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Using Ecologically Scaled Landscape Indices to Assess Biodiversity Consequences of Land-Use Decisions

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CHAPTER OVERVIEW

If maintenance of biological diversity is to be given serious consideration by land-use planners, ecologists need to provide planners with metrics for comparing alternative scenarios in terms of their consequences for species persistence. We explore the utility of ecologically scaled landscape indices (ESLIs) as measures of relative suitability of proposed land-use scenarios. ESLIs integrate landscape structure with measures of species mobility and area requirements. They can be computed for individual habitat patches or for an entire landscape. To illustrate, we compute ESLIs for species occupying fragmented agricultural landscapes in the Netherlands and in Indiana, USA. For forest mammals in Indiana, extirpated species, or those with the lowest patch occupancy were characterized either by ESLIs with low connectivity scores, indicative of sensitivity to fragmentation, or with low carrying capacity scores, indicative of sensitivity to habitat destruction. Values of ESLIs suggested greater carrying capacities but lower connectivities for the landscape-species combinations in the Netherlands. For the combined sample of 21 species of plants and animals from the two continents, a significant proportion of variation in the fraction of patches occupied was accounted for by a linear combination of ESLIs and their interaction term. We discuss the interpretation of ESLIs in the context of metapopulation dynamics and suggest modifications to improve their predictive capabilities. Finally, we provide suggestions for transforming vectors of ESLI scores into ecological ratings of land-use scenarios that can be used by land-use planners.

Key Words—Agriculture, biological diversity, species persistence, ecologically scaled landscape indices, fragmentation, landscape structure, land-use planning, metapopulation

INTRODUCTION

Humans have altered landscapes dramatically by developing land for agricultural, residential, and commercial purposes (Andersen *et al.* 1996; Collinge 1996; Farina 2000). In the midwestern United States, for example, agricultural practices have resulted in large-scale deforestation, drainage of wetlands, and conversion of native grasslands (Burgess and Sharpe 1981; Iverson 1988; Andersen *et al.* 1996) in the last 150–175 years. Recently, landscape alteration has consisted of expansion of housing developments into prime agricultural areas, especially in sites associated with woodlands. In the Netherlands, as in much of Europe, the same processes have taken place over much longer periods. Deforestation and conversion into agricultural fields began there thousands of years ago. In the past decades, landscape alteration mainly has featured a loss of small landscape elements such as woodlots, hedgerows, and ponds, and an intensification of agriculture that has resulted in declines in quality and increases in isolation of the remaining habitat fragments. As a result of human activities, landscapes on both continents now contain remnant patches of native vegetation surrounded by land converted for human use (Saunders *et al.* 1991). Habitat loss often results not only in a reduced amount of native habitat, but also in a change in its configuration in a landscape. Habitat fragmentation refers to the subdivision of native habitat into smaller pieces (Mönkkönen and Reunanen 1999), although the structure of gaps between suitable habitat may be more important than the structure of habitat patches (With and King 1999*a*). Habitat loss and fragmentation often are considered jointly, but they are capable of operating independently (Trzcinski *et al.* 1999) and can be distinguished by changes in landscape structure (Figure 6-1). Three biologically relevant aspects of fragmentation include declines in the connectivity (or conversely, increases in isolation) of native habitat, increases in the amount of native habitat adjacent to other habitat types, i.e., edge habitat, and reduced mean size of remnant habitat patches (Figure 6-1). Agriculturally induced fragmentation of landscapes often results in small patches of remnant vegetation and linear corridors such as fencerows and drainage ditches embedded within the cropland matrix (Forman 1995).

Both in the midwestern United States and in Europe, habitat loss and fragmentation are ongoing, but increasingly efforts are being directed at "defragmentation" via the establishment of habitat networks (e.g., PEEN: Pan European Ecological Network) and mitigation and compensation efforts for new and existing infrastructure and other biodiversity-threatening impacts. Predicting the ecological consequences of habitat loss and (de-)fragmentation is important for the conservation and management of species (Dooley and Bowers 1998; Nupp and Swihart 2000). This is especially true

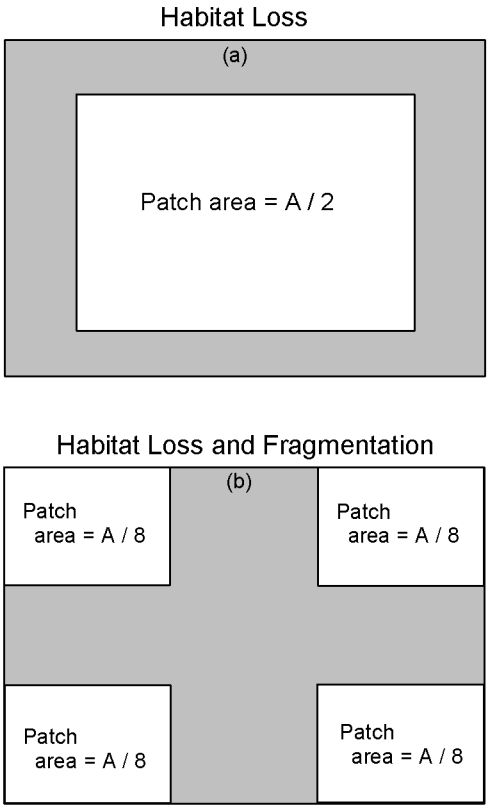

Figure 6-1. A homogeneous landscape subjected to 50% habitat loss (a) and habitat loss and fragmentation (b). Shaded areas represent those portions of the landscape that formerly were native habitat but which now exist as a matrix. Note the three changes that occur in landscape (b) relative to landscape (a): (1) mean patch area is reduced; (2) connectivity is reduced; and (3) edge:area ratio is increased (Hunter 1996). The latter point can be seen by denoting the width of the landscape by W. Then edge:area for native habitat in (a) is $4\sqrt{2}/W$. For a fragmented landscape (b), edge:area is $8\sqrt{2}/W$, or a twofold increase relative to (a).

in human-dominated landscapes, where decisions on land use presumably are made with much narrower margins for error when considering threshold effects of landscape fragmentation (*sensu* With and King 1999*b*). Thus, a challenge for ecologists is deriving metrics that can be used by land-use planners to assess the relative effects of alternative land-use scenarios on species sustainability. Several metrics have been suggested, and we briefly consider these below. In evaluating the utility of a metric as a land-use planning tool, we assert that it should exhibit the following characteristics: (1) a strong conceptual basis; (2) a transparent and repeatable method of computation; (3) an ability to quantify differences in landscape structure; and (4) an ability to quantify interspecific differences in sensitivity to habitat fragmentation.

