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Using an index of habitat patch proximity for landscape design

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Abstract

A proximity index (PX) inspired by island biogeography theory is described which quantifies the spatial context of a habitat patch in relation to its neighbors. The index distinguishes sparse distributions of small habitat patches from clusters of large patches. An evaluation of the relationship between PX and variation in the spatial characteristics of clusters of patches showed that reduction in the isolation of patches within a cluster produced exponential increases in PX, and that increase in the size of those patches produced a more modest linear increase in PX. Simulations using neutral model landscapes were used to determine the effect of the scale of analysis on PX. Increased size of the neighborhood considered around a habitat patch (proximity buffer) produced linear increases in PX, the slope being dependent on the proportion of the habitat of interest on the landscape. The proximity index was used to evaluate three alternative conservation reserve designs in an agricultural landscape, and comparisons were made among designs consisting of the same area of forest habitat added to the landscape. The 'single, large' reserve design produced the greatest increase in mean PX values among forest patches on the landscape when the total area of forest added was ≥ 842 ha, and the 'several, small' reserve design produced the greatest increase when the total area of forest added was ≤ 716 ha. The 'string-of-pearls' reserve design produced mean PX values approximately equal to those of the 'single, large' configuration when the total area of forest added was ≤ 716 ha and the proximity buffer was ≥ 2.1 km, since the 'string-of-pearls' configuration produced a higher total number of neighbors around the added reserves, which helped offset the smaller size of each reserve. Large reserves have more area, but their influence is limited to fewer neighbors. There appears to be a size threshold where the increased area of single, large reserves produced higher PX values than other configurations that influence more neighbors. Visualization of the spatial distribution of PX values across the landscape can reveal how organisms with specific movement scales might perceive the effective fragmentation of the landscape (spatial variability of PX), further aiding conservation reserve planning and design.

Keywords: Habitat patch; Landscape design; Proximity index

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1. Introduction

Terrestrial ecosystems around the world have undergone varying degrees of fragmentation as a result of human land use conversion that has disrupted the continuity of natural habitats (Lord and Norton, 1990). This fragmentation has had detrimental effects on some components of the biota due to reduction in habitat area, isolation of habitats, increased proportion of edge relative to interior conditions, and an increase in unsuitable environments within a landscape (Burgess and Sharpe, 1981; Harris, 1984; Wilcove et al., 1986). Landscapes dominated by agriculture often contain simplified natural ecosystems that are vulnerable to further disturbance (Forman, 1987; Saunders et al., 1991).

Island biogeography and metapopulation models suggest that barriers to movement between habitat fragments can affect communities such that, over time, more species will be locally extirpated, and biodiversity will be less (MacArthur and Wilson, 1967; Patterson, 1987; Pulliam, 1988; Burkey, 1989; Pulliam and Danielson, 1991; Verboom et al., 1991). Stability of many metapopulations requires periodic immigration to local populations in marginal habitats, and the restriction of movement by physical or perceived barriers can increase the rate of local extinctions (Terborgh, 1974; Brown and Kodric-Brown, 1977; Den Boer, 1981; Stacey and Taper, 1992).

Much of the study of conservation reserve design is based on the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) which includes the idea that, all other things being equal, species richness is likely to be higher on a large island closer to a source of immigrants than on a smaller, more isolated island. This concept has routinely been extended to terrestrial habitat islands, although few objective measures of the spatial context of habitat patches are in use in the ecological study of fragmented landscapes (see Knaapen et al., 1992, for a recent exception). In this paper, we present a proximity index (PX) to quantify the spatial relationship of

habitat patches to other neighboring patches. This index complements other indices commonly used to quantify various aspects of landscape spatial pattern (e.g. habitat diversity, habitat abundance, core area and amount of edge habitat) important in conservation planning.

The relative merits of a single, large reserve versus several smaller reserves has generated considerable discussion (Wilcove et al., 1986; Quinn and Hastings, 1987; Gilpin, 1988; Simberloff, 1988; Wright, 1990), but the primary concern has been the preservation of viable populations of species with large area requirements, or that exist in low densities. Other work has focused on the relationship between movement scales of organisms and the effective connectedness of habitat on landscapes by applying percolation theory to models of resource use in fragmented environments (O'Neill et al., 1988; Gardner et al., 1989, 1993). Little attention has been paid to strategies for developing conservation reserves in highly fragmented landscapes to restore more natural ecosystems and enhance an impoverished biota.

Biodiversity issues are ultimately concerned with the higher-level processes suggested by hierarchy theory, and are rightly addressed over broad spatial scales and long time-frames (Urban et al., 1987; Rahel, 1990). Although threatened species may be maintained by local and short-term strategies, stable ecosystem functioning is possible only when broad-scale conditions are addressed to maintain long-term ecosystem integrity. The design of conservation reserve systems must consider the spatial relationships of habitat reserves in the context of the broader landscape.

The objectives of this study were (1) to describe a quantitative index of the spatial context of habitat patches (PX), (2) to evaluate the relationship between PX and variation in the spatial characteristics of clusters of patches, (3) to determine the effect of the scale of analysis on calculations of PX, and (4) to demonstrate the use of PX to evaluate alternative landscape designs in an agricultural landscape.

2. The proximity index

The proximity index (PX) distinguishes sparse distributions of small habitat patches from clusters of large patches. The index is most suited to evaluation of 'high contrast' landscapes where the habitat of interest is distinct from the surrounding matrix. In this paper we use forests as the patch type of interest, but any patchy habitat type could be evaluated. A PX value is calculated for each forest patch by identifying each forest patch i whose edge lies at least partially within a specified number of pixels (proximity buffer) of the patch being indexed. PX is calculated using area (S_i) and the edge-to-edge distance from patch i to its nearest-neighbor forest patch (z_i) of each of the n forest patches identified within the buffer, including the patch being indexed:

$$PX = \sum_{i=1}^n (S_i / z_i)$$

PX is large when the patch is surrounded by larger and/or closer patches, and decreases as patches become smaller and/or more sparse (Fig. 1). For each forest patch, a unique proximity buffer is delineated to identify the forest patches to be included in the calculation. Note that PX incorporates the isolation (z_i) of each forest patch within the proximity buffer, rather than the distance from the patch being indexed to each of those patches (as in Whitcomb et al., 1981). The index evaluates the landscape context of forest patches at a specific scale of analysis that is determined by the size of the proximity buffer. When the edge of the map lies within the proximity buffer, calculated PX values do not reflect the presence of patches that may exist outside the map.

