

## Forest Patch Size, Land Use, and Mesic Forest Herbs in the French Broad River Basin, North Carolina

SCOTT M. PEARSON,<sup>1</sup> ALAN B. SMITH,<sup>1</sup> and MONICA G. TURNER<sup>2</sup>

<sup>1</sup>Biology Department, Mars Hill College, Mars Hill, North Carolina 28754;

<sup>2</sup>Department of Zoology, University of Wisconsin, Madison Wisconsin 53706

### ABSTRACT

The effect of forest fragmentation on cove-forest herbs was studied in the Southern Blue Ridge Province. Patches of mesic forests were sampled with 4 ha study plots. The coverage and density of herb species were greater in large patches (>200 ha) than in small patches (<10 ha). Several ant-dispersed species, such as *Disporum maculatum* and *Uvularia grandiflora*, were more likely to be absent from small patches than from large patches. Wind-dispersed species, such as ferns and composites, were not affected by patch size and isolation. Small patches had reduced amounts of organic matter in the soil, suggesting that small patches have experienced more disturbance than large patches. Otherwise, there were no other differences in soil characteristics between patch sizes. Mechanisms hypothesized to have affected these populations include (a) disruption of population dynamics due to habitat fragmentation, (b) habitat degradation, and (c) anthropogenic disturbance via land use. Disturbances may have affected herb populations directly by increasing mortality rates and by degrading habitat. These habitat changes were confounded by the small size and isolation of small forest patches.

### INTRODUCTION

Land use is the leading cause of landscape change. Landscape-level changes often result in habitat loss and fragmentation (Skole et al. 1994, Turner et al. 1994, Sinclair et al. 1995). Both worldwide and in the United States, land cover is altered principally by direct human use—through agriculture, pasture, forestry, and development (Meyer and Turner 1992). Land use patterns affect both terrestrial and aquatic systems (Reiners et al. 1994, Cooper 1995) and influence biodiversity for several reasons (Turner et al. 1997). First, land-use activities may alter the relative abundances of natural habitats and result in the establishment of new land-cover types. Species richness may be enhanced by the addition of new cover types, but natural habitats are often reduced, leaving less area available for native species (Walker 1992). Exotic species may become established and outcompete the native biota. Second, the spatial pattern of habitats may be altered, often resulting in fragmentation of once-continuous habitat. Species using a particular habitat may respond individualistically to these changes. Species that differ in their patterns of survival, fecundity, and dispersal, as well as in habitat needs, will likely differ in their response to habitat loss and fragmentation. Species having specialized habitat needs, requiring a large area for home range, or having limited vagility, will be impacted more than generalist species that disperse well and can live in small isolated patches (Terborgh 1992, Dale et al. 1994). Clearly, the conservation of native species and their habitats requires a landscape-level solution (Franklin 1993, 1994; Tracy and Brussard 1994).

Ecologists are beginning to develop techniques for assessing the complex impacts of landscape changes on biodiversity. Generalizations are difficult to obtain because habitat fragmentation affects species in different ways (Pearson et al. 1996). Assessing spatial and temporal changes in biodiversity by monitoring a suite of species having different habitat requirements has emerged as a useful technique. For example, patterns of deforestation in Rondonia, Brazil, were interpreted from the perspective of species having different area requirements and dis-