POTENTIAL METRICS FOR ASSESSING LAND-USE EFFECTS ON SPECIES

Existing approaches to spatial modeling can be categorized according to (1) whether they emphasize structure or process, and (2) the magnitude of data required for their parameterization. Using these criteria, we consider the relative merits of five methods for assessing the consequences of land-use decisions.

Strategic Models

Strategic models typically capture only the basic elements of spatial processes, resulting in rules-of-thumb predictions that may be useful because of their more general applicability. Numerous strategic models have been proposed for linking landscape structure with ecological processes. For individuals, strategic models have linked spatial structure to foraging decisions (With 1994; Adler and Kotar 1999) and dispersal decisions (Gustafson and Gardner 1996; With and King 1999*a*). Metapopulation models have been important in the development of general predictions regarding threshold effects on species persistence in fragmented landscapes (Hanski and Gilpin 1997; Bascompte and Solé 1998*a*; Swihart *et al.* 2001; Feng and DeWoody–Chapter 4), and some modeling efforts have explored the linkage of individual behavior to population dynamics in a spatially structured context (e.g., Fryxell and Lundberg 1998). Further refinements of spatial strategic models have been made recently by incorporating heterogeneity among patch (or matrix) types (Haydon and Pianka 1999; Vandermeer and Carvajal 2001) and dynamic landscapes (Keymer *et al.* 2000). Ives *et al.* (1998) demonstrated the utility and limitations of analytical approximations derived from strategic models as surrogates for tactical models. Strategic models provide insight and a general framework for linking landscape structure to ecological characteristics of species. However, their practical utility is limited because they lack explicit links to real landscapes and species-specific responses of real organisms to spatial structure and scale issues (Vos *et al.* 2001).

Tactical Models

In contrast to strategic models, tactical models link landscape structure to the probability of population persistence by calibrating demographic processes of focal species in relation to specific classes of habitat or other features of the landscape (Dunning *et al.* 1995). In addition to incorporating habitat-specific demographic parameters, these models are spatially explicit. Risk assessment analyses, such as population viability analysis, stem from the use of tactical models, in which a frequency distribution of abundance is generated after a

specified period of time. Thus, tactical models lend themselves to investigations aimed at determining the relative impact of future land-management strategies on conservation objectives (Boyce 1992; Akçakaya and Sjögren-Gulve 2000; Brook *et al.* 2000).

One weakness of previous spatially explicit tactical models has been their treatment of habitat and nonhabitat as a binary variable. In truth, many organisms perceive the suitability of different landscape elements along a continuum, including the matrix separating habitat patches (Gustafson and Gardner 1996; Ricketts 2001; Vandermeer and Carvajal 2001). Another limitation of risk assessments based on spatially explicit tactical models is their general failure to treat landscapes dynamically. Rather, successional dynamics often are ignored (Fahrig and Merriam 1994). Considerable advances in model realism could be made by incorporating habitat complexity and dynamics of landscape-cover change into spatially explicit tactical models. Models of landscape dynamics already exist (e.g., LANDIS, He *et al.* 1999) as a potential complement to spatially explicit tactical models of metapopulations (e.g., RAMAS GIS, Akçakaya 1998) or metacommunities (e.g., SHALOM, Ziv 1998).

Of course, enhancing realism comes at a cost in terms of the amount of data required to parameterize a model and in terms of the model's generality. Just as overparameterizing of a regression model can reduce model performance by producing imprecise estimates of coefficients (Draper and Smith 1998), so too can the additional data requirements of more realistic tactical models lead to large standard errors for parameter estimates and thus affect the utility of model outputs (Maxwell and Costanza 1994; White 2000). Moreover, tactical modeling is extremely time-consuming and costly, outcomes often are hard to calibrate with field data, and validation is not an option because of stochastic effects and long time frames. Last but not least, the complexity of tactical models usually leads to a lack of transparency of relations between input and output. If risk assessments for many species are sought, or if species are not critically imperiled, we believe that the increased data requirements of tactical models may often outweigh their value as a means of quantifying the relative impacts of land-use and land-cover change on species persistence. In the landscape-planning process, tactical models are only useful if there are one or two focal species, if considerable information exists for both distributional patterns and underlying processes, and if there is plenty of time for assessing the impact of land-use decisions (Verboom *et al.* 1993).

Incidence-based models occupy an intermediate position between strategic and tactical models. They are relatively simple yet have the pretension to be realistic. Potentially useful results for conservation of metapopulations have been developed from these models, including rules-of-thumb metrics such as mean lifetime (Frank and Wissel 1998, 2002) and metapopulation capacity (Hanski and Ovaskainen 2000), and guidelines for

reserve design in fragmented landscapes (Etienne and Heesterbeek 2001; Etienne 2003). The problems with these patch-occupancy models are the same as with the tactical models; namely, parameters are difficult to estimate, results are impossible to validate, uncertainties typically are quite large, and results can be sensitive to uncertainty in estimates (Knauer *et al.*, unpublished; ter Braak *et al.* 1998).