It should be noted that any configuration containing non-habitat gaps has the potential for 'impermeable' barriers to organism movement to develop, such as high-density urban development. Such a barrier might severely restrict organism movement, and reduce the value of conservation reserves placed to enhance movement. The proximity index is insensitive to the type of boundaries that exist within the landscape matrix.

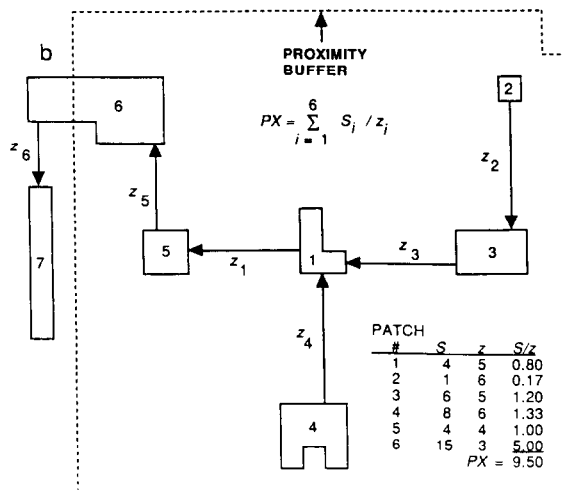
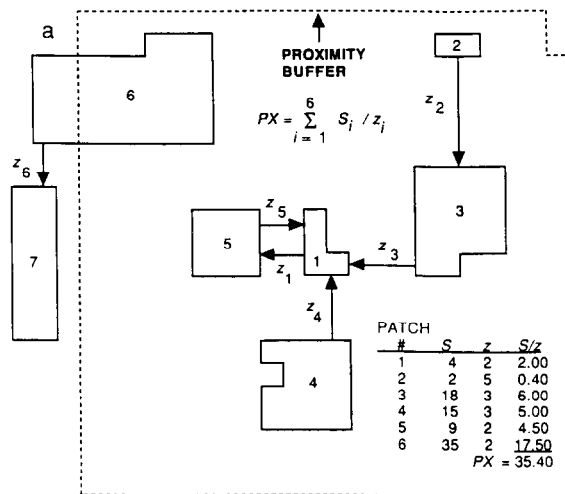


Fig. 1. Schematic diagram of the calculation of the proximity index of a single forest patch (Patch 1) on two hypothetical landscapes. The proximity buffer is 10 pixels from the edges of Patch 1, and Patches 1-6 are used in the calculation of PX, while Patch 7 is not used since it lies entirely outside the proximity buffer. S_i is area of Patch i (in pixels), z_i is distance to nearest neighbor of Patch i (in pixels), where i represents Patches 1-6. Hypothetical landscape (a) represents a configuration where patches are less isolated and there is a greater abundance of forest habitat, and (b) reflects a lower abundance of forest habitat and greater isolation of patches. In both cases, the PX value calculated is for Patch 1 only.

3. Methods

3.1. Simulations

To evaluate the effects of the size, isolation, and number of patches within the proximity buffer on the value of PX, we calculated PX for a hypothetical patch surrounded by other patches, and systematically varied the size and isolation of the neighboring patches, and the total number of patches within the proximity buffer. To assess the influence of proximity buffer size, we generated a series of neutral model landscapes, each 120×120 pixels. Landscapes were generated at each proportion (*p*) of a habitat of interest *i*, from $p_i=0.1$ to 0.8 in 0.1 intervals ($N=3$ for each, except $N=4$ for $p_i=0.5$ and 0.6) such that randomly placed rectilinear clumps of random lengths and widths were added until p_i was reached (as in Gustafson and Parker, 1992). The PX value of each patch was calculated using buffer widths of 4, 14, 24 and 34 pixels, and the mean PX value for each landscape was calculated and plotted.

3.2. Reserve design

The evaluation of alternative landscape designs was conducted using a 143 244 ha landscape in the Kankakee Marsh region in northwest Indiana, USA, an area that was formerly one of the largest wetland forest ecosystems in the midwestern USA (Meyer, 1936), but which has been largely drained and converted to agriculture, leaving forest habitats fragmented and relatively isolated. The study area included the area around the Jasper-Pulaski and Winamac State Fish and Wildlife Areas, which are the largest blocks of forest in the study area. We used the proximity index to evaluate three alternative conservation reserve designs that were digitized onto a digital land cover map, and the simulated reserves were recoded to represent forest. The simulated reserves were located so that they were spread evenly between the two fish and wildlife areas, the distance between reserves depending on the number of reserves added. The designs tested were: (1) a 'single, large' reserve design,

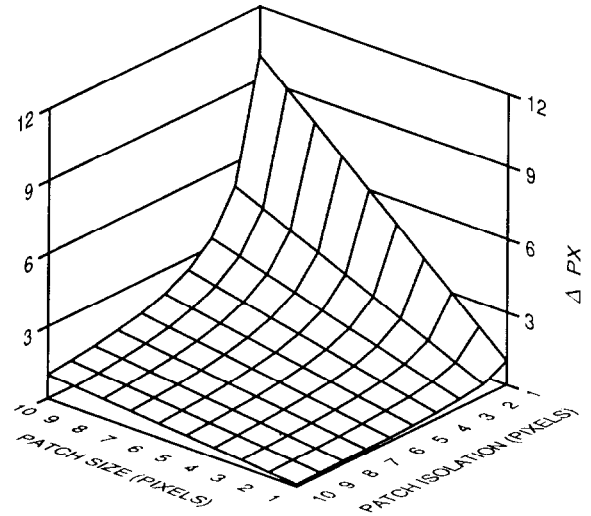


Fig. 2. The change in the PX value (ΔPX) of a habitat patch as a function of the size (*S*) and isolation (*z*) of a patch added within the proximity buffer.

