

ASSESSING HABITAT SUITABILITY AT MULTIPLE SCALES: A LANDSCAPE-LEVEL APPROACH

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Abstract

The distribution and abundance of many plants and animals are influenced by the spatial arrangement of suitable habitats across landscapes. We derived habitat maps from a digital land cover map of the $\sim 178,000 \text{ km}^2$ Chesapeake Bay Watershed by using a spatial filtering algorithm. The regional amounts and patterns of habitats were different for species which occur in 'woody', 'herbaceous', and 'woody-edge' habitats. Habitat for finerscale species (~5 ha home ranges) was twice as abundant and more evenly distributed than habitat for coarserscale species (~410 ha home ranges) in a 11,000 km² sub-region. Potential impacts of land cover changes on habitats in different parts of the region were assessed by the frequency distributions of habitat suitability for smaller ($\sim 3000 \text{ km}^2$) embedded watersheds. The methods described in this paper can be applied to several scales of digital land cover data, and used to derive multiplescale habitat suitabilities for a number of species or guilds. © 1997 Elsevier Science Ltd

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INTRODUCTION

Landscape ecologists have made considerable progress in quantifying landscape pattern (e.g. Krummel et al., 1987; O'Neill et al., 1988a; Turner & Gardner, 1991). Insight has also been gained into pattern formation through random processes (Gardner et al., 1987), disturbance (Turner et al., 1989, 1993), and land use history (Wallin et al., 1994). However, although landscape pattern and process are linked (Turner, 1989), it has proven more difficult to move from spatial patterns to assessments of changes in ecological processes (Wiens et al., 1993). Because society values ecosystem structure and function rather than abstract properties of pattern

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(Gardner et al., 1993; Dale et al., 1994), application of landscape concepts often demands ecological interpretation of pattern (Hunsaker et al., 1990). Traditionally, within-site habitat quality has been used to evaluate habitat suitability. But spatial pattern among sites is also important in determining the suitability of habitat for a range of species (Cutler, 1991; Flather et al., 1992; McCollin, 1993; Kattan et al., 1994; Koopowitz et al., 1994; Short & Turner, 1994). Furthermore, fragmentation of habitats has been implicated in overall declines of species richness and individual species across the globe. Fragmentation results in decreased sizes of continuous habitat (e.g. interior forests) and decreased connectivity among metapopulations (Verboom et al., 1991). As distances between patches of suitable habitat increase, the probability of extinction increases for individual populations, and the probability of recolonization by surviving populations decreases (Verboom et al., 1991). The result of fragmentation is the loss of populations and species over time (Kattan et al., 1994; Koopowitz et al., 1994; Short & Turner, 1994).

Within a geographic region, species respond differently to habitat changes because of differences in habitat requirements and the scales at which they interact with the environment (Kattan et al., 1994; Koopowitz et al., 1994). The differences in habitat requirements reflect fundamental differences in individual species' life-history requirements and population structure (Hanson & Urban, 1992; Wiens et al., 1993). The MacArthur and Wilson (1967) general equilibrium model predicts that species with large patch requirements and low mobility are lost first, whereas species with small patch requirements and high mobility will persist in fragments of suitable habitat. Such extinction patterns have been described for mammals (Cutler, 1991) and reptiles (Jones et al., 1985). For this reason, it is important to understand changes in patch sizes and connectivity at the scales at which a species interacts with the landscape. Although a broad-scale approach is sometimes used as a first approximation to ecosystem management, a single scale cannot be equally appropriate for all

species over large and heterogeneous regions (O'Neill et al., 1988b).

In the present paper we explore landscape pattern interpretations as they relate to habitat suitability and ecological assessments. Regional maps of suitable 'woody', 'herbaceous', and 'woody-edge' habitat are derived for the Chesapeake Bay Watershed from a digital land cover map by using a spatial filtering algorithm. We demonstrate how the scale at which habitat is evaluated affects the apparent landscape variability and configuration of habitats as perceived by different organisms. Examples are given to show how these habitat maps can be used to assess the possible impacts of land cover changes on different species. By evaluating habitat suitability, we move from abstract spatial pattern to the potential for a landscape to support a community of organisms, and we gain insight into managing the spatial distributions of habitats when designing reserves.