Statistical Models

Ecologists and managers have expended considerable effort in developing habitat suitability models for organisms with the objective of forecasting abundance, occurrence or vital rates. These models do not link occupancy or abundance data directly to demographic processes; rather, they rely upon local or landscape variables as surrogates for variation in demographic processes and thus are inappropriate for making causally based inferences. The incorporation of spatial structure into habitat suitability models has occurred only in the last 20 years, in conjunction with the ascendancy of geographic information systems (Lancia *et al.* 1982, 1986). As predicted by Van Horne and Wiens (1991), integration of habitat and landscape features into forecasting models has become increasingly common in the past 10 years (e.g., Donovan *et al.* 1997; Akçakaya and Atwood 1997; Gehring and Swihart 2003*a*; Johnson *et al.* 2002; reviewed by Stauffer 2002). Multi-scale studies are critical in human-dominated landscapes if forecasting models are to be useful in identifying and implementing conservation strategies. For example, Lindenmayer (2000) demonstrated that for an endangered marsupial, *Gymnobelideus leadbeateri*, effective conservation would require large-scale conservation efforts within ash-type eucalypt forests, landscape-scale efforts targeting large reserves and corridors within wood-production areas of ash-type eucalypt forests, and habitat-scale efforts to enhance availability of foraging and denning sites within forest stands. Future improvements in statistical treatment of model accuracy (Fielding 2002; Pearce *et al.* 2002), extrapolation to unsampled sites (Rotenberry *et al.* 2002), and incorporation of uncertainty in detection (Stauffer *et al.* 2002) will enhance the practical utility of statistical models of habitat and landscape suitability. Although a time series of data is desirable, statistical models often rely on a static representation of a system, which limits their utility in predicting species persistence (ter Braak *et al.* 1998). Despite advances in statistical modeling, these models likely will remain difficult to extrapolate to other landscapes or population conditions (reviewed by Boone and Krohn 2002). For the landscape-planning process, the main weakness is that statistical relationships do not require causality. For instance, in the Netherlands both the occurrence and births of white storks have increased. However, a causal mechanism underlying the correlation remains unidenti-

fied. Moreover, scenario assessment often means using a regression model outside the range of values for which it was calibrated upon, leading to planning assessments of dubious value (Verboom *et al.* 1993).

Landscape Indices

Landscape ecologists have focused considerable effort on describing the complex physical structure of landscapes, with a goal of summarizing the spatial heterogeneity embodied by an arrangement of spatial elements into statistics that have ecological significance. The intent is based on the empirical foundation that spatial pattern can have dramatic effects on ecological processes. Software for generation of summary statistics is widely available (e.g., FRAGSTATS*ARC, J. Berry *et al.* 1998; RULE, Gardner 1999). Descriptors of patch attributes, such as area, shape, edge:interior, or degree of isolation, summarize attributes that may influence occupancy or abundance in a patch (Forman and Godron 1986). Landscape ecologists recognize the importance of scale in affecting ecological processes, and methods aimed at detecting the scale of spatial patterning are reasonably well developed (e.g., Musick and Grover 1991; Turner *et al.* 1991; Cressie 1993). In addition, statistics describing patch structure, such as adjacency (He *et al.* 2000), connectivity (Gustafson and Parker 1992; Schumaker 1996; Tischendorf and Fahrig 2000*a*,*b*), and minimum-spanning tree (Urban and Keitt 2001) provide summaries of potentially important information regarding the juxtaposition of habitat elements. The pattern and spatial scaling of gap sizes, i.e., lacunarity analysis (Plotnick *et al.* 1993), also may be important to understanding effects of landscape structure on animal movements (With and King 1999*a*). A strength of landscape indices is the straightforward manner in which they characterize landscape structure (Gustafson 1998). A significant weakness, though, is their failure to account explicitly for interspecific differences in responses to landscape structure. Moreover, the ecological significance of most landscape indices is unclear (Vos *et al.* 2001).

Ecologically Scaled Landscape Indices

The importance of landscape structure on population persistence is widely recognized from a theoretical perspective (Levin 1992; Durrett and Levin 1994), and field research has demonstrated that the size, arrangement of patches, and composition of the landscape around patches can affect a species' distribution, abundance, interspecific interactions, and movement patterns (e.g., Sheperd and Swihart 1995; Debinski and Holt 2000). Moreover, habitat fragmentation caused by human disturbance is not scale-limited (Lord and Norton 1990). The scale at which habitat fragmentation operates is dependent upon species' perceptions and responses to landscapes. Considerable

interspecific variation in responses exists; for example, numerous studies have documented differential responses of mammalian species to habitat fragmentation (e.g., Harris and Woollard 1990; Hansson 1991; Andrén 1994; Laurance 1995; Dunstan and Fox 1996; Nupp and Swihart 1998, 2000). In judging the impact of land-use decisions on species, then, a metric is needed that combines measures of landscape structure with ecologically relevant characteristics of species that reflect the scales at which they respond to landscape structure. Integrated metrics of this sort are termed ecologically scaled landscape indices (ESLIs).

Metapopulation theory provided the basis for two ESLIs introduced by Vos *et al.* (2001). The incidence of a species in a patch, P, is given by $P = C/(C+E)$, where C and E are colonization and extinction rates, respectively (Hanski 1994). The viability of a metapopulation is determined by the ratio C/E, which for many species are isolation-dependent (C) and area-dependent (E) processes. Vos *et al.* (2001) linked landscape structural features with ecologically relevant measures of a species' sensitivity to isolation and area effects. They defined the carrying capacity of patch i as:

$$ESLI_{K_i} = \frac{A_i}{IAR_i}, \tag{1}$$

where A_i is the area of patch i and IAR_i is the area in patch i required by one reproductive unit of a species (e.g., a mated pair). An index of the average carrying capacity of a patch in a landscape containing n patches is obtained as:

$$ESLI_{\overline{K}} = \frac{\sum_{i=1}^{n} ESLI_{K_i}}{n}. \tag{2}$$

To link isolation effects to species mobility, Vos *et al.* (2001) defined the connectivity of patch i as:

$$ESLI_{C_i} = \sum_{\text{all } j \neq i}^{n} A_j e^{-\alpha d_{ij}}, \tag{3}$$

where d_{ij} is the distance between focal patch i and another patch j, and $1/\alpha$ is the mean dispersal distance for the species. Thus, C_i is an area-weighted sum of the probability of immigration from j to i. An index of the average connectivity of a patch in a landscape is provided as:

$$ESLI_{\overline{C}} = \frac{\sum_{i=1}^{n} ESLI_{C_i}}{n}. \tag{4}$$

Equations (1) and (3) provide a means of quantifying the suitability of individual patches for a species in terms of their likely contribution to metapopulation persistence, whereas equations (2) and (4) provide a means of comparing landscapes in terms of the overall suitability for sustaining a species.

The ESLIs defined by Vos *et al.* (2001) provide several advantages as metrics for assessing landscape suitability. They are rooted in the theory of metapopulations and are process-dependent inasmuch as mobility and energetic or social factors influence C and E. They explicitly link ecologically relevant characteristics of species to landscape structure, providing a scaling that allows comparisons across species or landscapes (Figure 6-2).

