

Assessing Risks to Biodiversity from Future Landscape Change

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Abstract: We examined the impacts of possible future land development patterns on the biodiversity of a landscape. Our landscape data included a remote sensing derived map of the current habitat of the study area and six maps of future habitat distributions resulting from different land development scenarios. Our species data included lists of all bird, mammal, reptile, and amphibian species in the study area, their habitat associations, and area requirements for each. We estimated the area requirements using home ranges, sampled population densities, or genetic area requirements that incorporate dispersal distances. Our measures of biodiversity were species richness and habitat abundance. We calculated habitat abundance in two ways. First, we computed the total habitat area for each species in each landscape. Second, we calculated the number of habitat units for each species in each landscape by dividing the size of each habitat patch in the landscape by the area requirement and summing over all patches. Species richness was based on presence of habitat. Species became extinct in the landscape if they had no habitat area or no habitat units, respectively. We then computed ratios of habitat abundance in each future landscape to habitat abundance in the present for each species. We also computed the ratio of future to present species richness. We then calculated summary statistics across all species. Species richness changed little from present to future. There were distinctly greater risks to habitat abundance in landscapes that extrapolated from present trends or zoning patterns, however, as opposed to landscapes in which land development activities followed more constrained patterns. These results were stable when tested using Monte Carlo simulations and sensitivity tests on the area requirements. We conclude that this methodology can begin to discriminate the effects of potential changes in land development on vertebrate biodiversity.

Evaluación de Riesgos para la Biodiversidad Debido a Cambios Futuros en el Paisaje

Resumen: Examinamos los impactos en la biodiversidad de un paisaje debidos a posibles patrones de modificación del suelo. Nuestros datos de paisaje incluyen un mapa del área de estudio actual derivado de sensores remotos y seis mapas de distribuciones futuras del hábitat que resultan de diferentes escenarios de desarrollo del suelo. Nuestros datos de especies incluyen listas de todas las especies de aves, mamíferos, reptiles y anfibios del área de estudio, sus asociaciones de hábitat y los requerimientos de espacio para cada una de ellas. Estimamos los requerimientos de área usando rangos de hogar, densidades de poblaciones muestreadas o requerimientos genéticos de área que incorporan distancias de dispersión. Las medidas de biodiversidad fueron la riqueza de especies y la abundancia del hábitat. La abundancia del hábitat fue estimada en dos formas. Primero, estimamos el área total del hábitat para cada especie en cada paisaje. Segundo, calculamos el número de unidades de hábitat para cada especie en cada paisaje dividiendo el tamaño de cada parche de hábitat en el paisaje por el requerimiento de área y sumando para todos los parches. La riqueza de especies

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se basó en la presencia de hábitat. La extinción de especies en un paisaje ocurrió cuando la especie no tenía área de hábitat o unidades de hábitat respectivamente. Posteriormente estimamos la proporción entre la abundancia del hábitat en cada paisaje futuro y la abundancia de hábitat en el presente para cada especie. También estimamos la proporción entre riqueza de especies futura y presente. Se desarrolló un resumen estadístico para todas las especies. La riqueza de las especies cambió poco del presente al futuro. De cualquier manera, existieron grandes riesgos distintivos para la abundancia de hábitat en paisajes que fueron extrapolados a partir de tendencias actuales o patrones de zonificación opuestos a paisajes en los cuales las actividades de desarrollo siguieron patrones restringidos. Estos resultados fueron estables al ser evaluados usando simulaciones Monte Carlo y pruebas de sensibilidad para requerimientos de áreas. Concluimos que esta metodología puede iniciar la discriminación de efectos en la biodiversidad de vertebrados debido a cambios potenciales en el desarrollo del suelo.

Introduction

Land-use practices are a major cause of the decline in biodiversity in recent decades (Soulé 1991). Conservation efforts have focused on maintaining biological diversity primarily by minimizing exposure to human activities through establishment of networks of protected areas. Gap Analysis (Scott et al. 1987, 1993) is a comprehensive approach to assessing conservation needs over large geographic regions. This approach has pioneered the use of vegetation maps, species-habitat associations, and geographic ranges of species to model the predicted distribution of native terrestrial vertebrate species in order to identify "gaps" in biodiversity protection. By overlaying maps of currently protected areas, Gap Analysis determines the number of species currently not protected. The long-term conservation of biological diversity is dependent not only on establishment of protected areas, however, but also on maintaining hospitable environments and viable populations within managed landscapes (Noss & Harris 1986; Western 1989; Hansen et al. 1991; Shafer 1994).

Impacts of habitat loss and fragmentation associated with some land-use practices, for example, agriculture, have been well studied for some species, particularly birds, in remnants of native vegetation (e.g., forests, marshes, prairies) (Freemark 1995; Martin & Finch 1995). Only a few recent studies, however, have attempted to systematically and quantitatively assess risks to biodiversity at the landscape scale. Best et al. (1995) used species-habitat associations to assess the impact of different agricultural landscapes on numbers of bird species potentially nesting in Iowa farmland. Hansen et al. (1993) developed an approach to identify bird species at risk in forests in western Oregon and Washington at present and under four disturbance-management scenarios over a 140-year period. They used habitat maps, species-habitat associations, and other natural history characteristics of species to quantify habitat suitability for each bird species. For present conditions species at risk were inferred from shortages of suitable habitat. Risks posed by alternative futures were inferred from patterns of habitat diversity and richness.

Methods are needed for predicting potential impacts of human activities on biological diversity across a hierarchy of spatial and temporal scales to make land use planning both clearer and better informed (Hansen et al. 1993; Dale et al. 1994; Freemark 1995). We present an approach for estimating potential risk to biodiversity from future landscape change associated with land development. The essential components of the approach are (1) a large, representative sample or enumeration of species; (2) natural history characteristics of the species, specifically their habitat and area requirements; (3) a map of habitats; (4) future landscape alternatives that can be mapped as changes in habitat; and (5) a method to assess potential risk posed by future landscapes compared to the present using summary statistics of changes in species richness and habitat abundance.