STUDY AREA AND METHODS

Digital land cover map

We investigated habitat suitability in the Chesapeake Bay Watershed, which is located in the eastern United States (Fig. 1). This region was selected because an extensive (large area) yet relatively fine-grained (high resolution) land cover map was available in digital format, and because it contains a wide range of habitat conditions associated with geophysical and historical land use patterns. The study was part of a larger effort by the United States Environmental Protection Agency in the Mid-Atlantic region to assess exposure to stress using patterns of wildlife habitat suitability as an indicator.

The digital land cover map was derived from Landsat Thematic Mapper images from 1988, 1989 and 1991 during leaf-on periods (Environmental Protection Agency, 1994). In an Albers conical equal-area projection, the pixel (picture element) size was 0.0625 ha $(25\times25 \text{ m})$. The study area was $\sim178,000 \text{ km}^2$ and contained ~285 million pixels. Six land cover classes were recognized: woody, herbaceous, exposed land, water, high-intensity developed and low-intensity developed for which the overall, per-pixel classification accuracy was 80% (Environmental Protection Agency, 1994). The woody class includes forest and woodland. and the herbaceous class includes agricultural lands and fallow fields. Exposed land includes bare ground, large rock outcrops, and beaches. The water class includes lakes, rivers, estuaries, reservoirs and canals. The highintensity developed class is mainly urban centers, and the low-intensity developed class includes suburban and residential areas.

The woody and herbaceous classes occupied about 56% and 33%, respectively, of the total study area (which includes water surface area). The water class

occupied about 7%, and the low-intensity developed class about 3% of the area. The remaining two classes together comprised less than 1% of the area. The woody class predominated in the north and west, whereas the east is primarily a matrix of woody and herbaceous classes. Major urban centers include Norfolk, Richmond, Washington DC, Baltimore, Harrisburg and Binghamton (Fig. 1).

Habitat models

We analyzed habitat suitability for three archetypic species: woodland, herbaceous/field, and woodland edge. The habitat analysis started with a window which represents a potential 'home range' for a species. The window was a square, fixed-area neighborhood placed somewhere on the land cover map. A habitat suitability score was calculated from the land cover amounts and patterns within the window. The 'woody habitat' function was the proportion of woody cover in a window, the 'herbaceous habitat' function was the proportion of herbaceous cover, and the 'woody-edge habitat' function was the proportion of edges (of those between cardinally-oriented pairs of pixels in the window) which joined the woody class with a non-woody class.

By sliding the window in steps, one pixel at a time, over the entire digital coverage, it was possible to enumerate the habitat scores for all possible home ranges. These scores were stored on a map (rather than in a list) so that their spatial patterns could be analyzed; the storage location was the center pixel of a given window. Strictly, the map themes were area density for woody land cover, herbaceous land cover, and woodyedge occurrence. We interpreted them as maps of potential habitat suitability.

Multiple window sizes were used to model habitat suitability for species which sense the landscape at different scales. The window sizes used were approximately 5 ha (9×9 pixels; 5.0625 ha), 46 ha (27×27 pixels; 45.5625 ha), and 410 ha (81×81 pixels; 410.0625 ha). We tested the effects of window (or home range) size for the woody habitat function only, using just a portion ($\sim11\,000$ km²) of the study region for illustration.

Data reduction

Maps of habitat can exhibit structure at many scales. Our interest was on very broad-scale, regional patterns. Patterns at this scale do not depend on local irregularities in a surface map. In fact, fine-scale peaks and valleys could be interpreted as 'noise' in a regional analysis. A median filter (e.g. Gonzalez & Woods, 1992) was used as a smoothing function. Briefly, the median pixel score was calculated for all 81 pixels in a 9×9 pixel window. The median value was then assigned to a single pixel in a new map for which the unit pixel area was defined as 5.0625 ha (i.e. the area of the original 9×9 pixel window). The window was moved in steps, one window at a time, over the entire map. By extracting the median value, information about variation within the

window has been lost. This is accounted for by a decrease in data resolution. The procedure simplified subsequent analysis by reducing the number of pixels in each map to ~ 3.5 million.