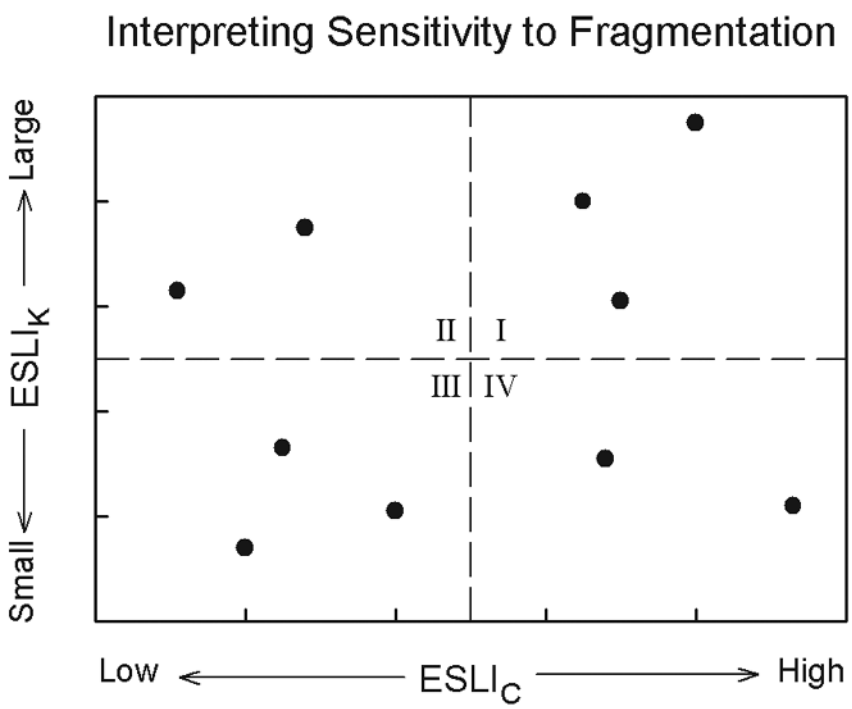

Figure 6-2. Ecologically scaled landscape indices (ESLIs) can be useful in comparing sensitivities of species to habitat fragmentation. For a hypothetical assemblage (species indicated by filled circles), species in quadrant I are characterized by relatively high connectivities and large carrying capacities. Quadrant I thus includes species with ecological traits that are insensitive to the level of fragmentation exhibited in the focal landscape. In contrast, species in quadrant III exhibit relatively low connectivities and small carrying capacities, suggesting a heightened sensitivity to the level of fragmentation exhibited in the landscape. Quadrant II contains species that can be characterized as relatively isolation sensitive (low $ESLI_C$), whereas quadrant IV contains species that are area sensitive for the landscape in question (small $ELSI_K$).

For instance, species capable of attaining high local densities (i.e., characterized by low per capita resource requirements) will exhibit greater values for indices (1) and (2) than species constrained to lower local densities by greater resource requirements. Similarly, species with well-developed dispersal capabilities (i.e., small α) will exhibit larger values of connectivity indices (equations 3 and 4) than relatively poor dispersers. Thus, for a given landscape, species falling in the lower left portion of a plot of ESLIs (Figure 6-2) are most sensitive to habitat fragmentation. Of course, variation of spatial structure between landscapes can produce different levels of ecologically scaled carrying capacity or connectivity, providing a valuable tool for assessing the likely consequences of alternative land-use scenarios. An assessment plot of alternative landscapes also could be portrayed for species co-occurring in a region by using a generalized distance between vectors of ESLI values and some baseline (e.g., the current status of species in the landscape), thereby permitting comparison of the overall suitability of various scenarios in terms of their impact on the assemblage. We explore this and alternative methods further in the concluding section.

EXAMPLES OF ECOLOGICALLY SCALED LANDSCAPE INDICES

To illustrate the utility of ESLIs, we present results of field studies conducted in agricultural landscapes on two continents. A guild of forest-dwelling granivorous rodents has been studied in west-central Indiana, USA, since 1992, with the intent of examining effects of agriculturally induced habitat alteration on individuals, populations, and communities (Sheperd and Swihart 1995; Nupp and Swihart 1996, 1998, 2000; Goheen 2002). Additional studies (Page *et al.* 1998, 2001*a,b,c*; Gehring and Swihart 2003*a*) have focused on the raccoon (*Procyon lotor*), a carnivore that relies on forest patches for denning sites and foraging. We summarized the dispersal capabilities and individual area requirements of these species using information from our own studies and from the literature (Table 6-1). For comparison, we selected two additional forest mammals that occurred historically in the area but which became extinct in the region over a century ago, coincident with the advent of large-scale destruction of forests by humans: a rodent (porcupine, *Erethizon dorsatum*) and a mesocarnivore (fisher, *Martes pennanti*).

Occupancy data were collected and ESLIs calculated for an area within the Indian Pine Natural Resources Study Area of the upper Wabash River basin (Figure 6-3). The area is flat to gently rolling, with fertile soils. Historically, the area was characterized by a confluence of ecoregions, including the savannah transition zone from hardwood forest to tall-grass

TABLE 6-1.
Ecological characteristics and ecologically scaled landscape indices for forest-dwelling mammals and an agricultural landscape in west-central Indiana, USA, and for plants, invertebrates, and vertebrates in agroecosystems of the Netherlands (Vos *et al.* 2001).

