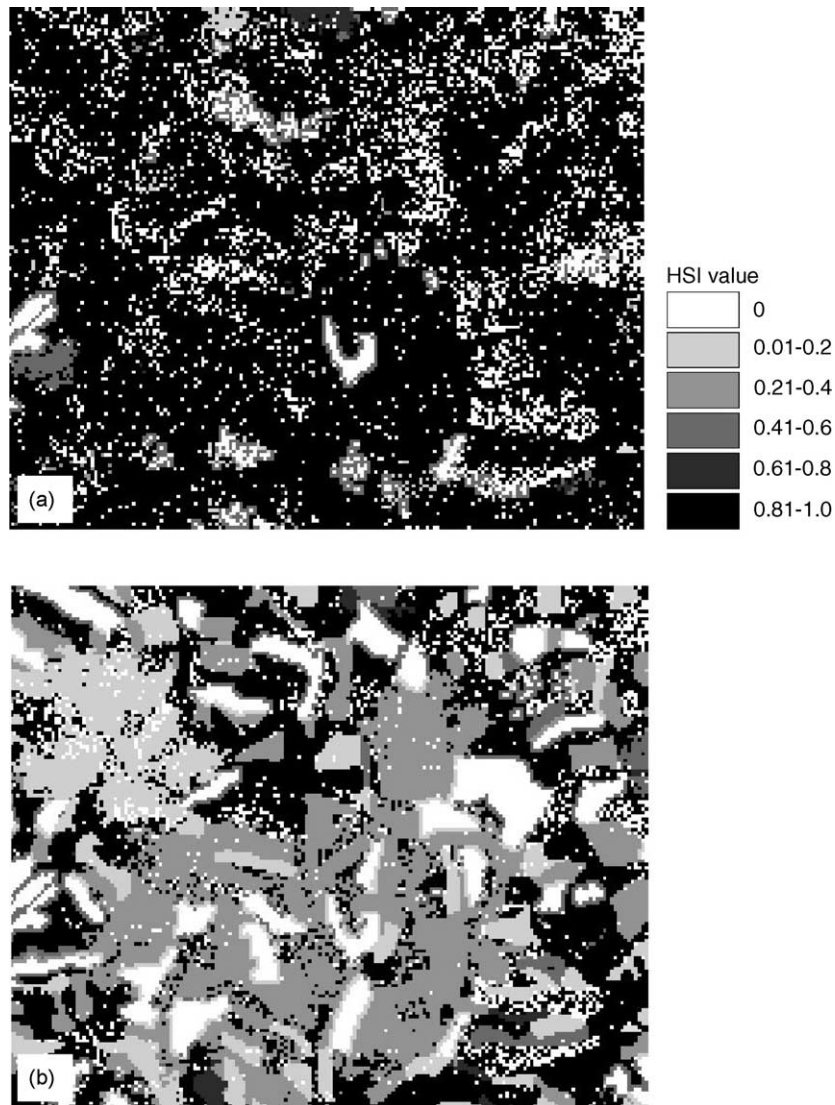
Fig. 2. Ovenbird habitat suitability index (HSI) values in a portion (∼5 km wide) of the southern Missouri study area in year 50 when they differed in magnitude and spatial distribution between the simulated no harvest ((a) mean HSI = 0.74) and even-aged ((b) mean HSI = 0.56) management scenarios.

suitability, and density dependence) indicated a population growth rate of $\lambda = 1.048$, or an annual increase of 4.8%. The viability model, when parameterized for the no harvest management scenario using the best habitat suitability estimates, was most sensitive to changes in the adult survival rate (Table 1). It was nearly equally sensitive to first-year survival, fertility, and the mean HSI threshold at which relative fecundity was 1.

Abundance and viability results from the model were relatively insensitive to changes in carrying capacity, initial abundance, and the temporal variation in vital rates.