Geographical Setting

This study was conducted in Monroe County, Pennsylvania, which is approximately 1580 km² in area and lies in the northeastern part of the state (Fig. 1), forming the core of the Poconos region. This region is defined physi-

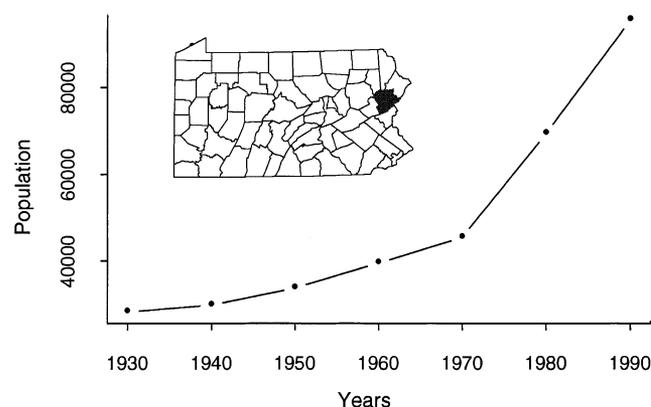


Figure 1. Human population growth in Monroe County, Pennsylvania (US Bureau of the Census 1930–1990). Inset shows the location of Monroe County in Pennsylvania.

cally by the Pocono Plateau, an uplifted sedimentary basin about 600 m in mean elevation at the southern edge of the Wisconsin glaciation. The plateau covers about 40% of the county and is characterized by lakes and forests. In addition to the plateau, the county has two other regions. The region to the east of the plateau is part of the Allegheny uplands, an area similar to the plateau but with a mean elevation of about 300 m. The southern 40% of the county is part of the ridge and valley region of Pennsylvania. The natural history of the Poconos region is described in Oplinger and Halma (1988) and its significance for conservation in Smith and Richmond (1994). Monroe County is divided politically into 20 municipalities comprised of 16 townships and four boroughs. The boroughs are smaller areal units with higher densities of human population. Most land-use decisions are made at the level of the municipalities.

The Poconos region has been a prominent recreation and vacation area since the nineteenth century for people from large metropolitan areas that are within several hours travel time by train or automobile. With the introduction of the interstate highway system in the 1960s and 1970s the number of permanent residents has increased along with recreational use. The population trend for the county shows a noticeable inflection upward at the census of 1970 (Fig. 1). This region represents a classic situation of potential loss of natural habitat due to increased human activities.

Habitat Map and Future Alternatives

Smith and Richmond (1994) prepared a habitat map for the county in conjunction with the Cornell Laboratory for Environmental Applications of Remote Sensing (CLEARS). The source material for the map is a portion of a single Landsat Thematic Mapper scene from 21 June 1991 covering all of Monroe County. The CLEARS registered and classified the TM scene according to standards of the GAP program (Scott et al. 1993); the spatial resolution was 25 m. The final classification contained 13 habitat classes (Table 1).

Six possible alternative versions of the landscape and habitats of Monroe County in the year 2020 were prepared by Steinitz et al. (1994). These came from a study that had the objectives of describing the patterns and significant human and natural processes affecting the landscape of the county, constructing geographic information system models to simulate these processes and patterns, creating changes in the landscape by forecasting and by design, and evaluating how the changes affect pattern and process using the models. The study identified six kinds of issues in the future development of the landscape of the county: geological, biological, visual, demographic, economic, and political. These issues

became the basis for evaluating the existing conditions of the county and developing alternative futures.

The alternative future landscapes were based on a modified version of the Smith and Richmond land-use/land-cover map. Steinitz et al. represented low density residential development more accurately than on the Smith and Richmond map by using digital road data and other sources. They represented wetland areas more accurately than on the Smith and Richmond map by using National Wetlands Inventory maps. With these changes they created a more accurate map of existing conditions in the county. We used this map as the baseline for our biodiversity analysis and called it the "present" landscape (Fig. 2).

The future landscapes described by Steinitz et al. (1994) differed both in degree and spatial distribution of human impact. These landscape alternatives all assumed a doubling of the human population by the year 2020, a projection based on the current rate of growth (Fig. 1). The future alternatives represented different ways in which this population increase might be accommodated. The Monroe County Planning Commission staff assisted Steinitz et al. in preparing the future scenarios. Two future alternatives were derived by extrapolating from current trends and zoning patterns (Fig. 2). The "plan-trend" alternative was based on implementation of the county comprehensive plan of 1981 and extended the pattern of land development that has occurred since that time. This pattern included deviations from the plan in some cases. The "buildout" alternative started with the current zoning plans for each municipality and assumed that the full development allowed in each plan would occur. This alternative represented an extreme level of human impact where most remaining undeveloped, but developable, land in Monroe County would be developed. The only large patches of land not developed in these two future landscapes were existing national park, state park, state forest, and state game lands. By the year 2020 the county would then resemble suburban areas in neighboring New Jersey or near Philadelphia.

Table 1. Number of species in major groups assigned to each habitat class.*

Habitat class	Herps	Birds	Mammals	All verts
Commercial-industrial	1	9	10	20
Residential	12	84	32	128
Agricultural	13	82	41	136
Lacustrine limnetic	14	19	4	37
Lacustrine littoral	22	26	5	53
Palustrine	27	28	14	69
Shrublands (successional)	26	64	38	128
Hemlock	20	53	40	113
White Pine	22	66	42	130
White Pine-hardwoods	27	95	46	168
Oak-heath	28	95	44	167
Sugar Maple-Red Oak	27	101	49	177
Sugar Maple-Ash-Basswood	27	98	49	174

*Smith and Richmond (1994)