Species	*Individual area requirements (ha)*	*Mean dispersal distance (km)*	*Average patch carrying capacity (log_e)*	*Average patch connectivity (log_e)*	*Fraction of patches occupied*
Indiana, USA					
White-footed mouse (*Peromyscus leucopus*)	0.05	0.1	4.35	8.21	1.00
Southern flying squirrel (*Glaucomys volans*)	2.5	0.05	0.46	2.24	0.14
Eastern chipmunk (*Tamias striatus*)	0.1	0.1	3.66	8.21	0.86
Red squirrel (*Tamiasciurus hudsonicus*)	1	0.3	1.36	12.01	0.30
Gray squirrel (*Sciurus carolinensis*)	2	0.2	0.68	11.15	0.19
Fox squirrel (*S. niger*)	2.5	0.5	0.46	12.98	0.86
Porcupine (*Erethizon dorsatum*)	150	3	–3.16	15.24	extirpated
Raccoon (*Procyon lotor*)	5	3	–0.22	15.24	0.64
Fisher (*Martes pennanti*)	2500	23	–4.34	26.54	extirpated
Netherlands					
Root vole (*Microtus oeconomus*)	0.01–0.1	0.6	6.89 4.92	3.59 0.94	0.71 0.59
Nuthatch (*Sitta europea*)	1	2	0.99	4.16	0.42
Reed warbler (*Acrocephalus scirpaceus*)	0.01–0.1	2	3.74	1.23	0.67
Tree frog (*Hyla arborea*)	0.001–0.01	0.6	3.12	–1.27	0.10
Moor frog (*Rana arvalis*)	0.001–0.01	0.6	5.59	0.05	0.67
Trunk ant (*Formica truncorum*)	1	0.2	0.79	–0.22	0.24
Grayling (*Hipparchia semele*)	0.01–0.1	0.6	7.22	4.93	0.57
Green hairstreak (*Callophrys rubi*)	0.01–0.1	0.6	7.32	4.77	0.89
Silver-studded blue (*Plebejus argus*)	0.001–0.01	0.2	9.51	4.44	0.34
Bog bush cricket (*Metrioptera brachyptera*)	0.001–0.01	0.2	6.15	–1.39	0.51
Meadow grasshopper (*Chorthippus parallelus*)	0.0001–0.001	0.2	8.60	1.94	0.72
Honeysuckle (*Lonicera periclymenum*)	0.1–1	0.02	2.86	–2.66	0.09
Bird cherry (*Prunus serotina*)	0.1–1	0.2	2.86	–1.27	0.09

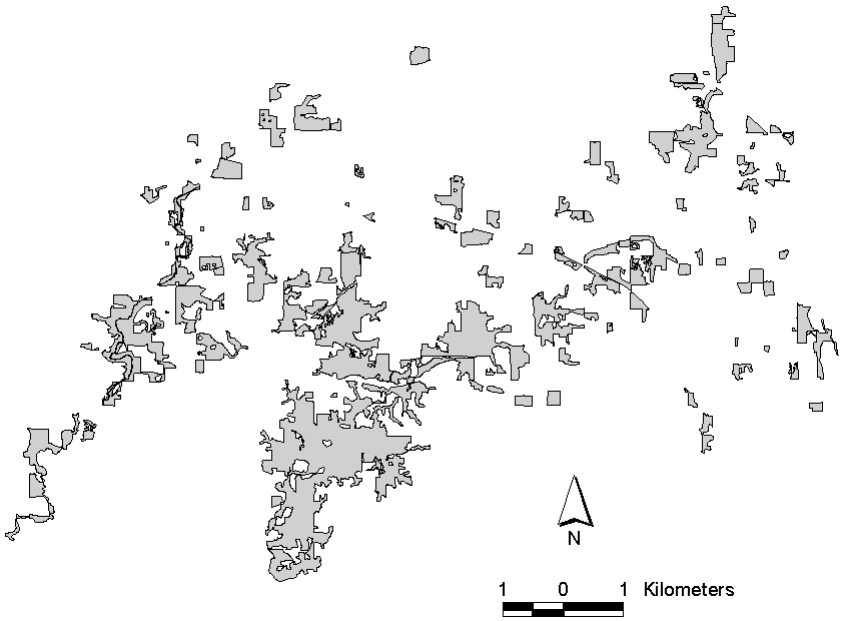

Figure 6-3. Forest patches in west-central Indiana, USA, used to compute ecologically scaled landscape indices for forest-dwelling mammals. The matrix is predominantly agricultural. Only forest patches are illustrated.

prairie, the southwestern extent of the northern hardwoods (dominated by *Acer* and *Fagus grandifolia*), and the northern edge of the central hardwoods (dominated by *Quercus* and *Carya*) (Petty and Jackson 1966; Ricketts *et al.* 1999). A substantial portion of the watershed (ca. 20%) originally consisted of wetlands and swales (Ulrich 1966). Today, human land use dominates the watershed with approximately 12% of the area in human developments and 70% in agricultural production, principally corn (*Zea maize*) and soybeans (*Glycine max*). Considerable clearing of forests and draining of wetlands have occurred over the past 150 years, and native grasses have largely been replaced by cool-season exotics. Currently, forests, grasslands, and wetlands comprise approximately 10%, 4%, and 1% of the area, respectively. Fencerows and drainage ditches bisect some of the agricultural fields, providing varying levels of connectivity between forest and grassland patches and comprising 3% of the area (Gehring and Swihart 2003*a*).

Data from the Netherlands come from fragments of natural habitat in agricultural landscapes dominated by meadows and arable land across the country. Corn is the dominant crop. Natural habitat comprises only a small percentage of the landscape (ca. 10%), and only parts of that are suitable as habitat for the species considered. The study species occur in various types of forest (e.g., nuthatch, *Sitta europea* in old deciduous forest), wetlands (e.g., reed warbler, *Acrocephalus scirpaceus*), heathlands (e.g., butterfly species) and grasslands (e.g., meadow grasshopper, *Chorthippus parallelus*). The proportion of landscape suitable as habitat varied among

species and landscapes from 0.2% for specialists such as reed warbler, which needs water with reed cover, to 25% for generalists such as green hairstreak (*Callophyrs rubi*), a butterfly of heathlands studied in an area with large heath remnants. The landscapes have undergone many centuries of habitat loss and fragmentation.

ESLIs were computed for each species in Table 6-1 using equations (2) and (4), with one exception. ESLIs for each patch (equations 1 and 3) were subjected to logarithmic (base e) transformations before averaging across patches. Least squares regression was used to assess the relation between the ESLIs and the proportion of patches occupied.

Forest-Dwelling Mammals

Forest mammals of Indiana exhibited a negative correlation between the ESLI for landscape connectivity and carrying capacity (Figure 6-5, top panel). A regression model, fraction of patches occupied = $0.01 + 0.16\ln(ESLI_{\overline{K}}) + 0.03\ln(ESLI_{\overline{C}})$, was significant ($R^2 = 0.71, F = 7.40$, d.f. = 2, 6, $P = 0.02$), although only $\ln(ESLI_{\overline{K}})$ was a significant predictor ($t = 3.52, P = 0.01$). The standardized coefficient of 1.14 for $\ln(ESLI_{\overline{K}})$ was 2.28 times larger than the standardized coefficient of 0.50 for $\ln(ESLI_{\overline{C}})$, providing an indication of the relative importance of the two indices in predicting patch occupancy by forest mammals in Indiana.