Suitable habitat thresholds

Threshold values were selected to define 'suitable' habitat as the area of the highest peaks on the maps of habitat potential. Segmenting maps into regions above

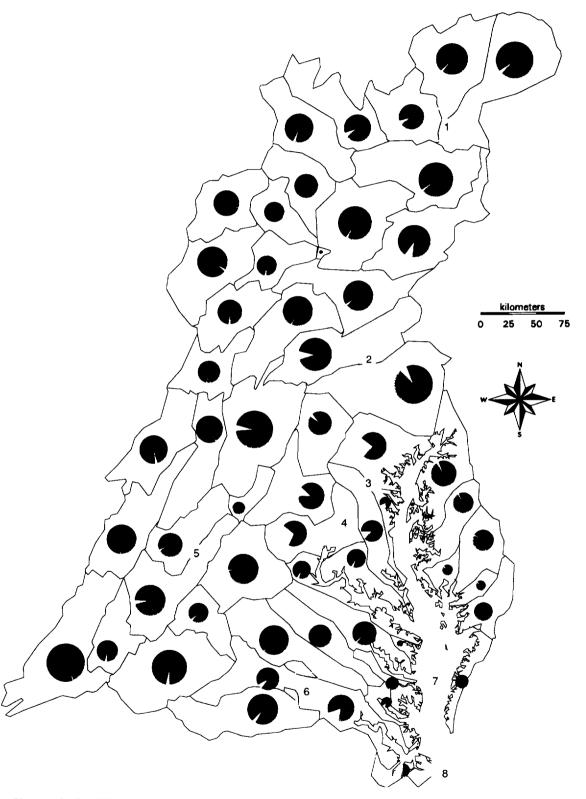


Fig. 1. The Chesapeake Bay Watershed study region. Pie charts show the area of woody (black), herbaceous (gray), and developed (white) land cover within USGS 8-digit hydrologic units (watersheds, Seaber et al., 1984). Landmark features referred to in the text are: (1) Binghamton; (2) Harrisburg; (3) Baltimore; (4) Washington DC; (5) Shenandoah Valley; (6) Richmond; (7) Chesapeake Bay; and (8) Norfolk.

and below a threshold value creates sharp distinctions between patches of apparently suitable and unsuitable habitat, making it simpler to describe their patterns. On a median-filtered map, a suitable pixel for a given threshold value represents a set of 81 'home range' windows for which the median habitat score was greater than the threshold value.

A window with 90% or more woody vegetation was considered to be suitable for the woodland archetypic species, a window with 90% or more herbaceous vegetation for the herbaceous/field species, and a window with 11% or more of the edges between woody and non-woody for the woodland-edge species. The 90% values were intended to identify the areas dominated by either woody or herbaceous land cover. The 11% value for the woody-edge habitat map corresponds to the percentage of edges necessary to traverse a 9×9 pixel window diagonally. These thresholds represent species with high habitat fidelity for the three types of habitat. Examples include woodthrush Hylocichla mustelina, woodpeckers Dryocopus pileatus and Picoides villosus, and nuthatches Sitta spp. (Whitcomb et al., 1981) (woody habitat), eastern meadowlarks Sturnella magna (Whitcomb et al., 1981) and garter snakes Thamnophis sp. (Conant, 1975) (herbaceous habitat), and cardinals Cardinalis cardinalis (Whitcomb et al., 1981) and black racers Coluber constrictor (Conant, 1975) (woody-edge habitat). Examples for the larger window analysis of woody habitat include scarlet tanager Piranga olivacea (46 ha) and goshawk Accipiter gentilis (410 ha) (Holling, 1992).

RESULTS AND DISCUSSION

Regional habitat amount and pattern

Regional patterns of woody (Fig. 2(a)) and herbaceous habitat (Fig. 2(b)) mirror each other and mimic the uneven distributions of land cover (compare to Fig. 1),

but woody edge habitat is about the same everywhere in the region (Fig. 2(c)). This happens because the same amount of woody edge is obtained by embedding one non-woody pixel in an otherwise contiguous woody area, or embedding one woody pixel in an otherwise non-woody area. Thus, woody-edge frequency can be the same in two regions dominated by different land cover classes, as long as there is at least some woody cover in both regions. From these observations, woody and herbaceous species may have a patchy (non-stationary) regional distribution, while woody-edge species are likely to be ubiquitous.