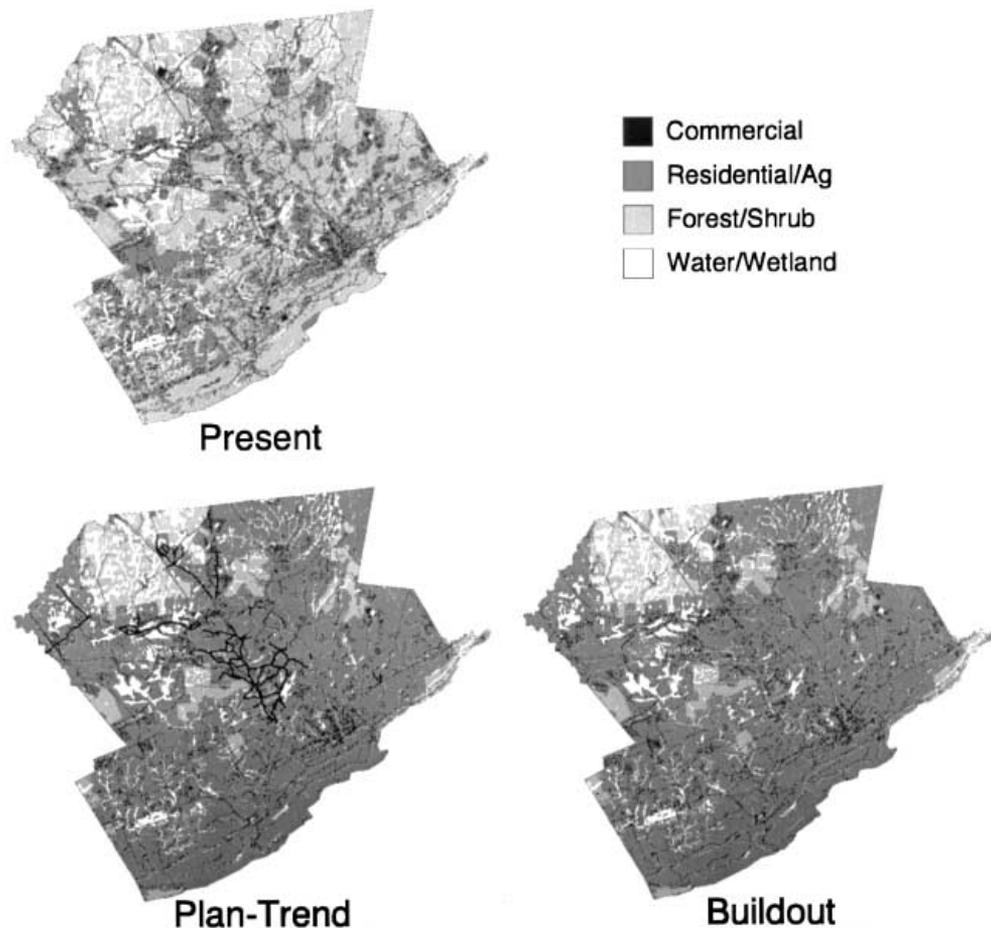


Figure 2. The present landscape and the two future landscapes that extrapolated land development either from the county comprehensive plan (plan-trend) or from current zoning (buildout). The 13 habitat classes were aggregated to 4. Agriculture was less than 4% of total land area and shrublands less than 2% in all landscapes.

Steinitz et al. (1994) presented four other possible ways in which land development in the county could occur (Fig. 3). At the opposite extreme from the plan-trend and buildout alternatives was the “park” future landscape that was predicated on the conservation of all existing undeveloped land, achieved by increasing densities of development in currently developed areas, and using savings in infrastructure costs to purchase development rights on undeveloped land. The three other alternatives attempted to balance development and conservation. The “township” alternative allocated development among the municipalities in accordance with their current development patterns by increasing densities in some cases, and developing new areas that least threatened landscape features in other cases. The “spine” alternative considered a proposal by interest groups in the area to re-establish a rail corridor between Scranton, to the northwest of the county, and the New York metropolitan area to the east. This corridor runs through the center of the county and would become, under this alternative, the focus for development activities. Finally, the “southern” alternative recognized the regional differ-

ences in the county by concentrating new development in the southern ridge and valley portion of the county that is already more developed for agriculture and for more intensive human activities, while conserving most of the northern part of the county.

Species Lists and Species-habitat Associations

Smith and Richmond (1994) prepared lists of vertebrate species (excepting fish) for Monroe County. For bird species, the list was the union of the species lists from the *Pennsylvania Breeding Bird Atlas* (Brauning 1992) for all atlas blocks contained in or intersecting the county. Reptiles and amphibian lists were developed from the dot maps in McCoy (1982) and mammals from range maps in Merritt (1987). These lists contain 40 species of reptiles and amphibians, 153 species of birds, and 55 species of mammals, for a total of 248 species. Smith and Richmond (1994) also prepared a species-habitat association table for all species, interpreting the land-use/land-cover classes as habitats (Table 1). We ex-