Extirpation or low levels of patch occupancy were not tied exclusively either to carrying capacity (Figure 6-4, middle panel) or to connectivity (Figure 6-4, bottom panel). For example, *M. pennanti* and *E. dorsatum*, the species with the largest area requirements and thus lowest ESLI values for carrying capacity, also exhibited the largest connectivity values. In these species, extirpation appears to have been mediated by deforestation rather than fragmentation. In contrast, the southern flying squirrel (*Glaucomys volans*) exhibited a much lower connectivity value than the other species, in keeping with its limited ability to move through unforested areas due to its gliding form of locomotion (Swihart *et al.* 2003*a*). This species appears to be limited in distribution by its inability to traverse the cropland matrix between forest fragments. However, sensitivity to forest patch size also may play a role in the low patch occupancy of *G. volans* (Nupp and Swihart 2000). Relative to the other two species most similar to it in size (*Tamias* and *Peromyscus*), *G. volans* displayed a much smaller value for carrying capacity (Figure 6-4, top panel). Experiments have shown that in more northerly portions of its range, *G. volans* can reduce energetic costs 36% by huddling in communal groups of six individuals during winter, thereby shortening the extent and frequency of nonshivering thermogenesis (Stapp *et al.* 1991; Merritt *et al.* 2001). If groups are needed to ensure survival of individuals during harsh winters, threshold sizes of forest patches for viable populations of *G. volans* may be considerably larger than for species such as *Tamias* and *Peromyscus* that do not rely on such a strategy.

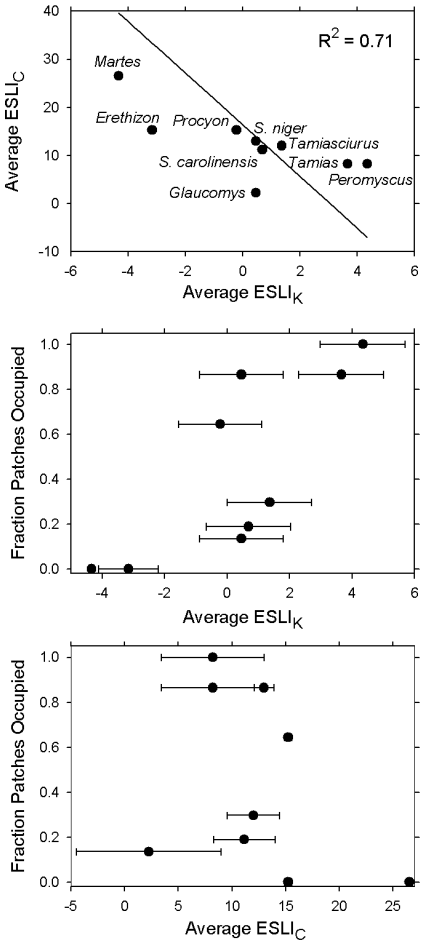

Figure 6-4. Ecologically scaled landscape indices (log-transformed) computed for mammals in an agricultural system of Indiana, USA. The landscape for which ESLIs were calculated is depicted in Figure 6-3. The regression line in the top panel depicts combinations of ESLI values yielding predicted occupancy of ½ of patches. Values of ESLIs are from Table 6-1.

Intercontintental Comparisons

How general are the relationships observed for the set of forest mammals we examined? When data on plants and animals from the Netherlands were added to the analysis, two items immediately became apparent. First, organisms from the Netherlands tended to have larger ESLIs for carrying capacity and lower ESLIs for connectivity (Figure 6-5), either as a consequence of occupying larger but more isolated habitat patches, as a result of smaller individual area requirements and more restricted mobilities, or due to a combination of these factors. Second, data from the two continents followed the same general patterns. A multiple regression model including both ESLIs,

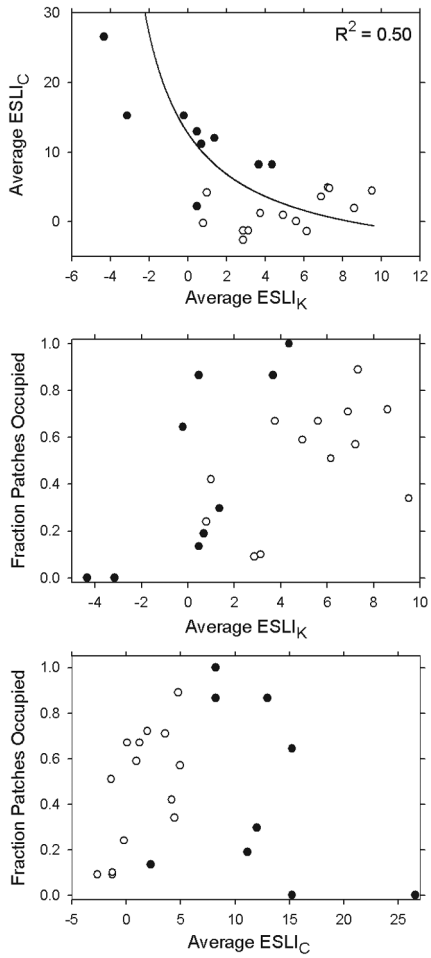

Figure 6-5. Ecologically scaled landscape indices for Indiana mammals (•) and for plant and animal species inhabiting agroecosystems in the Netherlands (o). The regression line in the top panel depicts combinations of ESLI values yielding predicted occupancy of ½ of patches. ESLI values are from Table 6-1 and from Vos *et al.* (2001).

interactions of their standardized scores, and an indicator variable for continental identity provided no support for the hypothesis that differences existed between the continents in terms of effects on the fraction of patches occupied ($t = -0.34$, $P = 0.74$). A regression model fitted after removing the variable for continental identity yielded: fraction of patches occupied $= 0.12 + 0.06\ln(ESLI_{\overline{K}}) + 0.04\ln(ESLI_{\overline{C}}) + 0.10(ESLI_{\overline{K}}ESLI_{\overline{C}})$. The model was significant ($R^2 = 0.50$, $F = 6.26$, d.f. = 3, 19, $P = 0.004$), as were all estimates of parameters except the intercept. Standardized coefficients of 0.70 for $\ln(ESLI_{\overline{K}})$ and 0.88 for $\ln(ESLI_{\overline{C}})$ were comparable, indicating that connectivity and carrying capacity were approximately equal in terms of

their importance as descriptors of patch occupancy for the broad array of species we considered.