Mean simulated populations increased from their initial abundance of $K/2$ at the beginning of all model runs except in the even-aged management scenario when the low habitat suitability estimate was used.
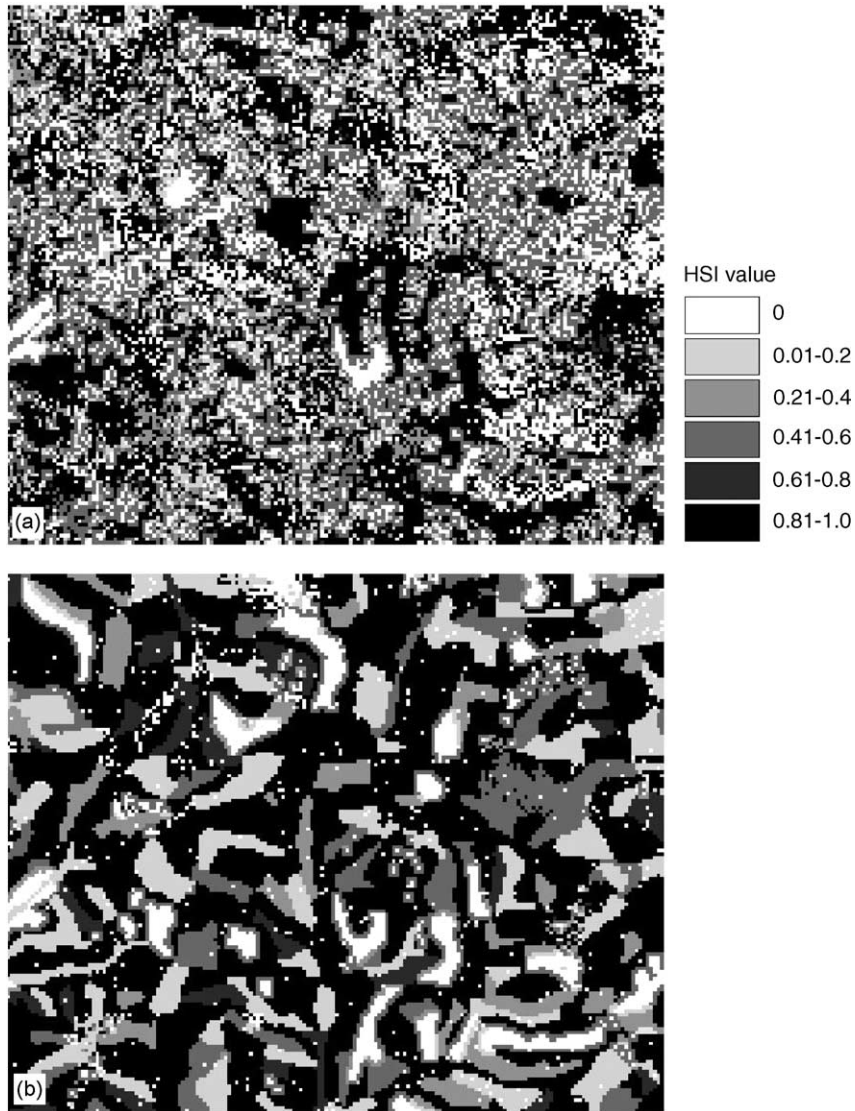
Fig. 3. Ovenbird habitat suitability index (HSI) values in a portion (∼5 km wide) of the southern Missouri study area in year 100 when they were similar in magnitude but were different in spatial distribution between the simulated no harvest ((a) mean HSI = 0.54) and even-aged ((b) mean HSI = 0.56) management scenarios.

When habitat quality was relatively high during the first 70 years of the no harvest scenario, simulated populations were limited by carrying capacity (Fig. 5a). They also responded with increases in abundance, after a lag of approximately 5–10 years, to less substantial increases in habitat quality that occurred in years 130 and 200 of the no harvest scenario. Carrying capacity and the mean HSI value of available habitat were relatively