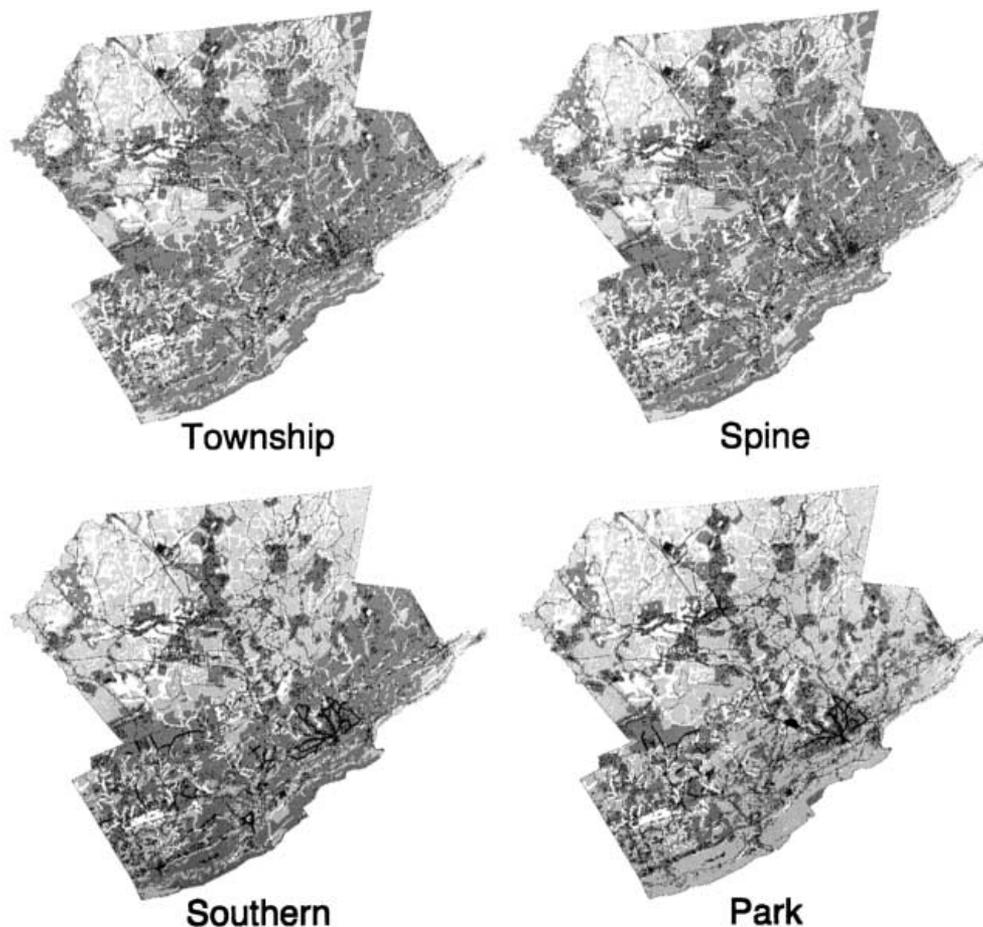


Figure 3. Four future landscapes that incorporated “designed” patterns of land development: township, growth centered in the municipalities; spine, growth along a central rail corridor; southern, south developed, north preserved; and park, intensified in current locations only, remainder conserved. See Fig. 2 for the key.

cluded from our analyses 8 species introduced by humans plus 9 species for which we were unable to obtain area requirements. Therefore we used a total of 231 species: 40 species of herpetofauna, 147 species of birds, and 44 species of mammals.

In mapping the future alternatives, Steinitz et al. (1994) used several classes of residential development and several classes of roads to represent their scenarios more accurately. The total number of classes in the union of their classifications was 35. The Smith and Richmond species-habitat association table, however, only assigned species to the 13 classes on the Smith and Richmond map. Therefore we reduced each of the Steinitz et al maps from 35 classes to 13 by assigning all Steinitz et al. classes to one of the Smith and Richmond classes.

Species Area Requirements

As an initial step toward incorporating a more complete approximation of natural history and demographic characteristics of species, we estimated an area requirement

(Mühlenberg et al. 1991) for the species in our study. Area requirements represent an initial estimate of space required for a reproductive or breeding unit of a species. Breeding units may be individuals (females), a breeding pair, or some set of individuals such as a deme or a colony. We defined area requirements as home ranges, territory sizes, sampled population densities, or dispersal distances, depending on the type of reproductive unit. For each major taxonomic group we consulted appropriate literature and adapted the area requirement concept accordingly. Because the reported area requirements for many species have a range of values, we used both minimum and maximum values for each species; for some species these were the same. Across all species the minimum values and the maximum values ranged from 0.002 to 19,600 ha. The median of the minimum values was 1.1 ha and the median of the maximum values was 5.0 ha.

We based our estimates of area requirements for amphibians and reptiles on reported dispersal distances, assuming that a circle with this distance as diameter would encompass minimal home ranges for breeding, summer

activity, or wintering. We used the following sources in compiling the area requirements for amphibians and reptiles: Society for the Study of Amphibians and Reptiles (1971 et seq.), Berven (1980), Berven and Grudzien (1980), Gregory (1982), Semlitsch (1983), Smith et al. (1983), DeGraaf and Rudis (1986), Halliday and Verrell (1988), and Hardy and Raymond (1991). For species for which there were no reported values, we used phylogenetic criteria to estimate the area requirements. We searched for published references on other species of the same genus, using the single range or average of ranges, depending on the availability of data. For birds, we obtained home range size, sample density, territory size, and diet type from DeGraaf and Rudis (1986). When measured home range sizes were not available, we used sampled population density, and if no density data were available we used territory size (see Ferry et al. 1981). For species for which no data were available, we estimated home range sizes based on regression equations that relate body weight and home range size, following earlier work by McNab (1963), Mace and Harvey (1983), and Holling (1992). We fit separate regressions for carnivore and for non-carnivore species. For mammals we used two compilation sources, Merritt (1987) and DeGraaf and Rudis (1986) for species not adequately covered in Merritt (1987).

Methods of Analysis

The objective of our analysis was to measure the possible changes in species richness and habitat abundance between the present and each of the six future landscapes. We regarded habitat abundance as a potential index of the abundance of breeding units. We examined change in habitat abundance in two ways: first, by using the total habitat area assigned to each species without regard to spatial configuration and, second, by analyzing each patch of habitat for each species using its area requirements. Thus, we used four methods in our analysis: (1) species richness using habitat area only; (2) species richness using area requirements; (3) habitat abundance using habitat area only; and (4) habitat abundance using area requirements.

A principal objective of our work was to develop a quantitative assessment of risk to biodiversity. We formulated this risk as $1 - (\text{future biodiversity}/\text{present biodiversity})$, obtaining a proportion of biodiversity as measured by one of our methods, at risk in the future. We applied this risk formulation using all of our methods (Table 2). For methods 1 and 3, we examined the change in area of habitat assigned to each species between the present and the future. If habitat disappeared completely in a future landscape, the species was assumed to suffer local extinction, and the species richness for the study area in that landscape was decreased

Table 2. Symbolic descriptions of algorithms for computing comparative risk scores for species richness and habitat abundance using habitat area only and using area requirements.