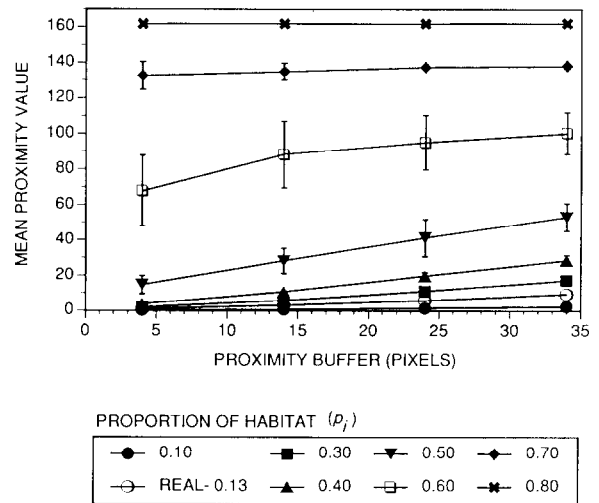


Fig. 3. Effect of proximity buffer width on mean PX values, calculated for neutral model landscapes. The points denoted 'REAL' refer to the study area landscape, which was 13% forested. Error bars represent 1 standard deviation.

where the reserve was located approximately 9.4 km from each of the two state fish and wildlife areas; (2) a 'several, smaller' reserve design, where the reserves ($N=4$) were approximately 3.75 km apart; (3) a 'string-of-pearls' design of 14 small reserves, approximately 0.9 km apart.

The total area of the added reserves was held constant among design configurations to allow comparison of the alternative designs, and three levels of total reserve area added were simulated (590, 716 and 842 ha) for a total of nine scenarios. The purpose was to demonstrate a potential 'what-if' analysis using PX that might be conducted by a conservation agency considering land acquisition in this area.

The digital map of existing land cover was derived from a 7 June 1989 Landsat Thematic Mapper image, with a pixel resolution of 30 m, using a combination of unsupervised and supervised classification techniques (Lillesand and Kieffer, 1987) and PC-ERDAS (ERDAS Inc., Atlanta, GA) image processing software. Classes delineated were: bare soil; grass cover (pasture, hay, or winter wheat); forest (>70% canopy closure); water; urban. Classification accuracy was assessed by comparing the classification map with reference data derived from NAPP (Na-

tional Aerial Photography Program) color infrared aerial photographs (1:40 000) taken in 1987 and 1988, and USDA Agricultural Stabilization and Conservation Service color slides taken in 1989. Test polygons representing the boundaries of the land cover patches found at 637 randomly selected locations (mean size 14.2 pixels, encompassing 1.0% of the classified pixels) were digitized from the reference data and compared to the classification map. The overall classification accuracy was 88.9%, and the classification accuracy for forest was 94.8%. Landsat data were selected because they cover large areas, and because digital data are well suited to computer analyses.

Forest patches were identified as clusters of contiguous forest pixels (pixels with common edges or corners), and the proximity index (PX) was calculated for each patch on each map using a computer program written in FORTRAN. We were forced to make a trade-off between map

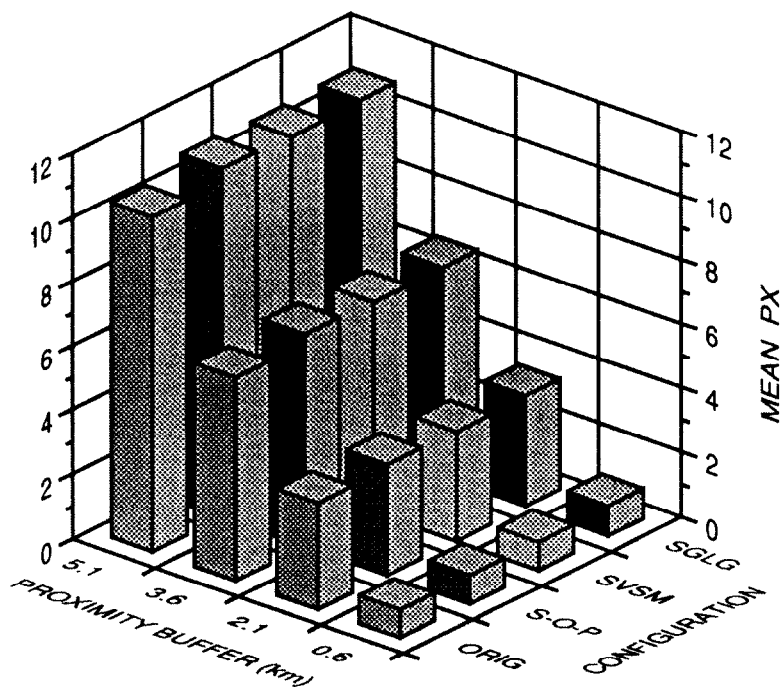
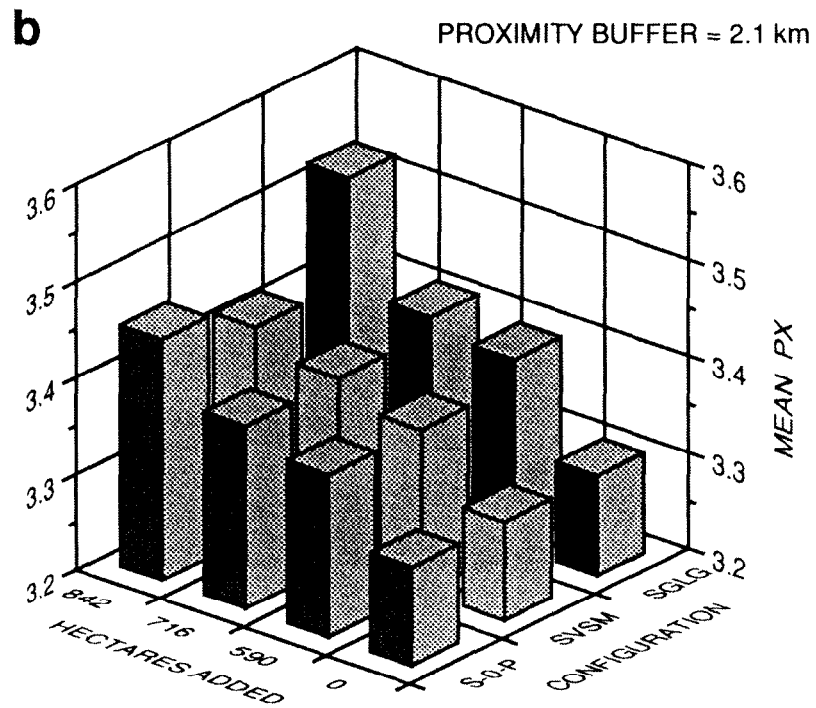
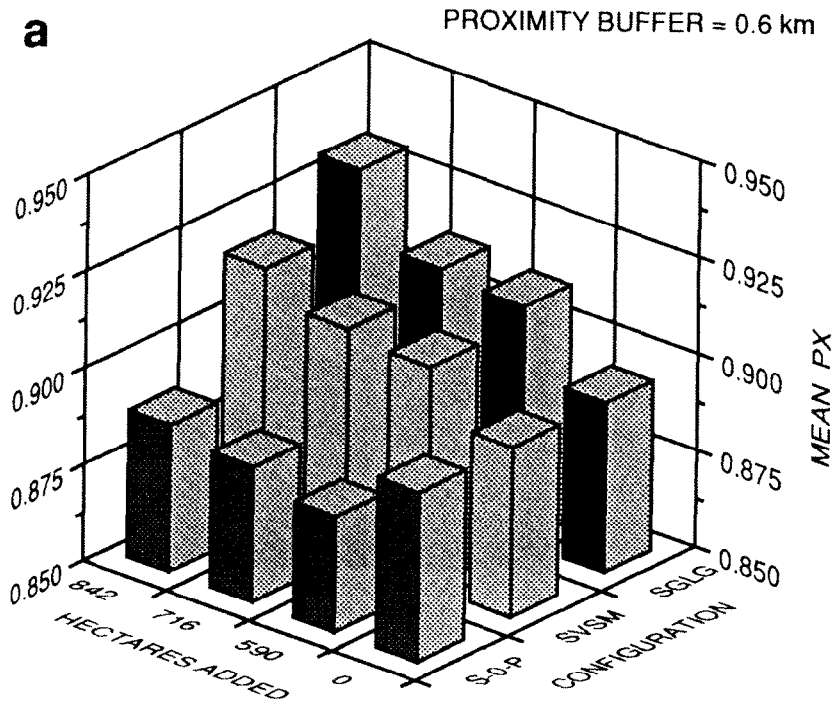