The segmented habitat suitability maps (Fig. 2(d), (e), (f)), obtained by applying the threshold values) illustrate regional habitat patterns for archetypic organisms with high fidelity for woody, herbaceous, and woodyedge habitats. Over the entire study area, the overall proportion of suitable habitat was 36, 15, and 20% for woody, herbaceous, and woody-edge habitat, respectively (Table 1). The connectivity statistics indicate that suitable woody habitat is more likely than the others to be contiguous ('clumped'). This is also reflected in the numbers and sizes of suitable patches (regions of contiguous suitable pixels) for different habitat types. Average suitable patch size varied from 23 ha (woodyedge habitat) to 150 ha (woody habitat). The largest suitable patch of woody habitat was two orders of magnitude larger than the largest woody-edge patch.

Table 1 shows two additional statistics that describe the combined patterns of suitable and unsuitable habitat for each habitat type. Fractal dimension, estimated by perimeter-area scaling (e.g. Krummel et al., 1987), measures the complexity of patch perimeters; the patches on the map of woody-edge habitat had the most complicated perimeters. Contagion (O'Neill et al., 1988a; Li & Reynolds, 1993) is an entropy measure of the attribute adjacency matrix that is related to angular second moment (Gonzalez & Woods, 1992) or fine-scale image texture (Riitters et al., 1995). The herbaceous

Table 1. Descriptive statistics for suitable areas of woody, herbaceous, and woody-edge habitats in the Chesapeake Bay Watershed according to the habitat models described in the text

	Habitat type		
	Woody	Herbaceous	Woody-edge
Suitable habitat:			
Area (ha)	6 446 699	2 637 887	3 474 713
Percent of total area	36	15	20
Connectivity ^a	0.68	0.48	0.31
Number of patches	42 933	51 105	148 779
Largest patch size (ha)	372 367	60 163	6065
Average patch size (ha)	150	52	23
Overall image:			
Fractal dimension ^b	1.47	1-51	1.60
Contagion ^c	0.24	0.49	0.32

^aGiven a pixel of suitable habitat, the percentage of neighboring pixels also of suitable habitat.

^bA measure of perimeter complexity for patches larger than four pixels that do not touch the map border, estimated as twice the slope of the log-log regression of patch perimeter on patch area. ^cLi & Reynolds (1993).

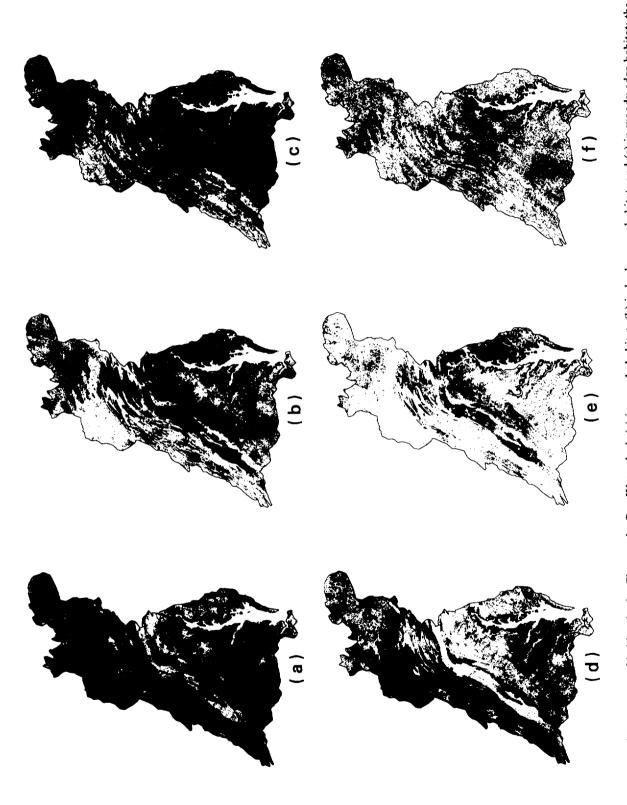


Fig. 2. Regional patterns of three types of habitat in the Chesapeake Bay Watershed: (a) in woody habitat; (b) in herbaceous habitat; and (c) in woody-edge habitat; the habitat scores in a 5 ha window are represented by shades of gray (white represents the lowest possible score, and the contrast has been stretched in (c). In (d) suitable woody habitat; (e) suitable woody edge habitat, the scores have been segmented (see text) using threshold values of (d) 90%; (e) 90%; and (f) 11% to indicate suitable habitat.

habitat map had the coarsest fine-scale texture by this measure.