constant over time in the even-aged management scenario (Figs. 4a and 5b). Simulated populations in the even-aged management scenario, however, increased in abundance initially until year 18, and then they decreased until year 100 before stabilizing at approximately $K/2$ during the second century of the scenario. This indicated that a mean HSI value of 0.65, corresponding to a relative fecundity of 0.93 and a fertility
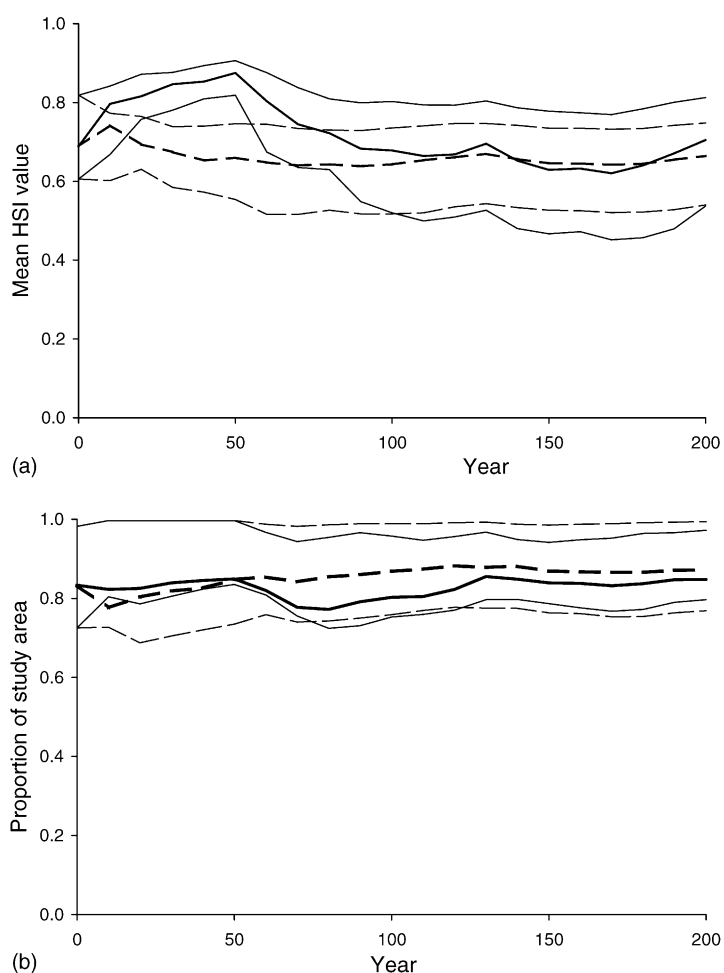
Fig. 4. Temporal trends in (a) mean HSI values and (b) proportions of the southern Missouri study area providing ovenbird habitat under the simulated no harvest (solid line) and even-aged (dashed line) forest management scenarios. Dark lines indicate the best estimate of habitat suitability, whereas light lines indicate upper and lower bounds on habitat suitability estimates.

Table 2
Abundance of adult female ovenbirds after 200 years of simulated forest management

Habitat suitability estimate	Forest management scenario	Percentiles		
		5th	50th	95th
Upper	No harvest	48186	62316	62316
	Even-aged	35491	58725	58725
Best	No harvest	3850	23889	46995
	Even-aged	1954	21267	45715
Lower	No harvest	0	0	12
	Even-aged	0	0	7

Initial abundance was 31,760 for the upper habitat suitability estimate, 22,680 for the best estimate, and 17,365 for the lower estimate.
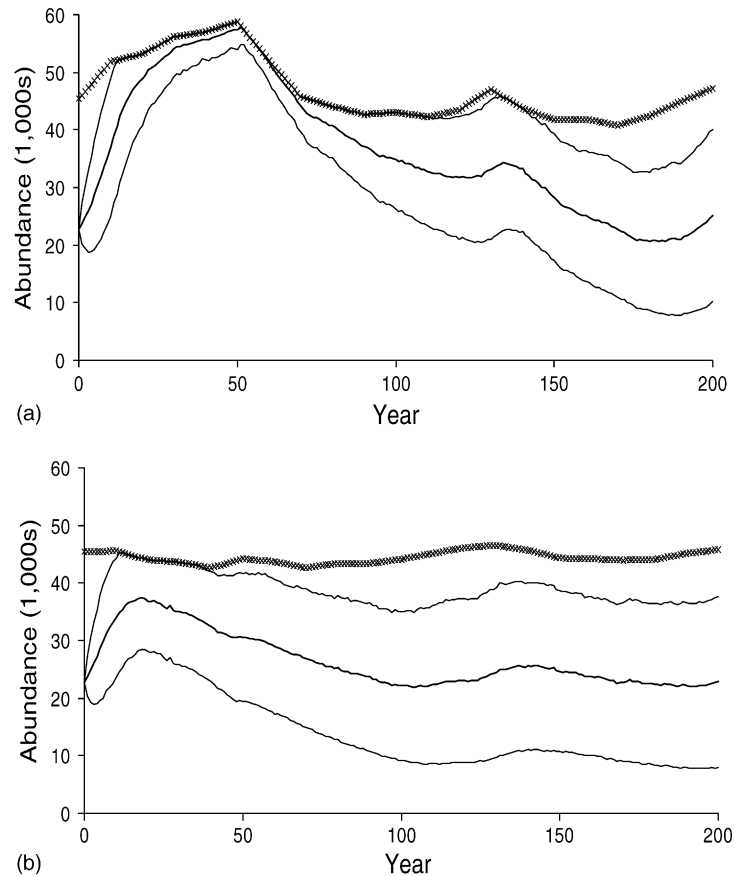
Fig. 5. Temporal trends in simulated abundance of and carrying capacity (×) for ovenbirds in the southern Missouri study area under simulated no harvest (a) and even-aged (b) forest management scenarios. Dark lines are mean abundances, and light lines are ±1 S.D.