MODIFICATIONS OF ESLIs

Our examination of ESLIs suggests that they can serve as useful summary statistics for linking patch occupancy with landscape structure and ecologically relevant characteristics of organisms. Of course ESLIs, like any statistical summary, have limitations. Three problem areas, and methods of addressing them, deserve more detailed consideration here: time lags, stochasticity at the metapopulation level, and variation among patches.

ESLIs do not take into account the possible existence of time lags in responses of occupancy to habitat fragmentation. Differences in the time scale at which fragmentation has operated may explain differences between European and U.S. data. The European landscapes have been fragmented for a much longer time than the U.S. landscapes, resulting in European metapopulations that more closely approximate equilibrium conditions with the current landscapes and U.S. metapopulations lagging behind predicted occupancy levels due to extinction debts still awaiting payment. These extinction debts produce greater levels of occupancy, because faunal loss is still occurring. Comparable patterns have been observed for North American mammals occupying oceanic islands, mountaintops, and terrestrial-habitat islands that differ in time since patch formation (Swihart *et al.* 2003*a*). Generally speaking, persistence will be overestimated if static or declining patterns of patch occupancy are mistakenly attributed to dynamically stable metapopulation processes (ter Braak *et al.* 1998; Clinchy *et al.* 2002). Time lags and effects on metapopulations are discussed in more detail by Nagelkerke *et al.* (2002), and the conditions and implications associated with extinction debts are considered by Tilman *et al.* (1994). For our purposes, time lags limit the applicability of ESLIs as absolute predictors because they may yield overoptimistic results. For land-use planning and ranking of scenarios, however, time-lag phenomena do not hamper the use of ESLIs in comparing alternative plans.

The current ESLI classification system, which incorporates $ESLI_{\overline{K}}$ and $ESLI_{\overline{C}}$, does not account for demographic stochasticity at the metapopulation level (immigration-extinction stochasticity and regional stochasticity; *sensu* Hanski 1991). Consequently, metapopulations with high values for one or both indices and a corresponding large predicted fraction of patches occupied can become extinct if the number of patches in a network is too small, say less than 20 (Hanski 1991). This problem can be solved by considering only situations with fairly large numbers of patches.

Alternatively, an additional ESLI has been proposed as a measure of demographic stochasticity at the metapopulation level (Opdam *et al.* 2003).

The ESLI classification system for landscapes that we used does not take into account differences between patches. Because arithmetic means are taken of all patches, this may in some cases produce incidental artefacts. For example, adding a small and isolated patch to a landscape will decrease the value of both indices while this should not influence, or should influence positively, the sustainability of the metapopulation. It will indeed lower the proportion of occupied patches, but this should not be interpreted as a drop in landscape quality. Solutions to this problem include focusing on large or key patches (Verboom *et al.* 2001), disregarding very small and/or isolated patches, or considering the variance in connectivity and carrying capacity. However, the latter approach did not improve the variation explained in earlier analyses (Vos *et al.* 2001).

As currently formulated, ecologically scaled measures of landscape connectivity treat uniformly all matrix types separating patches of habitat. Models constructed by Vandermeer and Carvajal (2001), however, predict that the quality of the matrix can be an important factor determining population dynamics in landscapes where animals must cross areas of unsuitable habitat to reach suitable patches. Several experimental and observational studies support the hypothesis that the composition of the matrix can affect patch occupancy (Åberg *et al.* 1995; Hokit *et al.* 1999; Pope *et al.* 2000). Refinements in $ESLI_C$ to permit differential permeabilities among matrix types likely would improve the degree to which $ESLI_C$ accurately predicts colonization of empty patches, as would the explicit consideration of corridors that might reduce levels of isolation for adjacent patches (Miller and Russell–Chapter 8).

The ESLIs formulated by Vos *et al.* (2001) enable quantification of connectivity and carrying capacity for individual patches and for landscapes. Other factors also may contribute to variation in patch occupancy independently of connectivity and carrying capacity, and we briefly consider two possibilities. Interspecific interactions can be strong determinants of community structure at local levels and thus may explain a species' absence in suitable patches or presence in poorly suited patches (e.g., Hanski and Zhang 1993; Swihart *et al.* 2001). Likewise, a species' position in its geographic range may influence its occupancy of patches, irrespective of connectivity or carrying capacity. For many species, abundance tends to decline spatially from the core of a range to the periphery (Brown 1995). This pattern arises because core areas of a range presumably contain more suitable habitat in terms of niche requirements and more suitable abiotic conditions for the species' survival, resulting in lower rates of local extinction and colonization (Enquist *et al.* 1995; Pulliam 2000). An examination of

distributions of 32 species of vertebrates at our Indiana study site confirmed that proximity of the study site to a species' range boundary was a significant predictor of overall level of occurrence (Swihart *et al.* 2003*b*). Thus, accounting for the predicted occurrence or abundance of competitors and predators, and the position of species with respect to their range boundaries, may aid in strengthening observed relationships between ESLIs and patch occupancy.

IMPLICATIONS FOR CONSERVATION-BASED PLANNING

For planning purposes, ESLIs from multiple species need to be summarized in a form that permits comparisons among alternative land-use scenarios (Swihart and Slade–Chapter 1). Here we present two methods for assessing scenarios using ecological ratings (Figure 6-6). If no field data on species occupancy are available, an indirect ecological rating score can be computed easily for ESLIs representing average carrying capacity and connectivity of patches in a landscape (equations 2 and 4). Consider a matrix $\mathbf{E}^{i}_{\mathbf{kx2}}$ in which the rows contain ESLI values for the k species under consideration, with column 1 representing $ESLI_{\bar{K}}$ and column 2 representing $ESLI_{\bar{C}}$, computed under land-use scenario $i, i = 1, \ldots, m$. To permit stakeholders to assign differences among species in terms of their importance, either ecologically, economically, or aesthetically, construct a row vector of weighting coefficients, $\mathbf{w'}_{\mathbf{1xk}}$ such that the elements of $\mathbf{w'}$ sum to 1. Pairwise comparisons of alternative scenarios, or comparisons of each scenario to some baseline (e.g., current land use) can then be reduced to a pair of ecological ratings as $\mathbf{w'}(\mathbf{E^i} - \mathbf{E^j}) = \mathbf{r}$, where the first element of $\mathbf{r}$ is the sum of weighted differences in $ESLI_{\bar{K}}$ across species and the second element is the corresponding sum of weighted differences in $ESLI_{\bar{C}}$. A simple way to portray results of this indirect ecological rating is to compare each of the scenarios with a baseline (e.g., current landscape) and plot the resulting m vectors as a scatterplot (Figure 6-6).