Fig. 4. Relationship between mean PX values and the width of the proximity buffer (scale of analysis) for four conservation reserve configurations, where the total area of forest added in each configuration was 716 ha. ORIG is the original landscape with no reserves added, S-O-P is a 'string-of-pearls' configuration, SVSM is a system of 'several, small' reserves, and SGLG is a 'single, large' reserve.



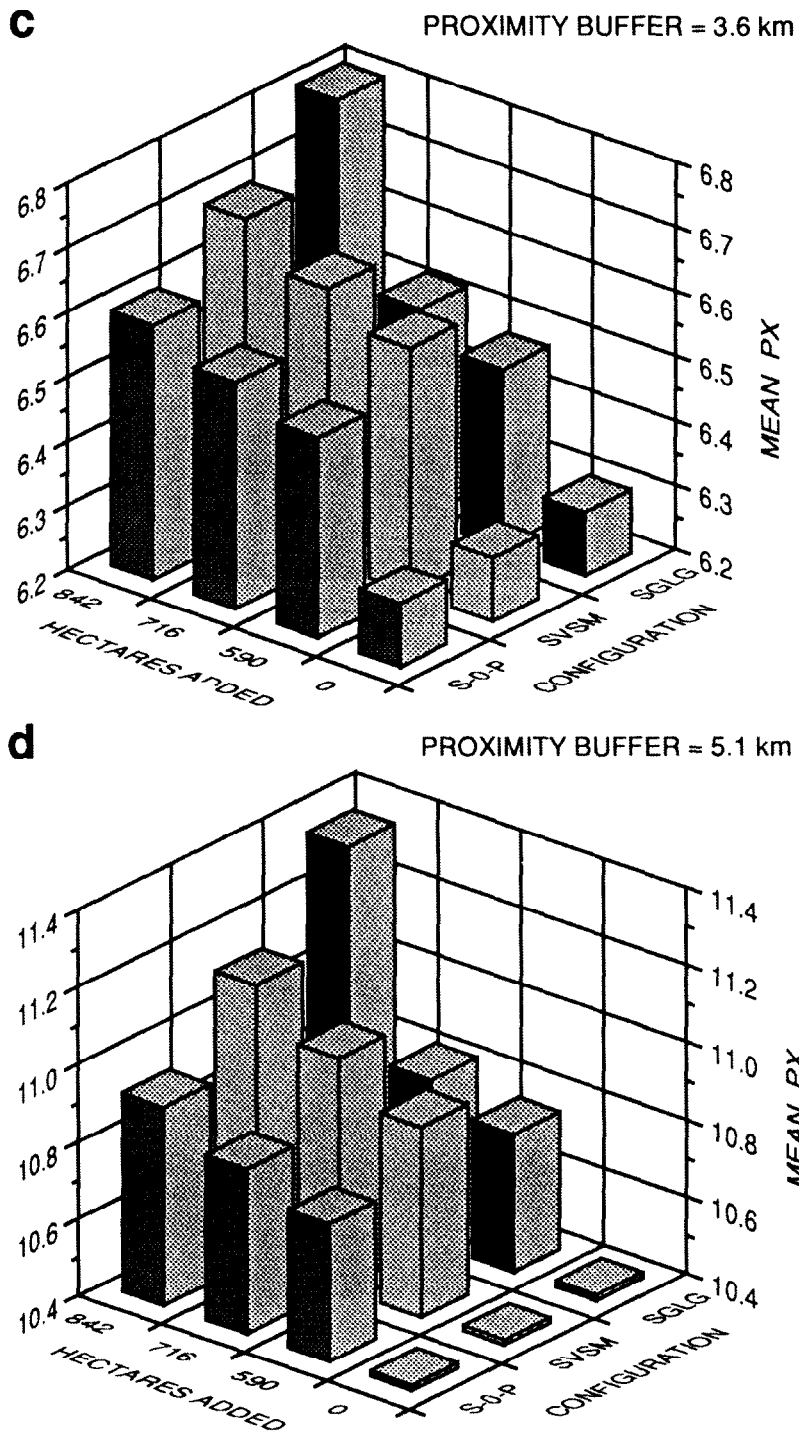


Fig. 5. Effect of conservation reserve configuration and the total area of forest added in reserves on mean PX values of forest patches. Zero hectares added refers to the original landscape with no reserves added. S-O-P is a 'string-of-pearls' configuration, SVSM is a system of 'several, small' reserves, and SGLG is a 'single, large' reserve. The results were calculated using the proximity buffer sizes indicated.