Many other statistics and models could be used to describe patterns of habitat and their implications. To go beyond the qualitative comparisons made here, statistical issues such as variance estimation and hypothesis testing must be addressed (Hess, 1994). When comparing patch sizes among different habitat maps, for example, it may be more informative to compare frequency distributions instead of average values. Simulation methods have proven useful for estimating variances of landscape pattern statistics (Wickham et al., in press).

Habitat functions and thresholds were selected for demonstration purposes. However, the approach will accommodate any number of habitat functions and thresholds needed to address specific species or communities. For example, one could evaluate habitat suitability for a particular species that required combinations of forest, herbaceous, and open water within a certain area. In addition, thresholds could be varied to represent habitat suitability for species requiring different degrees of 'interior' cover. Finally, the habitat function and threshold approach can be applied to more detailed land cover maps with finer grain and greater classification detail, such as those derived from fine-scale aerial photography.

Key to applying our landscape approach is the development of habitat suitability models. Only recently have we begun to understand how landscape pattern influences individual organisms, populations, and suites of species (Hanson & Urban, 1992; Kattan et al., 1994; Baz & Garcia-Boyero, 1995; McIntyre, 1995), and how to apply such knowledge to specific habitat suitability assessments (Rickers et al., 1995). Development of new habitat suitability models should consider the relationships between landscape pattern and life history characteristics of individual species and population-level

dynamics (Hanson & Urban, 1992; Wiens et al., 1993; Enoksson et al., 1995; Rickers et al., 1995).

Sensitivity to window size

The effects of varying the 'home range' window size for the woody habitat function are illustrated for two smaller, embedded watersheds near Harrisburg, PA (Fig. 3). This region is defined by the boundaries of two United States Geological Survey (USGS) 8-digit hydrologic units (Seaber et al., 1984; unit codes 02050 305 and 02050 306) which together comprise about 11,000 km². In this sub-region, woody habitat is concentrated and nearly continuous along ridgelines in the 'ridge-and-valley' region in the north and west. In the 'piedmont' region in the southeast, woody cover occurs at a lower overall density and within a matrix (Wickham & Norton, 1994) of several land covers.

Suitable woody habitat for larger windows follows the regional patterns of land cover (Fig. 3), but there are important differences among window sizes. For the smallest (5 ha) window, there is at least some suitable habitat nearly everywhere, but suitable habitat for the largest window size (410 ha) is found only in restricted areas. As window size increases, the amount and pattern of suitable habitat changes (Table 2). The area of suitable habitat decreases by $\sim 50\%$ from the smallest to largest window size. Suitable habitat also becomes more 'clumped' as shown by trends in connectivity, average patch size, number of patches, and contagion. Patches in the large-window map have simpler perimeters than the smaller-window maps.

Figure 4 shows the frequency distributions of woody habitat scores (the pixel values after median filtering) prior to segmenting (Fig. 3 (a), (b), (c)). For the smallest window, individual windows are more clearly either 'suitable' or 'unsuitable'. This is consistent with a finer-scale perception of habitat potential. There is a higher proportion of intermediate values for the two larger

Table 2. Descriptive statistics for suitable areas of woody habitat for three window sizes in a sub-region of the Chesapeake Bay Watershed near Harrisburg, PA, according to the habitat models described in the text

	Woody habitat window size (ha)		
_	5	46	410
Suitable habitat:		The state of the s	
Area (ha)	223 226	153 146	100 567
Percent of total area	20	14	9
Connectivity ^a	0.66	0.80	0.89
Number of patches	2346	445	38
Largest patch size (ha)	33 676	39 467	27 753
Average patch size (ha)	95	344	2646
Overall image:			
Fractal dimension ^b	1.42	1.31	1.27
Contagion ^c	0.45	0.62	0.74

^aGiven a pixel of suitable habitat, the percentage of neighboring pixels also of suitable habitat.

^bA measure of perimeter complexity for patches larger than four pixels that do not touch the map border; twice the slope of the log-log regression of patch perimeter on patch area.