rate of 1.3 female fledglings/female, was a threshold between positive and negative population growth.

The abundances of females in simulated populations were consistently but not substantially greater in the no harvest forest management scenario than in the even-aged scenario (Table 2). Abundances differed much more among the three levels of habitat suitability estimates within each scenario (i.e., best estimate and upper and lower bounds). Probabilities of quasi-extinction (i.e., that the abundance of a simulated population was below a specified threshold at some time during the 200-year simulation) also differed more by habitat suitability estimate than by forest management scenario (Fig. 6). The probability that a simulated population went below 5000 adult females was 0.16 greater in the even-aged management scenario than the no

harvest scenario when the best habitat suitability estimates were used. The probabilities under both scenarios, however, were 0.61–0.77 greater when the lower estimate of habitat suitability was used and 0.23–0.39 less when the upper estimate of habitat suitability was used.

4. Discussion

4.1. Effects of tree harvest scenarios on ovenbird viability

Ovenbird habitat quality in the study area differed between the no harvest and even-aged forest management scenarios during the first 100 years but was
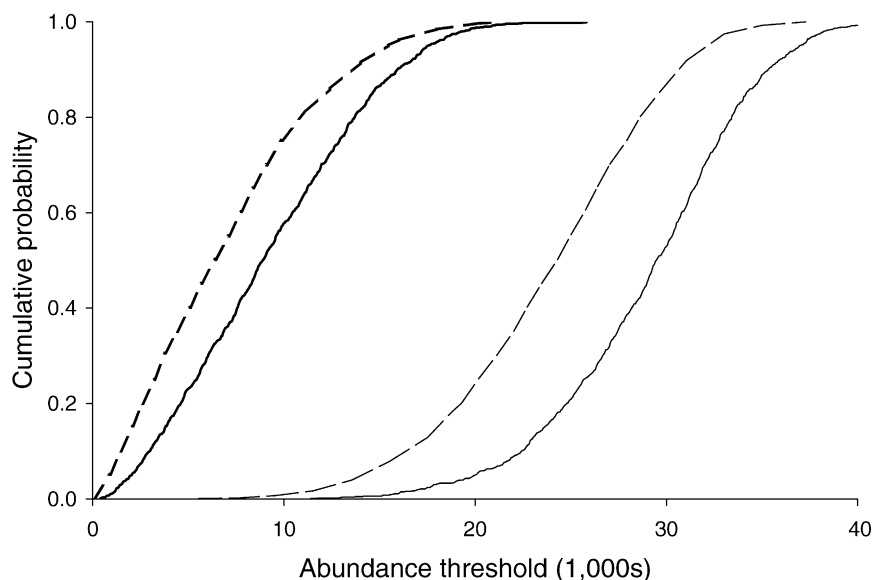
Fig. 6. Probability of quasi-extinction of simulated ovenbird populations in the southern Missouri study area under the simulated no harvest (solid line) and even-aged (dashed line) forest management scenarios. Dark lines are based on the best estimate of habitat suitability, whereas light lines are based on the upper bounds on habitat suitability estimates. Probability of quasi-extinction based on the lower bound on habitat suitability estimates was 1 for thresholds of 100 in the no harvest scenario and 200 in the even-aged management scenario.

similar during the second 100 years. Simulated trees in the unharvested forest aged from the initial condition during the first 50 years and provided increasing habitat quality. Even-aged management largely maintained the initial tree age structure, so habitat quality did not change substantially during that scenario. Habitat quality in the no harvest scenario declined between years 50 and 100 as overstory disturbances due to natural tree mortality, wind, and fire increased both the area dominated by regenerating young trees and the length of edge between habitat and nonhabitat in the study area.