resolution and computational resources, since at 30 m resolution there were $\approx 1.6 \times 10^6$ pixels, and > 5300 forest patches. The classification map was aggregated to a pixel size of 150 m for these analyses. This pixel resolution (grain) was considered appropriate for the spatial extent (51.9 km across) of the area studied, and the scales of analysis used, although the omission of woodlots < 2.2 ha may have changed the spatial characteristics of the landscape significantly as perceived by some species. Our analysis considers this landscape from the perspective of relatively mobile organisms and assumes that the patches delineated reflect forest patches as perceived by these organisms. Consideration of less mobile

species would require greater pixel resolution and involve a smaller spatial extent (Wiens, 1989).

A range of proximity buffer widths (4–34 pixels, representing 0.6–5.1 km) was used in the calculation of PX to assess the changes in PX values resulting from different scales of analysis. This range was chosen to include values large enough to capture some of the broad landscape structure that might affect organism movement dynamics at landscape scales, but also values small enough to reflect the scale of movement of relatively less mobile species. Thus the analysis examines the landscape as it might be perceived by a variety of organisms that have different dispersal and movement abilities.

a PROXIMITY BUFFER = 0.6 km

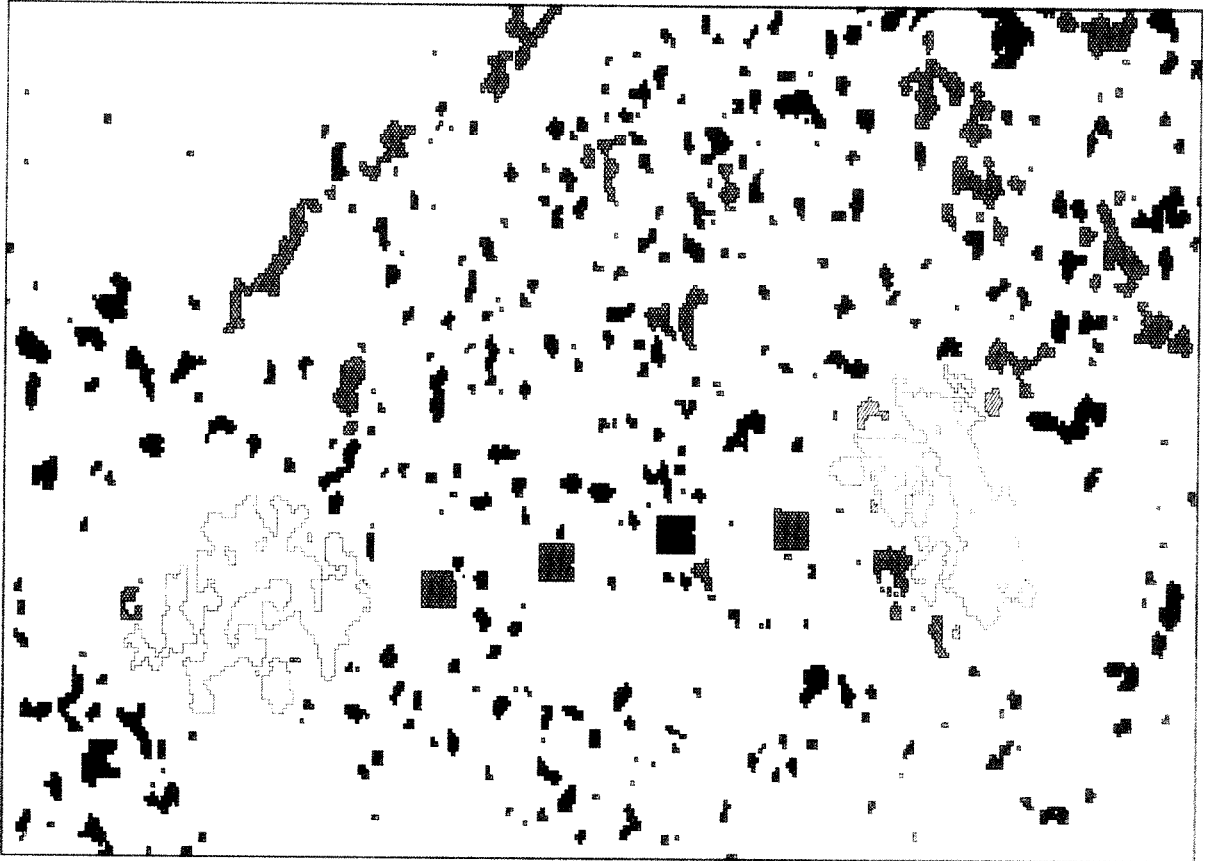


Fig. 6. Maps showing the spatial variability of PX of a 'several, small' reserve configuration calculated using the proximity buffer sizes indicated. The four forest reserves are located between the large blocks of forest in the Jasper-Pulaski (left), and the Winamac (right) State Fish and Wildlife Areas.

The mean PX value of all forest patches for each alternative design was calculated at each scale of analysis (proximity buffer) and plotted, and maps were produced showing the PX values of each forest patch on the landscape.

4. Results

4.1. Simulations

Increased size (S) of a single patch within the proximity buffer produced a linear positive change in PX (ΔPX), but reduction in the isola-

tion (z) of a single patch produced an exponential increase in ΔPX (Fig. 2). A linear relationship was found between an increase in the number of patches within the proximity buffer and ΔPX (not plotted, slope = S/z , $R^2 = 1.0$), when size and isolation of patches were held constant. PX is most sensitive to variation in isolation (z), especially when z is relatively small.