^cLi & Reynolds (1993).

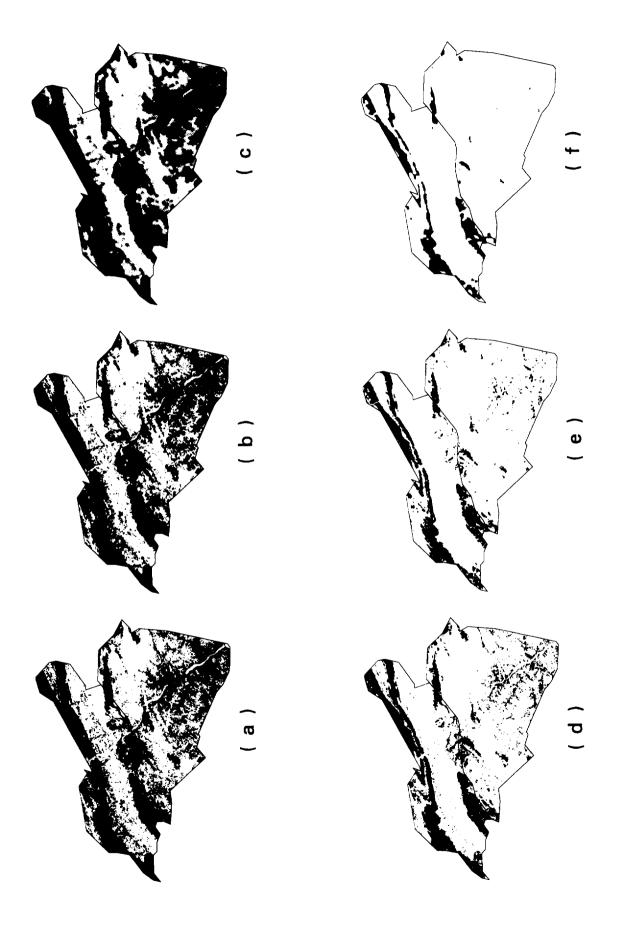


Fig. 3. Multi-scale woody habitat patterns as measured in different window sizes in a sub-region of the Chesapeake Bay Watershed. In (a) 5 ha; (b) 46 ha; and (c) 410 ha; the woody habitat scores are represented by shades of gray (white represents the lowest possible score). In (d) suitable, 5 ha; (e) suitable, 46 ha; and (f) suitable, 410 ha; the woody habitat scores have been segmented (see text) using threshold values of (d) 90%; (e) 90%; and (f) 11% to indicate suitable habitat.

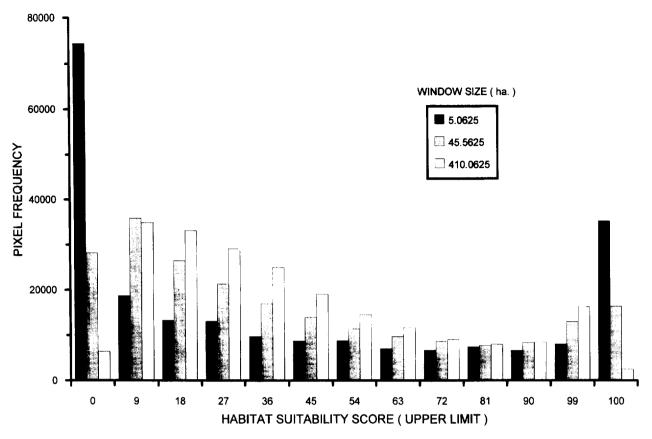


Fig. 4. Frequency distributions of woody habitat scores for three window sizes in a sub-region of the Chesapeake Bay Watershed.

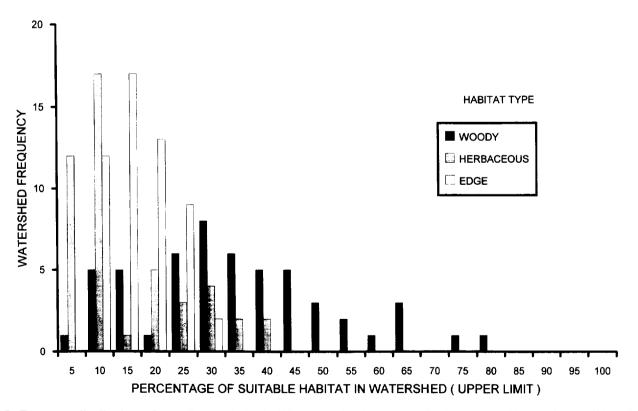


Fig. 5. Frequency distributions of overall watershed suitability rating for three types of habitat in the Chesapeake Bay Watershed.