<i>Formulas</i>	
Habitat abundance using habitat area only	
$\forall_i \forall_s:$	$b_{i,s} = \sum_c a_{i,c} \cdot i_{c,s}$
Habitat abundance using area requirements	
$\forall_i \forall_s:$	$b_{i,s} = \sum_h \text{floor}(a_{h,s,1}/r_s)$
Proportion of habitat abundance at risk (either method)	
$\forall_i \forall_s:$	$p_{f,s} = b_{f,s}/b_{0,s}$
$\forall_f:$	$k_f = 1 - \exp(\text{mean}[\ln(\mathbf{p}_f)])$
Proportion of species richness at risk (either method)	
$\forall_i:$	$n_i = \sum_s (\text{if } b_{i,s} > 0 \text{ then } 1 \text{ else } 0)$
$\forall_f:$	$j_f = 1 - n_f/n_0$
<i>Symbols</i>	
\forall	universal quantifier (i.e., for all elements...)
l	indexes all landscapes
0	indexes present landscape
f	indexes future landscapes (1/0)
s	indexes all species (or classes of species)
c	indexes habitat classes
h	indexes habitat patches
$i_{c,s}$	indicator variable for a species in a habitat class (0 = absent; 1 = present)
$a_{i,c}$	area of a habitat class in a landscape
$a_{h,s,1}$	area of a habitat patch for a species in a landscape
r_s	area requirement of a species
$b_{i,s}$	habitat abundance of a species in a landscape
$p_{f,s}$	proportion of species' present habitat abundance in a future landscape
\mathbf{p}_f	vector of proportions of all species' present abundances in a future landscape
k_f	risk to habitat abundance in a future landscape
n_i	number of species in a landscape
j_f	risk to species richness in a future landscape
floor	largest integer not greater than
exp	exponential function
mean	population mean
ln	natural logarithm

(method 1). Otherwise, the habitat abundance for the species was the sum of the area of each habitat class assigned to the species (method 3).

Methods 2 and 4 started with the creation of a map of habitat for each species by aggregating all habitat classes assigned to it. Our model assumed that each habitat patch of connected pixels could potentially be filled with habitat units, that is, units large enough for breeding, for the species according to its area requirement. Patches of a size less than the area requirement would have no habitat units for a species and larger patches would have the number of habitat units that could be completely contained in the patch. A species became extinct in a landscape if there were no habitat units for it (method 2). The abundance of habitat units for a species in a landscape was the sum of the habitat units for all patches (method 4).

For methods 3 and 4, we converted the habitat abundances of each species in each landscape to comparative summary measures. First we calculated the proportion of habitat abundance for each species in each future

landscape relative to the abundance in the present landscape. Next we calculated summary statistics for these proportions. Because the skewed empirical distributions of the proportions appeared approximately lognormal, we transformed the proportions using natural logarithms. We then computed the mean for the set of species for each landscape of the transformed proportions. Next, we transformed the means in the logarithm scale back to geometric means on the original scale. The geometric mean of each set of proportions was used as the measure of central tendency. The final step was to subtract each geometric mean from 1.0 to obtain a measure of risk.

We performed several tests to examine the reliability of the area requirements. The first set of tests was a sensitivity analysis of the results using a Monte Carlo simulation of the effects of measurement errors in the area requirements. The parameters for these analyses were the number of repetitions of the simulation and the standard deviation of normally distributed measurement errors that were added to the logarithms of the area requirements. We used this model of measurement error because we suspect, although we have no way of knowing for certain, that these errors are multiplicative rather than additive, that is, they are proportional to the magnitude of the area requirements. For each repetition of the simulation we first produced a randomly perturbed version of each species' area requirement by adding the measurement error to the natural logarithm of the original area requirement. Next we transformed the perturbed area requirements from logarithm scale back to the original abundance scale with the exponential function. Then we conducted the analysis as described in Table 2. We performed this Monte Carlo simulation for a range of values of the standard deviation, with little change observed in the results. For the results reported here we used 1000 repetitions of the simulations and a standard deviation of 2.0 for the measurement errors. This value for the standard deviation corresponds to a coefficient of variation of about 7.3 (Gilbert 1987), or 730%, a substantial degree of variation.

In addition we conducted sensitivity tests in which we multiplied the minimum and maximum area requirements by several factors. For this series of tests we multiplied the minimum area requirements by 0.1 and 0.5, and the maximum area requirements by 2 and 10. In both the Monte Carlo simulations and the multiplicative sensitivity tests we estimated both species richness and habitat abundance.

Results

There was substantial change in mapped habitat classes from the present to the future landscapes (Fig. 4). The dominant changes were the increase in residential and the decrease in forest classes. Agriculture and shrubland

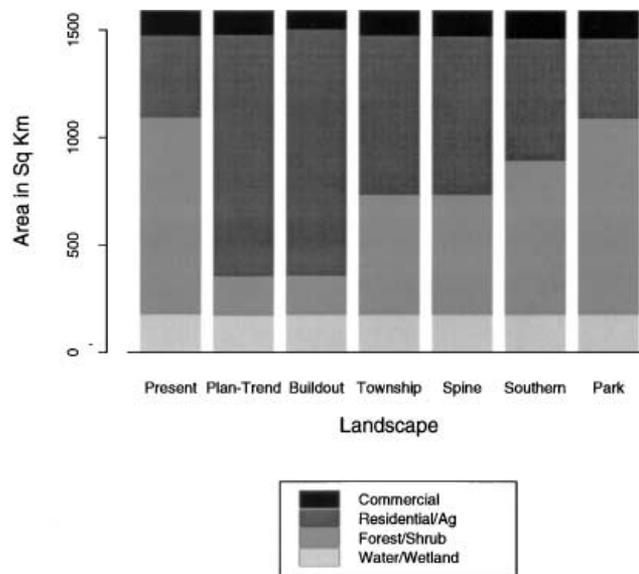


Figure 4. Area in each of four aggregated habitat classes for the present and future landscapes.

classes were small proportions of all landscapes. Future landscape buildout showed the greatest change and park the least. These changes may be significant in themselves but say nothing directly about species richness or habitat abundance.

When we measured changes in species richness using either method 1 or 2, we found little change from landscape to landscape, and in particular little or no change from present to future. Thus the risks for each taxonomic group for each of the future landscapes were either zero or very close to zero. Because species were eliminated in method 1 when no pixels of its habitat remained and because each landscape had at least one pixel of each habitat class, the risks using this method were all zero. In method 2 small numbers of species were eliminated (Table 3, columns 3 and 6). The species eliminated, however, were nearly constant across all landscapes including the present. Using the set of minimum area requirements, one bird species was eliminated. Using the set of maximum area requirements, two bird species and either two or three mammal species were eliminated. Because there was at most a change of one species in the total vertebrate species list between present and future, the risks were very close to zero.