PX increased linearly as buffer size was increased on neutral model landscapes (Fig. 3). The slope of the relationship increased as p_i increased ($0.1 < p_i < 0.5$). The decrease in slope associated with landscapes having $p_i > 0.6$ reflects the formation of a percolating cluster, a patch

b PROXIMITY BUFFER = 2.1 km

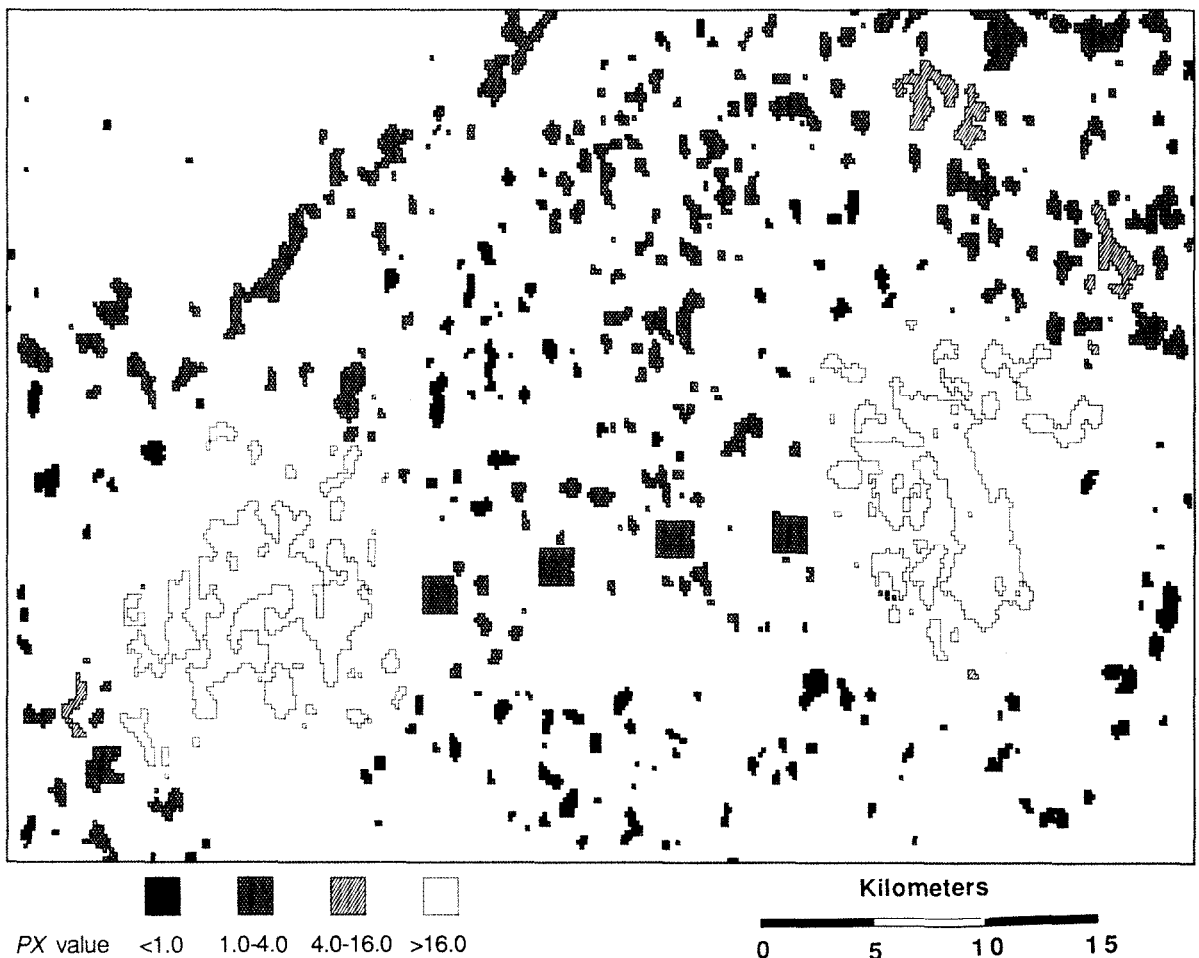


Fig. 6 continued.

that extends completely across the landscape grid due to the coalescence of randomly added clumps. For random grids generated with this algorithm, we found that the probability of the formation of a percolating cluster approached 1.0 when $0.55 < p_i < 0.59$. See O'Neill et al. (1988), Gardner et al. (1989) and Gustafson and Parker (1992) for discussions of percolation theory and landscape modeling. When $p_i > 0.6$, landscapes were dominated by a large percolating cluster, and increased buffer size resulted in few additional neighbors incorporated into the calculation of PX, and only modest increases in PX were realized. When $p_i = 0.8$ for example, there were typically only 4–7 patches on the landscape, and all were within 4 pixels of the large, percolating

cluster, so increased buffer size had no effect on PX.

4.2. Reserve design

Mean PX values of the alternative reserve configurations calculated using different buffer sizes show that variability caused by differences in the spatial arrangement of the reserves is negligible compared to the effects of changing the scale of analysis (Fig. 4). When the effects of the scale of analysis are separated from the effects of reserve configuration, the results show that as the area added in reserves increases, the mean PX value increases, and the rate of increase is greatest for the 'single, large' configuration (Fig. 5). In Fig. 5(a), the 'string-of-pearls' configuration