The watershed suitability rating is the proportion of suitable habitat a given watershed.

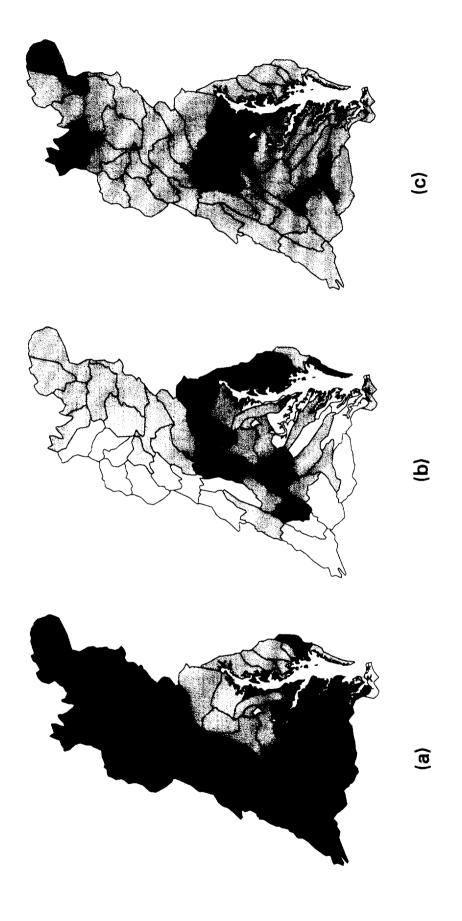


Fig. 6. Regional patterns of overall watershed habitat conditions for three types of habitat in the Chesapeake Bay Watershed: (a) woody; (b) herbaceous; (c) edge. The watersheds were rated based on the proportion of suitable habitat in a watershed: □, < 10%; ■, 10%-25%; ■, > 25%.

window sizes, as expected for a broader-scale perception. All of the distributions are skewed; a randomly chosen location is more likely to be unsuitable at all window sizes.

Our analyses of window sizes and habitat suitability suggest that landscape pattern change will have different consequences for species with different home ranges. Losses in suitable habitat for species with relatively large home ranges (e.g. some raptors, large predators, bears and large cats) can exceed the actual change in land cover at the finest scale of resolution. For example, a 35% loss of desert grassland habitat in southeastern Arizona resulted in a 70% loss of suitable habitat for pronghorn antelope; the difference was due to the spatial pattern of land cover change (Kepner et al., 1995). The comparative effects of fragmentation at different scales can be analyzed in this fashion.

The literal interpretation of a window as a 'home range' needs better justification. Home ranges are probably never exactly square, as was portrayed in these examples. The shape or pattern of home range could be taken into account if it were known, but that is rarely the case. An alternative is to apply home range size information to the maps of habitat suitability (i.e. after segmenting) which would eliminate otherwise suitable patches which fail to meet some size or shape constraint. With or without a 'home range' interpretation, windows of different sizes selectively enhance different scales of habitat information from the land cover map. Thus, they are a means to explore land cover changes which occur at different scales.

Watershed habitat suitability

Ecological management is sometimes practiced on a watershed-by-watershed basis (General Accounting Office, 1994). A different way of summarizing habitat suitability may be useful for that purpose. To accomplish this, the suitability maps for the woody, herbaceous, and woody-edge habitats were stratified by USGS 8-digit hydrologic units (watersheds, Fig. 1). Four small (<25,000 ha) watersheds were excluded, leaving 53 watersheds for analysis. The median watershed size was 3084 km², with a range from 622 to 6202 km². The percent of suitable habitat area was used to rate the overall habitat suitability of each watershed. Overall suitability was considered 'low' if the percentage was less than 10%, 'medium' if the percentage was between 10% and 25%, and 'high' otherwise. The same three values were used for all three habitat functions; they were arbitrarily chosen to illustrate the technique.