Using methods 3 and 4, we found the risks to habitat abundance to be positive and of varying magnitude both across landscapes and across taxonomic groups. Results from method 3 were consistent with the expectation that the more modified landscapes would show the greatest risks to species habitat (Fig. 5). In no case were risks less than zero, which would imply an average gain in habitat rather than loss. (Certain species, however, had increased habitat, particularly those assigned only to the

Table 3. Number of species not supported by at least one habitat unit in sensitivity tests.*

Landscape	Herpetofauna								Birds							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Present	0	0	0	0.0	0.7	0	0	1	0	0	1	2.2	6.1	2	4	13
Plan-trend	0	0	0	0.1	1.0	0	1	4	0	1	1	2.8	6.0	2	5	12
Buildout	0	0	0	0.1	1.0	0	1	4	0	1	1	2.8	6.0	2	5	12
Township	0	0	0	0.0	0.9	0	0	1	0	0	1	2.3	5.8	2	4	13
Spine	0	0	0	0.0	0.9	0	0	1	0	0	1	2.3	5.8	2	4	13
Southern	0	0	0	0.0	0.8	0	0	1	0	0	1	2.2	5.7	2	4	13
Park	0	0	0	0.0	0.7	0	0	1	0	0	1	2.2	6.1	2	4	13

Landscape	Mammals					All Vertebrates										
	1	2	3	4	5	1	2	3	4	5						
Present	0	0	0	0.5	2.7	3	3	5	0	0	1	2.8	9.5	5	7	19
Plan-trend	0	0	0	0.4	2.1	2	3	3	0	1	1	3.3	9.2	4	9	19
Buildout	0	0	0	0.4	2.1	2	3	3	0	1	1	3.3	9.1	4	9	19
Township	0	0	0	0.6	2.7	3	3	5	0	0	1	2.9	9.4	5	7	19
Spine	0	0	0	0.6	2.7	3	3	5	0	0	1	2.9	9.4	5	7	19
Southern	0	0	0	0.6	2.7	3	3	5	0	0	1	2.8	9.3	5	7	19
Park	0	0	0	0.5	2.7	3	3	5	0	0	1	2.8	9.6	5	7	19

*The tests are labeled 1 = 0.1 · minimum; 2 = 0.5 · minimum; 3 = minimum; 4 = mean of Monte Carlo on minimums; 5 = mean of Monte Carlo on maximums; 6 = maximum; 7 = 2 · maximum; and 8 = 10 · maximum.

residential class). The park alternative had the lowest risks because it most closely approximated the present. The township and spine alternatives performed somewhat worse than the southern alternative. Plan-trend and buildout had the greatest risks. Among taxonomic groups, herpetofauna had the greatest risks followed by mammals and then birds. The highest magnitude risk to habitat across all groups and landscapes was over 50% for herpetofauna in plan-trend and buildout. Results using method 4 with minimum area requirements were very similar to those of method 3; results using method 4 with maximum area requirements were only slightly less so (Fig. 5).

We also conducted a supplemental analysis asking the question of how many species were improving, declining, or remaining about the same with respect to change in habitat abundance. To examine this effect we calculated

$$\ln \left(\frac{\text{habitat abundance for species}_i \text{ in future}_i}{\text{habitat abundance for species}_i \text{ in present}} \right)$$

for each species in each future landscape, using data from method 4, and plotted histograms of these values by landscape (Fig. 6). These histograms show a consistent pattern with a set of species declining (values less than zero), a set improving (values greater than zero), and a set remaining about the same (close to zero). The only future landscape not showing this pattern was park, in which there was very little change. If we demarcate the divisions between these groups by the distinct breaks in the histograms and count the number of species in each group, the results are quite consistent

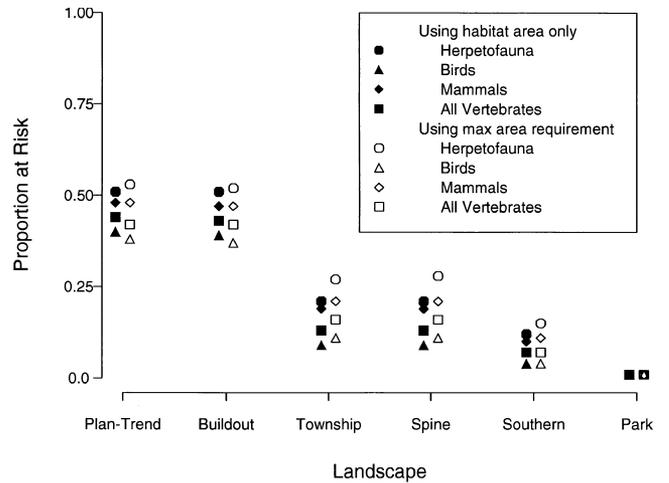


Figure 5. Risk to terrestrial vertebrate habitat, by future landscape and by taxonomic group, estimated using total habitat area only (method 3) and using maximum area requirements (method 4).

across landscapes. In all future landscapes (except park), 28 species improved. In plan-trend and buildout, 92 species declined and in township, spine, and southern, 85 species declined. By this analysis, plan-trend and buildout had slightly greater effects on species decline (3.3 times as many species declining compared to improving) than the other three landscapes (a ratio of 3.0).

The results were not strongly affected by perturbations in the area requirements in our sensitivity tests (Table 3). Changes in species richness were greater than 5% only in the sensitivity test that multiplied the maximum area requirements by a factor of 10 (Table 3, column 8). In that test approximately 8% of the total number of terrestrial vertebrate species suffered local extinction. Furthermore, total vertebrate species richness was not affected differentially across landscapes by these sensitivity tests. That is, the numbers of species (of all terrestrial vertebrates) lost differed at most by one between the present and all six future landscapes. Within taxonomic groups there were larger differences in some cases. For example, in the 10 times maximum test, three more herpetofauna species were lost in buildout than in the other landscapes. However, one less bird species and two less mammal species were lost. Because of the small numbers of species lost and the small differences between present and future landscapes, the risks to species richness were zero or very close to zero for all tests.