Despite the relatively short-term effects of simulated forest management on tree age structure and ovenbird habitat quality, the viability (i.e., quasi-extinction probability) of the simulated ovenbird populations was noticeably lower under the even-aged management scenario. The PVA results, however, do not support a conclusion that clearcut tree harvests should be eliminated if maximizing ovenbird viability is the management goal because uncertainty is so great in the estimation of habitat suitability. Even if the range of ovenbird viability between the upper and lower bounds on HSI values were half as conservative (i.e., wide),

the range would still be greater than the difference in viability between the forest management scenarios.

Results of the ovenbird HSI model, and therefore the PVA model, were sensitive to the assumption that negative edge effects occurred around a forest opening as small as a single 30 m × 30 m cell. It is unknown how large an opening in a contiguous forest needs to be to cause edge effects. If it is larger than 0.09 ha, the numerous but relatively small tree-fall gaps that occurred after year 50 in the no harvest scenario should not have reduced ovenbird habitat suitability as much as they did in our models.

4.2. Demonstration of the modeling approach

We demonstrated the use of three successive stages of modeling in a comprehensive analysis of a practical management question. Each stage has its benefits and limitations. Many criticisms of models are due to the fact that models are imperfect representations of reality and require several assumptions to be valid before inferences about the real world can be made from their results. Landscape, habitat, and viability models rely on assumptions that their initial conditions, or

input data, are accurately portrayed and that the data and processes incorporated in the models are sufficient to address the management question. Uncertainty exists in both the structure (i.e., which variables are and are not included) and parameterization (i.e., the values assigned to the variables) of our models. Results from models like the ones we described, therefore, are more appropriately interpreted in relative rather than absolute terms. Whereas the specific projected landscape condition, habitat quality, or wildlife abundance in some future year is quite uncertain, comparison of the results among alternative scenarios allows stronger inference because the uncertainties are at least consistent among the scenarios.

More specifically, our GIS-based habitat model relies on the assumption that potentially important microhabitat features, such as ground cover, are adequately represented by larger scale variables, such as ecological land type and the age and species of overstory trees. Furthermore, we assumed that the overstory trees on a raster cell were adequately characterized by a single species and age. Tree age is indicative of general forest size classes (i.e., seedling, sapling, pole, sawlog, old growth) and these have been shown to be related to habitat for neotropical migrant birds (Thompson et al., 1992). Age-dependent size classes are also indicative of stages of stand development (e.g., stand initiation, stem exclusion, understory reinitiation) that are associated with properties of vegetation structure (Johnson et al., 2002).

True validation of habitat models is difficult and rarely conducted, which increases the importance of providing an assessment of uncertainty in, or sensitivity of, the model (Bender et al., 1996; Burgman et al., 2001). We assessed uncertainty in the parameterization of the variables in the habitat model but not uncertainty in the structure of the model (i.e., which variables were included and excluded).

Our population viability model for ovenbirds was as sensitive to the relationship between fecundity and habitat suitability as it was to rates of first-year survival and fertility itself. Habitat-based viability models and the wildlife studies they support, therefore, would benefit greatly from improving the accuracy and precision of habitat suitability estimates. Morrison (2001) recommended that wildlife scientists should focus habitat studies on specific resources and the factors that may limit a species' ability to use them. We recommend

that habitat studies also attempt to quantify the relationships between the availability of critical resources and wildlife fitness parameters (e.g., survival and fecundity) that are used directly in PVAs.

The benefits of the modeling process we demonstrated outweigh the potential limitations. Landscape simulation models are sufficiently sophisticated to realistically project the effects of disturbances and land use patterns on spatially explicit landscape structure and composition. Such simulations represent a significant advancement over other means of evaluating potential landscape change. Whereas assuming linear increases or declines in the amount of habitat may be useful in a PVA (Akçakaya and Raphael, 1998), other PVAs have benefited from incorporating specific forest management simulations (Liu et al., 1995; Moore et al., 2000). Benefits of using LANDIS to simulate landscape conditions for analysis of wildlife habitat include its user-defined spatial resolution, which can be quite high, and its specific accounting of multiple tree age classes and species groups within a raster cell. Such detailed landscape information gives wildlife biologists the flexibility to aggregate the information in a variety of ways and only to the extent necessary for specific needs. For our ovenbird models we summarized the tree data in each cell as the age of the oldest trees of the dominant species group. Habitat models for other species may require the use of more specific tree data available from LANDIS, whereas other habitat models may require aggregating data among adjacent cells (e.g., to define homogeneous cover types for forest stands).