C PROXIMITY BUFFER = 3.6 km

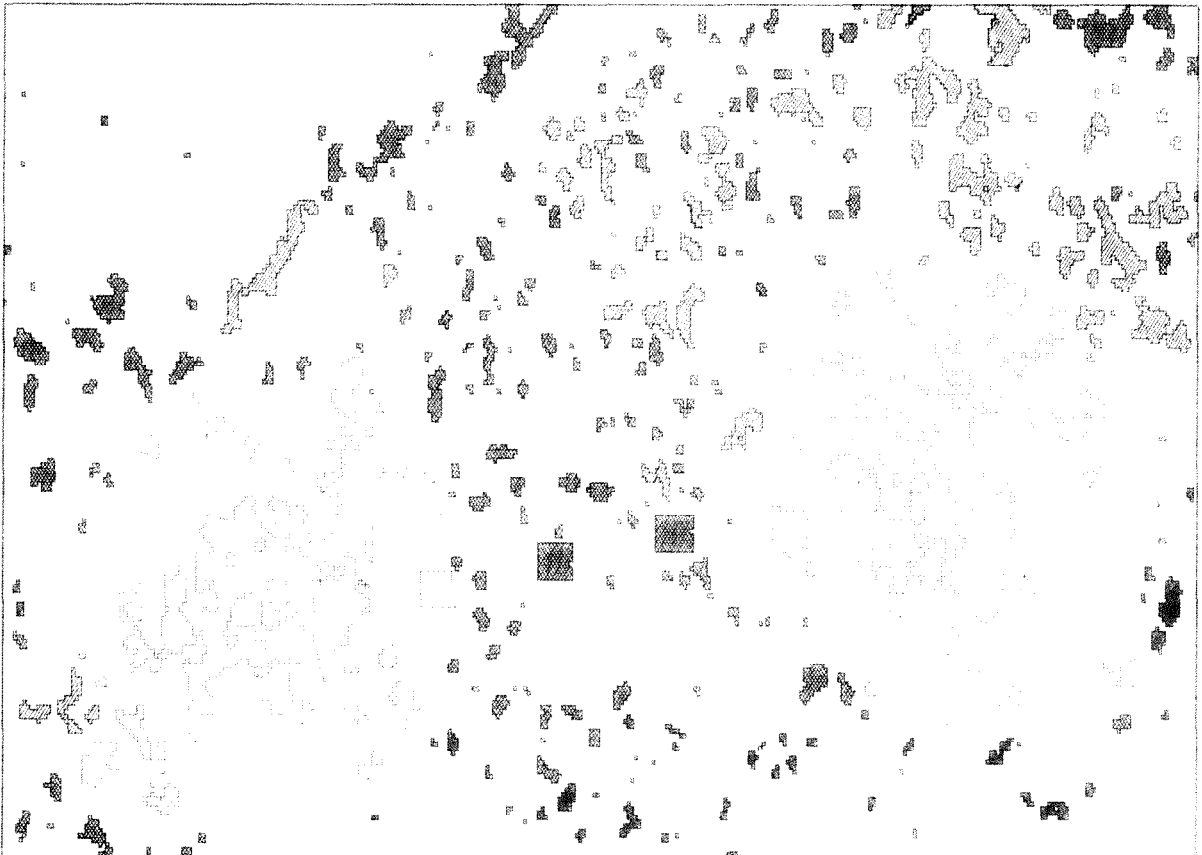


Fig. 6 continued.

has a lower mean PX value than the original landscape when the buffer width is 0.6 km, since these reserves are more than 0.6 km apart, and their PX values are less than the average PX values of the original landscape. The 'several, small' configuration and the 'single, large' configuration had approximately the same mean PX value, except when the area added as reserves was 842 ha. In Fig. 5(b), the mean PX values of each configuration was approximately the same except when the area added as reserves was 842 ha. Figs. 5(c) and 5(d) show that the 'several, small' configuration had a greater mean PX than the 'single, large' configuration when the area added

as reserves was ≤ 716 ha. Since the four reserves in the 'several, small' configuration had a greater total number of neighbors than the single large reserve, the resulting PX was greater. However, when 842 ha were added, the 'single, large' configuration showed higher mean PX values than the 'several, small' configuration, suggesting that at some point the influence of the increased area of the large reserve overcomes the limited number of neighbors around it. This phenomenon also may explain the higher PX value for the 'string-of-pearls' configuration than for the 'several, small' configuration when 842 ha of forest were added in Fig. 5(b). It is important to note

d PROXIMITY BUFFER = 5.1 km

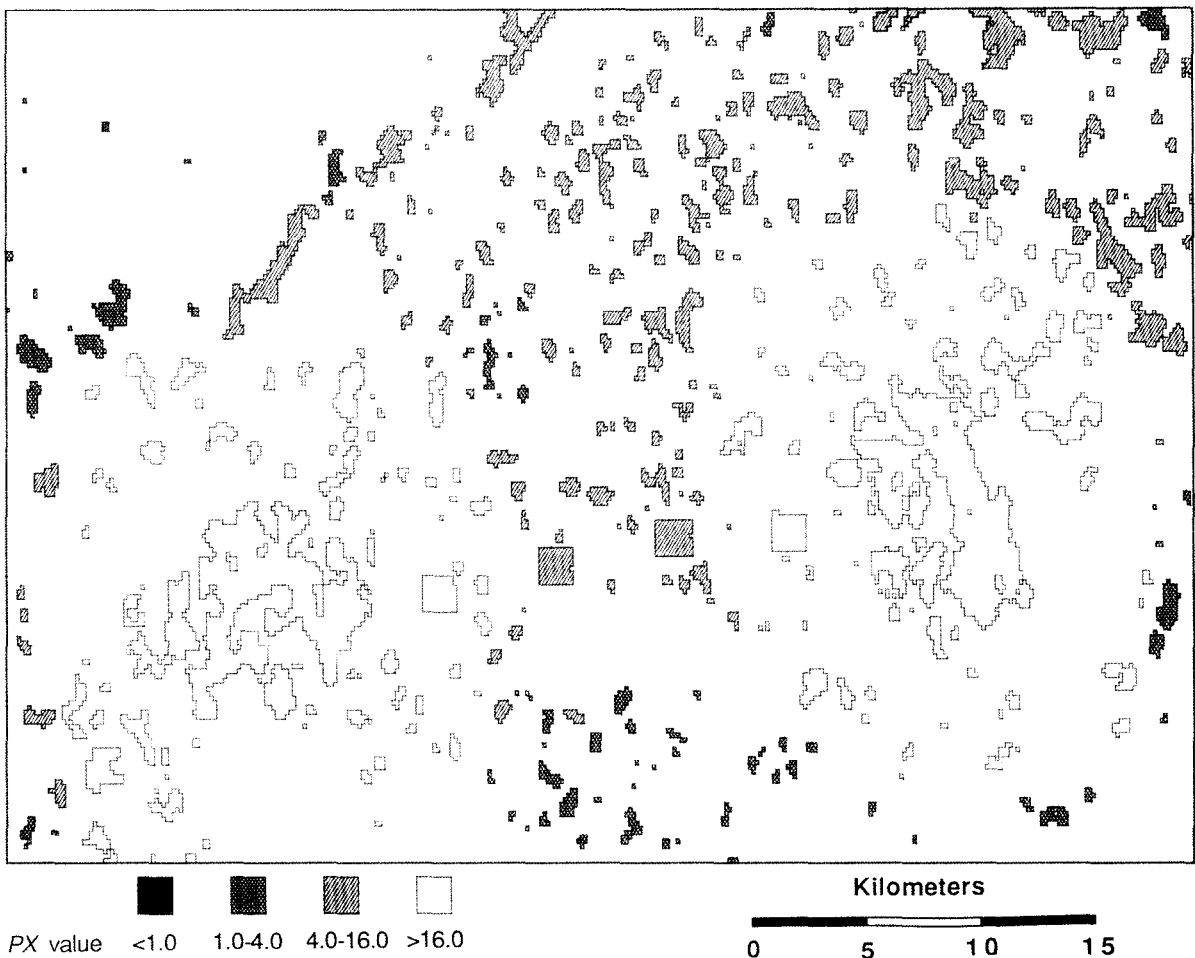


Fig. 6 continued.

that reserves became neighbors of each other when the buffer was ≥ 2.1 km for the 'string-of-pearls' configuration, and when the buffer equaled 5.1 km for the 'several, small' configuration.