Risks to habitat abundance were also robust with respect to perturbations in the area requirements (Fig. 7). The mean values of the risks obtained from the Monte Carlo simulations on the minimum area requirements were within one standard deviation of the original results using the minimum requirements. The mean risks from simulations on the maximum area requirements were within one standard deviation of the original re-

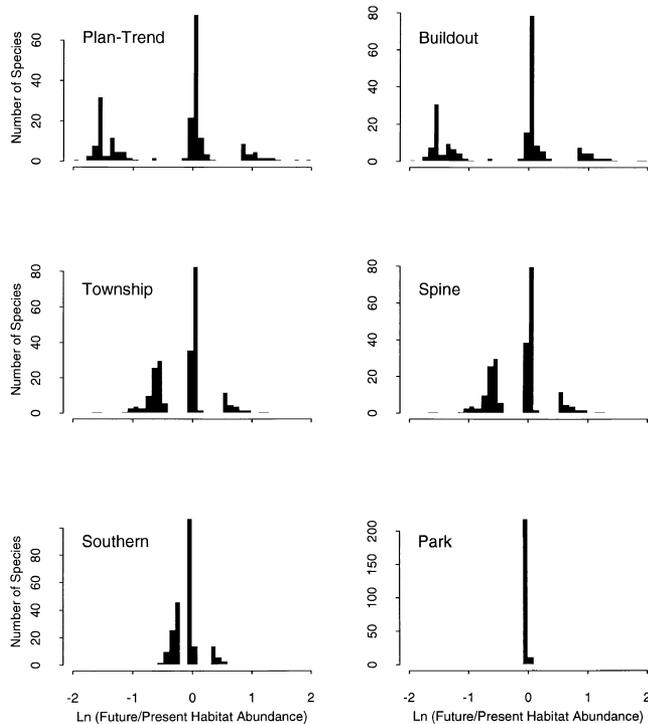


Figure 6. Distributions of natural logarithms of proportions of future to present habitat abundance for all species, using maximum area requirements, by future landscape.

sults in all cases (all 24 combinations of six future landscapes and four taxonomic groups) except for the risks to all vertebrates in the plan-trend and buildout landscapes. In these two cases the mean risks were within two standard deviations. In the multiplicative sensitivity tests, only at 10 times the maximum area requirements did the scores begin to change noticeably (Fig. 7).

Discussion

Although our study could have benefited from more ecological refinement, we believe we have started to develop a comprehensive and reasonable approach to assessing risks to biodiversity at a landscape scale. We found the following:

- We can begin to model risks to terrestrial vertebrate biodiversity at a landscape scale with an analysis of vertebrate species and their habitat requirements.
- Modeled risks of loss of species in our study area were very small using these types of analyses and available data.
- Modeled risks of loss of habitat, however, were significant, but similar when measured either by habitat area assigned to species or by habitat unit abundances calculated using area requirements.
- Modeled risks of loss of habitat to herpetofauna were generally greater than to that of mammals or birds.

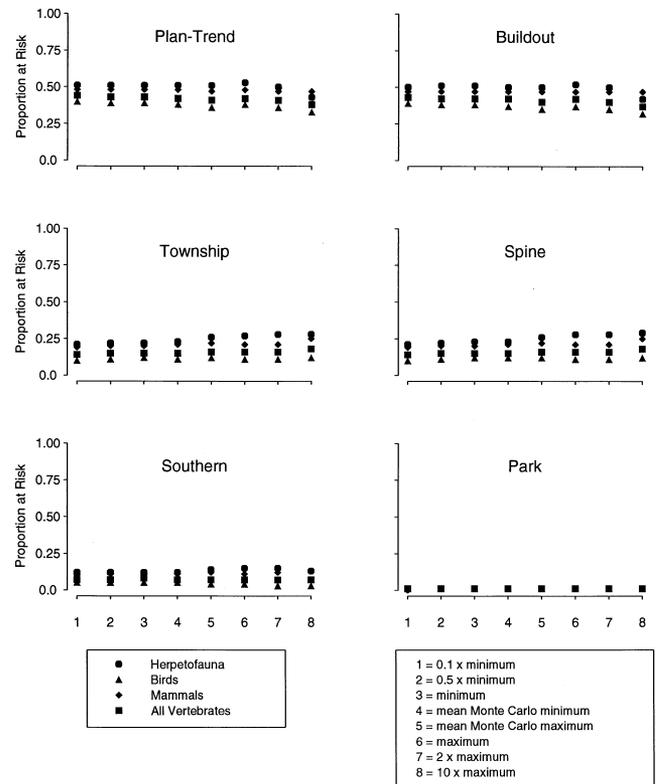


Figure 7. Sensitivity of habitat risks to measurement error in area requirements by future landscape and by taxonomic group. Results using the unmodified minimum area requirements are in position 3 of each x-axis and results using the unmodified maximum area requirements are in position 6. Positions 1 and 2 are the results of dividing the minimum area requirements by 10 and 2, respectively; positions 7 and 8 are the results of multiplying the maximum area requirements by 2 and 10, respectively. Positions 4 and 5 are the results of the Monte Carlo simulations on the minimum and maximum area requirements, respectively.

- Measurement errors in area requirements did not noticeably affect summary statistics of either species richness or habitat abundance.
- For this study area, strategically “designed” future landscapes had significantly lower risks to biodiversity than simple extrapolations from development trends or zoning patterns.

The estimated risks to species richness differed substantially from those to habitat abundance. The lack of risk to species richness may be a realistic reflection of likely changes. For example, the recorded number of vertebrate species extinctions over all of the eastern United States has been small (World Conservation Monitoring Center 1992). Nevertheless, over areas the size of this study, greater numbers of extinctions would proba-

bly be expected when human modification of habitat is great. Another reason for the small risk to species richness is that our definition of species loss was the absence of either all pixels of habitat or all patches of habitat equal to or greater than the area requirement of the species. The implication of this definition, using method 2, is that as long as one breeding unit of the species can be supported then the species is present. Without considering population effects this definition then requires almost complete elimination of habitat, not just enough to reduce populations below sustainable levels.