The population of watersheds is characterized by frequency distributions for each habitat type (Fig. 5). The median percentage for woody habitat was 36% (range 8-83%), while that for the herbaceous habitat was 12% (range 0-2-41%). The median percentage for the woodyedge habitat was 19%, with a range from 11 to 34%. Watershed suitability (low, medium, high) for each habitat type is shown in Fig. 6. In Fig. 6(a), the only

watershed with low woody habitat suitability is in the vicinity of Norfolk. Watersheds adjacent to the northern portion of the Chesapeake Bay have medium suitability, and the rest have high ratings.

In Fig. 6(b), the watersheds with low herbaceous habitat ratings are not simply the mirror image of those with high woody habitat ratings. Instead, a more complicated pattern emerges (because the population distributions of watershed ratings are not uniform). Watersheds with low herbaceous habitat suitability are found along the western and southern boundaries of the region, as well as in some watersheds along the western side of Chesapeake Bay. The sub-regions of high suitability are near the northern end of Chesapeake Bay (excluding those watersheds in the developed area around Baltimore and Washington) and in the Shenandoah Valley region west of Washington. The map of watershed suitability for woody-edge habitat has the least amount of regional pattern. Woody-edge habitat suitability is at least medium in all watersheds.

The maps shown in Fig. 6 can be interpreted as a preliminary assessment of the current status of watersheds with respect to wildlife habitat. Most of the east-central area has been lost as potential habitat for species requiring nearly continuous forest cover (Fig. 6(a)). This area has been converted into herbaceous or grassland habitat (Fig. 6(b)). Fragmentation has been extensive and moderately suitable edge habitat is located throughout the region (Fig. 6(c)). Complete coverage of the study region by remote sensing makes it possible to restratify the suitability maps at different scales for other purposes. For example, habitat suitability could be summarized by ecoregions, political regions, or landscape pattern type regions (Wickham & Norton, 1994).

CONCLUSION

This demonstration shows how spatial filtering of remotely-sensed land cover maps can be used to assess the status and trends of potential wildlife habitats. As in most areas, the amounts and patterns of habitat in the Chesapeake Bay Watershed are largely determined by the dynamics of forest, agriculture, and urban land uses at several scales. The Chesapeake Bay Watershed would approach a woody-cover dominated condition without human influence. However, humans have altered the spatial distributions of all land cover over time. The change can be temporary. For example, forest cover is created and destroyed at rates dependent on socioeconomic factors such as land value, conservation incentives, and public land policy. Changes in habitat associated with these factors can be evaluated by using the approach described here.

Spatially-explicit habitat assessments can identify 'islands' of relatively suitable habitat in otherwise unsuitable regions. These fragments may merit special

land use management to maintain regional metapopulations and biodiversity. Local extinction is normal for many species, and this will certainly occur as individual habitat fragments are lost. Strategies for maintaining regional populations may consider the surrounding fragments of suitable habitats to re-establish local populations in the context of a shifting mosaic of land use over time.

In addition to assessing current status, this habitat approach also has potential for identifying watersheds that will be sensitive to future change. Figure 5 depicts watersheds that are adjacent to habitat rating thresholds. These watersheds are at greatest risk for changing suitability category, given further land cover change. In the present study, these thresholds are arbitrary. If empirical thresholds could be developed, then sensitive watersheds might be identified for special attention.

With comparable digital land cover maps, the trends in habitat loss and fragmentation can be assessed. For example, a regional conversion of forest to agriculture or urban land cover can be directly related to the risk of losing forest interior species, and continued fragmentation can be related to the likelihood of sustaining biodiversity. In this manner, changing spatial patterns can be interpreted as risks to ecological and social values.

In the present exploratory study, the community was limited to three archetypic species. However, the approach clearly lends itself to application of more complex habitat modeling at multiple scales, which would require empirical information about habitat requirements (spatial and non-spatial) and about how species respond to patterns at different scales. As far as habitat requirements are known, and data available, a broad array of vertebrates and invertebrates could be considered and assessments could then be based on trends in community diversity. Species of particular interest, such as rare or endangered species, might have far more realistic habitat functions and assessments could then be based on the risk of losing a protected taxon.

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