A direct ecological rating can be derived from ESLIs if field data on occupancy are available. For a set of k species, a predictive model of prevalence (proportion of patches occupied) can be constructed as a function of $ESLI_{\bar{K}}$ and $ESLI_{\bar{C}}$, using the observed $k \times 1$ vector of prevalence values, $\mathbf{p}$, collected from sampling in the current landscape (as in the top panels for Figures 6-4 and 6-5). Alternative scenarios serve to generate new ESLI values for each species, which can then be used to compute a predicted prevalence value, $\hat{p}_i, i = 1, \ldots, k$. For each scenario, a reasonable sum-

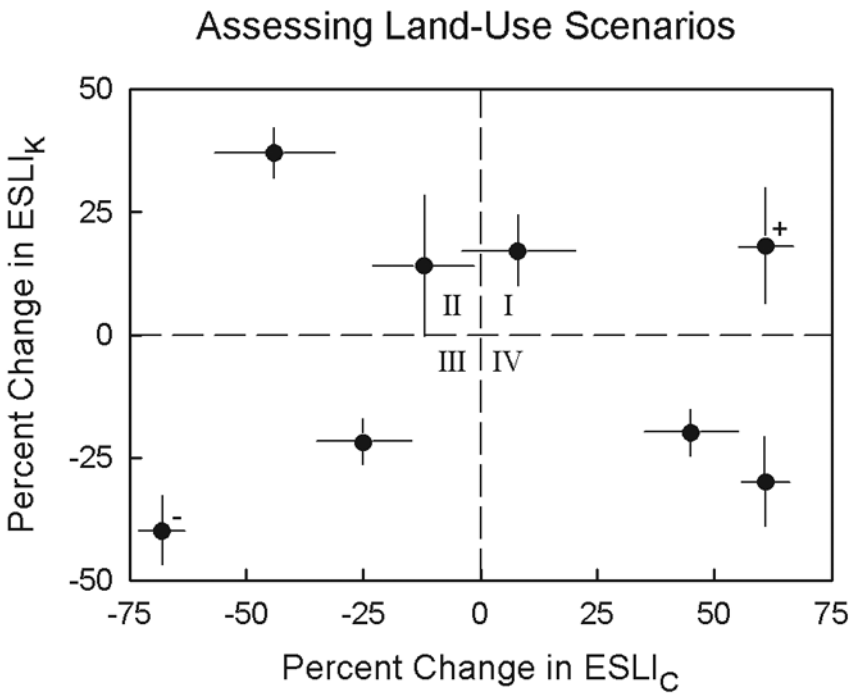

Figure 6-6. Depiction of the impact of eight hypothetical land-use scenarios on ESLIs of an assemblage such as the one illustrated in Figure 6-2. For each land-use scenario, ESLIs are computed for each species. For each species, the change in ESLI associated with a scenario is expressed as a percentage of the ESLI for the current landscape. Solid circles represent the mean percent change for all species; vertical bars represent ± 1 standard error in percent change for $ESLI_K$, and horizontal bars represent ± 1 standard error in percent change for $ESLI_C$. Thus, the scenario representing the greatest improvement in connectivity and carrying capacity, considering all species, is denoted by a "+", whereas the scenario with the greatest negative impact is denoted by a "–". Note that weightings could be applied to species to recognize differences in ecological, economic, or esthetic values.

mary statistic is $n_m \mathbf{w}'(\mathbf{p} - \hat{\mathbf{p}})$, where n_m is the number of habitat patches in scenario m.

Similar approaches can be used for patch-specific measures of carrying capacity and connectivity (equations 1 and 3). What we desire in this instance is a patch-by-patch rating of each scenario. In an analogous fashion to the indirect rating discussed above, we can construct for the ith scenario a $n \times k$ matrix $\mathbf{E}_\mathbf{k}^\mathbf{i}$ of $ESLI_K$ values with all of the possible patches as rows and species as columns. Note that for any scenario, some of the n patches may be absent, in which case the ESLI values equal zero. The differential effects of the scenarios on carrying capacity of each patch can be

summarized as $(\mathbf{E}_{\mathbf{k}}^{\mathbf{i}} - \mathbf{E}_{\mathbf{k}}^{\mathbf{j}})\mathbf{w} = \mathbf{r}_{\mathbf{K}}$, where each element of the $n \times 1$ column vector

$$\mathbf{r}_{\mathbf{K}} = \sum_{h=1}^{k} w_h ESLI_{K_h},$$

i.e., the weighted sum of the $ESLI_K$ values for a patch. Substitution of $ESLI_C$ yields a corresponding vector $\mathbf{r}_{\mathbf{C}}$. These vectors form the basis for subsequent graphical or geospatial comparisons of alternative scenarios at a detailed level.

A direct ecological rating can be derived from patch-specific ESLIs if field data on occupancy are available. Because the observed response variable is binary, a predictive model of patch occupancy can be constructed for each species as a logistic function of $ESLI_{K_i}$ and $ESLI_{C_i}$. From this series of k regression equations, a $n \times k$ matrix $\mathbf{P}^{\mathbf{i}}$ of predicted probabilities of occupancy can be generated for the ith planning scenario. A patch-by-patch comparison of scenarios i and j can be obtained as $(\mathbf{P}^{\mathbf{i}} - \mathbf{P}^{\mathbf{j}})\mathbf{w}$.

CONCLUSIONS

Our analysis suggests that ecologically scaled landscape indices can be useful predictors of patch occupancy in a variety of organisms occupying agricultural systems. We view ESLIs as practical tools for assessment of land-use planning scenarios, because they are derived from a solid theoretical foundation, are readily interpreted, and combine physical attributes of landscapes with ecologically relevant attributes of species. ESLIs thus provide planners with a valuable tool for incorporating biodiversity into the evaluation process. Of course, a more complete assessment also may require the use of tactical or incidence-based models, or other more detailed studies of potential impacts on biodiversity.

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