We hypothesized at the start of our study that the inclusion of more realistic models of species presence based on their area requirements and a patch by patch analysis of habitat might produce different results than the simpler analysis method using only total assigned habitat area for each species. One reason the results from these two methods differ very little appears to follow at least in part from the relationship between the distribution of the area requirements and the distribution of patch sizes on the habitat maps. As an example, the median patch size for the habitat type that consisted of all six forest classes plus shrublands was 0.18 ha in the present landscape and 0.44 ha in buildout. In contrast the median minimum area requirement for the 14 species assigned to this habitat type was 1.2 ha and the median maximum area requirement was 3.25 ha. If the typical area requirement is not much larger than the typical patch, we should not expect the method using area requirements to have an effect greatly different than the method using the sum of habitat area without regard to those area requirements.

Although the similarity of results between methods 3 and 4 suggests that, for some purposes and for some data, method 3 is not only adequate but sufficient, we want to reiterate some of the simplifying assumptions that we have made in order to analyze a large set of vertebrate species. These include the use of a limited set of habitat classes and a corresponding species-habitat association matrix that only assigns presence or absence in a habitat class; a set of area requirements each of which is constant for a species across all habitat classes to which it is assigned; and no consideration of the shape or context of a habitat patch. Each of these assumptions limits the realism of our analyses. For example, although habitat may serve as a useful indicator of vertebrate demography, the relationship is seldom perfect (Block et al. 1994; Wolff 1995). Biotic interactions (e.g., predation and competition), disturbances, chance demographic events, suitability of edge versus interior habitat (Temple 1986), differences in habitat quality and configuration (Noss 1987; Saunders & Hobbs 1991; Freemark et al. 1995), and other factors may all complicate assessments of species-habitat associations. Our model also assumes 100% occupancy of habitat units. Many species are relatively rare, even in their most preferred habitat

(Robbins et al. 1989; Vickery et al. 1994). Rare species are also those most often at risk of extinction (but see Tilman et al. 1994). For these reasons, it is important to validate species-habitat models to determine if the error level is acceptable (Hansen et al. 1993; Block et al. 1994).

We are assessing habitat abundance in this study as a first step toward a more complete assessment of population viability for a set of species. Population viability is strongly related to area of suitable habitat (Laurance 1991) and to population size (Pimm et al. 1988), which is often a function of habitat area. In an earlier study using this idea, Seagle (1986) assessed the effects of landscape and habitat change on species richness. He developed a simulation approach in which he computed a carrying capacity for a species in the landscape as the number of fixed size habitat patches in the species' niche (a range of habitat types and seral stages) divided by its territory size. Augmenting our approach with population viability analysis (PVA) would improve the assessment of risk by incorporating the persistence probability of species within landscapes. Because PVA requires additional life history information and the computation of persistence probability for each species (Armbruster & Lande 1993; Beier 1993), it may not be feasible to analyze as large a set of species as in this study. In conducting any PVA it is also critical to consider the regional context of the study area in relation to the range of the species' populations (Freemark et al. 1993; Ruggiero et al. 1994).

There were many possible sources of error or uncertainty in our analyses in addition to possible errors in the area requirements. Each set of input data may have been affected by error. The original land-use/land-cover map developed by Smith and Richmond (1994) may have suffered from errors in assigning habitat types to pixels. The refinements to this map by Steinitz et al. may also have suffered from similar errors. The species-habitat association table may have contained errors as well. And both the habitat maps and the species-habitat association table were affected by the classification system that was used. Certain habitats were likely to be better identified than others through the Thematic Mapper imagery, and certain species were likely to be better represented than others by the classes of habitat that were delineated on the map. Although we did not attempt to model any of these other sources of error, some of the error may have been mitigated in the analysis through the calculation of the ratio of species richness or habitat abundance in the future to the same quantity in the present. To the extent that these errors affected the future landscapes in a similar way to the present, then error effects may have been canceled in the ratio. A further contribution to the robustness of these results was the calculation of averages for habitat abundance across many species, an analysis strategy that may have helped to mitigate errors or weak assumptions for specific species.

Conclusions

Conservation biology is concerned with the impacts of human activities on the non-human biological world and with developing the scientific support for conservation policy and management decisions. It is difficult to analyze many of the possible effects of human activities, and much research in conservation biology does not explicitly attempt to do so. In a recent assessment of the status of the field, Caughley (1994) divides conservation biology research into two paradigms. The first paradigm addresses the problem of small populations and has developed substantial theory in population dynamics and population genetics. Risk assessment in the context of this paradigm is described by Burgman et al. (1993) and Akçakaya and Ginzburg (1991). The second paradigm is concerned with declining populations and has a strong empirical and applied history dealing with effects of habitat change, exotic species, overharvesting, and secondary extinctions (Diamond 1989; Soulé 1991). An inference from Caughley's argument is that both directions are necessary, and neither is sufficient by itself, for progress in species conservation. We believe that the approach outlined in this paper adds an important biodiversity perspective to the declining population paradigm and starts to link it with the small population paradigm by using habitat and area requirements of species to approximate the carrying capacity of landscapes.

Our approach should be useful for developing and engaging local support for land use planning based on biodiversity considerations. It provides a quantitative ranking of landscape alternatives using a methodology that is relatively simple with few parameters (Doak & Mills 1994) and is adaptable to different definitions of biodiversity. We used the presence and amount of habitat of terrestrial vertebrate species as our biodiversity response, however, emphasizing species known to be at risk may also be useful and important. Articulating goals or targets for landscape and ecosystem management is a critical activity in the development and evaluation of alternative land use scenarios that has received relatively little attention (Slocombe 1993). Our approach is sufficiently generic that it can be applied to other spatial and temporal scales and to other regions using data of different levels of resolution. As such, it can facilitate a more comprehensive and hierarchical approach to the development of land use plans for the proactive conservation of biological diversity.

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