Landscape-scale HSI models can incorporate important landscape structure and composition variables, such as habitat patch size, edge effects, and the juxtaposition and interspersion of habitat requisites. Habitat models implemented in a GIS allow scientists to view and analyze spatial and other statistical variation in HSI values across a landscape. Furthermore, our raster-based landscape and habitat models were not constrained by arbitrary or static patch boundaries, such as compartment or stand boundaries that are larger than the raster resolution. Habitat models, as current best summaries of wildlife–habitat relationships, produce useful and often realistic representations of habitat quality. Models that quantify habitat quality, rather than simply identify habitat and nonhabitat, are especially well suited for linking population viability to environmental (i.e., landscape) conditions.

In fact, habitat-based PVA models integrate spatial and temporal dynamics of habitat quality into the concepts of primary management interest, wildlife population dynamics and viability. Roloff and Haufler (1997, 2002) developed an approach to account for variable contributions to population viability made by home ranges that vary in size and quality. Their approach is an improvement over the use of a mean HSI value from an entire landscape in habitat–viability relationships, as we did using RAMAS GIS, because two landscapes with the same mean HSI value may result in drastically different levels of population viability. For example, a landscape with contiguous patches of high quality habitat may support higher population growth rates than a landscape with more habitat, if the habitat is fragmented or is of relatively low quality. Metapopulation structure and dispersal between isolated habitat patches can also be incorporated in habitat-based PVA models. Successful integration of habitat and viability information, however, requires specification of functional relationships between habitat quality and demographic parameters. We used linear relationships between habitat suitability and demography similar to those used by Akçakaya and Raphael (1998), whose PVA model incorporated habitat-dependence in carrying capacity, fecundity, and survival rates. In a slightly different modeling framework, Moilanen and Hanski (1998) used more sophisticated statistical functions to link habitat features to probabilities of extinction and colonization in an incidence function metapopulation model. Selected functional forms of the relationships between habitat quality and demographic parameters are usually limited by our knowledge of the processes involved, but ideally, the functions would be known and well understood.

Combining landscape, habitat, and viability models in a single analysis provides benefits beyond those of the individual modeling stages. A comprehensive analysis encompasses all components and processes of interest. If population viability is the management objective, it is insufficient to assess only changes in the landscape and their effect on habitat quality. It would also be much less informative to assess the effects of forest management on wildlife population viability by simply making assumptions about differences in forest structure and composition among management strategies than by conducting useful landscape simulations. Combining all 3 models also facilitates the propagation of uncertainty in the results. As was evident in our ovenbird example, conclusions based on the mean results from a single modeling stage may be different than conclusions based on results that account for uncertainty in the output of the previous stage of modeling. A comprehensive approach allows direct comparison of the relative levels of uncertainty in each stage of modeling. A PVA model may be most sensitive to uncertainty in estimates of vital rates, but if the PVA model was based on habitat quality, one might conclude that improving the habitat model would have a larger impact on increasing precision in the PVA results. Finally, the approach allows analysis of the economic benefits and costs of different land use plans (Marzluff et al., 2002), which may be affected by landscape management, habitat manipulation, and wildlife conservation efforts.

5. Conclusions

Using population viability, habitat suitability, and landscape simulation models in an integrated analysis for conservation planning is an important advancement because habitat quality is a critical link between human land use decisions and wildlife population viability. Benefits of this approach are currently limited by our understanding of wildlife–habitat relationships. The validity of habitat suitability models may be questionable, and the direct effects of variation in habitat suitability on wildlife vital rates are often unknown. It is important, therefore, that model users evaluate these uncertainties and make them explicit, so model results can be interpreted appropriately. Despite potential limitations, the modeling approach we demonstrated provides significant benefits. The effect of land use on the viability of wildlife populations is a common management concern. A comprehensive modeling approach can address the entire concern in the quantities of primary interest, namely wildlife abundance and viability, thereby avoiding partial answers, which may be misleading.

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