A map of the distribution of PX values among patches across the landscape provides a visualization of how organisms that move at a specific scale might perceive the fragmentation of a landscape. The example configuration given in Fig. 6 shows that the effective fragmentation (disconnectedness of habitats) changes with the scale of analysis. When the proximity buffer was relatively small (Fig. 6(a)) the variation in PX values among patches was greater, and transitions from regions of low PX to high PX were relatively abrupt. When the proximity buffer was large, the distribution of PX values was relatively more homogeneous (Fig. 6(d)), as the effective fragmentation of the habitat became less. In Fig. 6(a), the forest patches between the reserves have relatively low PX values, reflecting the smaller scale of analysis (0.6 km), while in Fig. 6(d) those same patches have relatively high PX values when the buffer width equals 5.1 km.

5. Discussion

The importance of the scale of analysis and its relation to the movement scale of organisms suggests that differences in the mobility of organisms may make reserve designs irrelevant to most organisms on the landscape unless they are designed to reduce fragmentation across a wide range of spatial scales (Lord and Norton, 1990). At specific scales there appears to be a tradeoff between the size of reserves added and the increased density of patches (increased number of neighbors around habitat patches) which results from a greater number of habitat patches added. When the total area to be added is relatively low, greater gains in PX are realized by reducing the isolation of patches, but when more habitat can be added, the concentration of habitat in larger patches produces greater increases in PX.

The proximity maps generated for each landscape were assumed to reflect the spatial varia-

bility in forest habitat accessibility such that forest patches with relatively high PX values were associated with configurations more conducive to the movement of organisms to and from the patch and more likely to support populations that are part of more stable metapopulations. Calculation of PX over a range of scales may provide an indication of the relationship between movement scale and the connectedness of a landscape. The PX map can be used to identify locations where low PX values may be effectively disconnecting the landscape at a specific scale of analysis. Analyses made for specific taxa can include land cover information at an appropriate scale, and a proximity buffer approximating the movement scale of those organisms can be chosen (see Gustafson et al., 1994, for an example using wild turkeys, *Meleagris gallopavo*). In these cases, specific hypotheses concerning reserve design can be generated and tested (Murphy and Noon, 1992).

To illustrate, consider that our analysis using a proximity buffer of 0.6 km could be used to assess the perception of the fragmentation of this landscape by white-footed mice (*Peromyscus leucopus*, dispersal distance 85–867 m; Krohne et al., 1984) or raccoons (*Procyon lotor*, mean dispersal distance 0.4 km, maximum <1.6 km; Butterfield, 1944). The proximity buffer of 3.6 km could be used to assess the landscape for ruffed grouse (*Bonasa umbellus*, dispersal distance 2.1–4.8 km; Small and Rusch, 1989), and the buffer of 5.1 km for bobcat (*Lynx rufus*, mean daily movement 5.6 km; McCord and Cardoza, 1982). An even larger buffer would be required for gray fox (*Urocyon cinereoargenteus*, dispersal distance up to 83.2 km; Sheldon, 1953) and white-tailed deer (*Odocoileus virginianus*, mean dispersal distance 40–50 km in agricultural habitats; Nixon et al., 1991). In Fig. 6, each map represents how organisms with the movement scale indicated might respond to the landscape, such that where woodlots have darker shading, dispersal would be inhibited and small habitat patches may have higher extinction rates. Mice and raccoons might find dispersal difficult and populations may be unstable (Fig. 6(a)), while gray fox and deer might have little difficulty

maintaining stable metapopulations (Fig. 6(d)).

PX is assumed to be an indicator of colonization dynamics predicted by island biogeography theory. The formulation of PX is somewhat arbitrary, and empirical studies may reveal a different relationship that will be more useful as an indicator of landscape context and organism movement. PX decreases negative exponentially as the interpatch distance (z) increases (Fig. 2), even though the formulation of PX is essentially linear. This finding is strikingly similar to those of deterministic models that apply island biogeography theory to the problem of colonization via stepping-stone islands (Gilpin, 1980). The precise nature of an appropriate relationship is not clear from island biogeography theory. Future empirical studies may show that PX has value as a predictor of species richness on habitat islands. For example, a high relative value of PX might predict those cases where area-dependent birds occur in smaller than expected forest tracts (the 'rescue effect'; Brown and Kodric-Brown, 1977; see also Askins et al., 1987). Until such studies are conducted, PX may be most useful as an indicator of habitat patch density and accessibility across a fragmented landscape, especially for organisms whose populations function as a metapopulation.

In highly fragmented agricultural landscapes, conservation goals are related to the development of a habitat configuration that can support more stable ecosystems, in which dispersal can be maximized and biodiversity enhanced. These goals are not fundamentally different from those for the preservation of threatened species except that the emphasis is shifted from the maintenance of a complex ecosystem, to a strategy that will most efficiently maximize metapopulation interaction as reserves are added over time in a simplified, human-dominated landscape. A first step may be to couple existing blocks of forest and reverse the disruption of ecological interdependencies caused by fragmentation (Lord and Norton, 1990). The configuration best suited for land acquisition depends on the conservation goals and the scale at which those goals can be realized.

The evaluation of the spatial distribution of

habitat across a range of spatial scales is critical to accurately model colonization dynamics and the long-term stability of natural populations in human-dominated landscapes. The proximity index is an example of a quantitative index, based in ecological theory, that facilitates computer analysis of spatial alternatives. The validity of this approach remains to be documented, but the utility of quantitative descriptions of the landscape spatial context of habitat patches appears to have the potential to aid the design of conservation reserve projects.

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