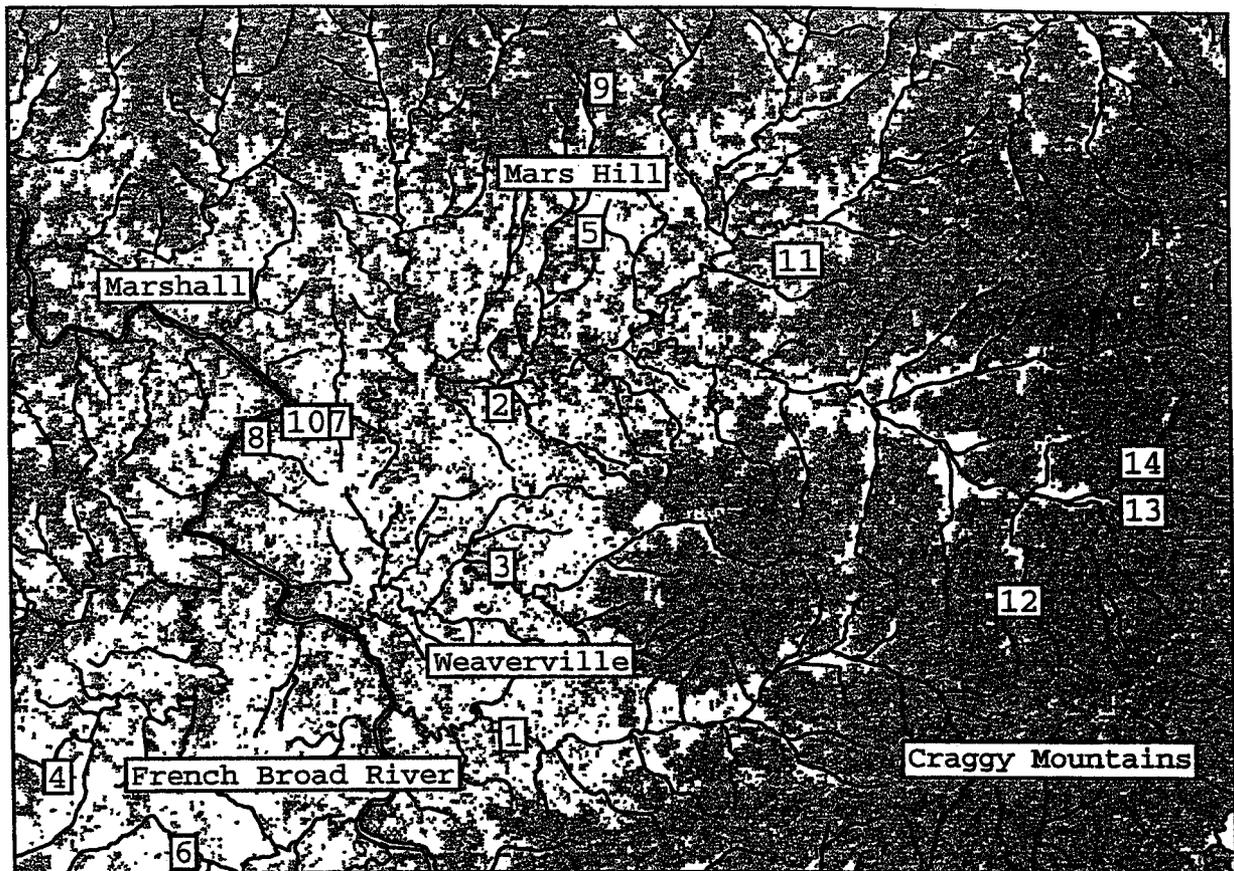


Figure 1. Forest cover in a portion of the French Broad River basin. The region shown is north of Asheville in northern Buncombe and southern Madison Counties, North Carolina. This map shows non-forest (white) and forest (grey) land covers for a  $35.9 \times 25.6$  km region. Streams are shown as black lines. Numbers show locations of study plots. Plots 1–8 were located in small patches of forest. Plots 9–14 were located in large patches.

persal capabilities (Dale et al. 1994). In low- to mid-elevation forests in the Pacific Northwest, risk to bird species under four different management scenarios was evaluated by quantifying suitable habitat for each species by using habitat maps, species-habitat associations, and other life-history requirements (Hansen et al. 1995). Avian diversity has been used as an indicator of the vertical and horizontal structural complexity of vegetation over a broad region (Flather et al. 1992). Butterflies (Kremen 1992, 1994) and birds and butterflies (Debinski and Brussard 1994) have been used as indicators of biodiversity. While species' responses to landscape patterns are complex, the collective response of many species produces the patterns of biological diversity observed on landscapes. Moreover, landscapes have patterns that change in both space and time. Disturbance influences species diversity in many landscapes, and a better understanding of the interaction between spatial pattern and disturbance is needed (Roberts and Gilliam 1995).

While the southern Blue Ridge Province currently has a high percentage of forest cover (approximately 70% forested, SAMAB 1996), forest cover in some regions, particularly in large river valleys, is fragmented by agricultural and suburban land uses. The central portion of the French Broad River basin, North Carolina is one such region (Figure 1). The present-day landscape consists of a mosaic of forest patches interspersed with agricultural and suburban land uses. This region has experienced sustained agricultural use for more than 100 years (Eller 1982), and more recently has experienced a growth of urban and suburban land uses. This region has demonstrated the unlikely combination of increasing human population size and increasing forest cover since 1950. Agricultural land uses have declined since the turn of the century and land formerly in agriculture has reverted to forest, especially since 1950 (Wear

and Bolstad 1998 submitted). At the same time, suburban land uses have increased to support a growing human population. This landscape, as a whole, presently has more forest cover than earlier in this century. In some areas, forest cover has increased due to the abandonment of agricultural land formerly in pasture and cultivation and has decreased in other areas due to suburban development (Wear and Bolstad 1998 submitted). While recognizing these historical patterns, we seek to understand the consequences of the present-day patterns of forest cover on plant communities.

This research seeks to investigate the impact of habitat fragmentation on herbaceous species characteristic of cove forests found in this landscape. The study addresses the following question: Are the diversity and abundance of native forest herbs correlated with the present-day forest patch size in this landscape? The goal of this study was to determine whether forest herb communities differed between plots located in small and large patches of mesic forest. Soil characteristics were also measured to determine whether any differences in the plant community could be explained by differences in soils. To achieve this goal, we compared the vegetation and soils sampled in a series of study plots located in either large or small patches of forest.

## METHODS

During 01 June–15 July 1995, 14 4-ha study plots were selected and sampled in forest patches ranging in area from 5 ha to >10,000 ha. The sampling units for this study were the 4-ha plot and 1-ha subplots within the larger study plot. The forests studied were located on both public and private lands in Madison and Buncombe counties of North Carolina. Three of the large forest patches were owned and managed by the USDA Forest Service. To control for coarse-level habitat variation, all plots were located in mesic forests at 600–920 m elevation. Plots located in forest patches <25 ha in area were classified as being in small patches (N = 8). Plots in patches >200 ha in area were classified as being in large patches (N = 6). Eight plots were classified as being in small patches, and each of these plots were located a different patch of forest. The mean  $\pm$  SE edge-to-edge distance to the nearest patch was  $42 \pm 8$  m for all patches in the study area. The nearest-patch distance for the small patches containing study plots was not significantly different from this mean. Three of the six large-patch plots were located in separate patches. The three remaining large-patch plots were located in the same forested patch that was >10,000 ha in area (Sites 12–14, Figure 1). The minimum distance between these three plots was >1.5 km, and mesic forest habitats were discontinuous between these plots. Therefore, these plots were treated as independent samples. Forest patch size was measured to the nearest ha using a land-cover map derived from a 1991 Thematic Mapper image (P. Bolstad and H. Pape-University of Minnesota, pers. comm.).

The same sized study plot (4 ha) was used to sample both large and small patches. This plot size covered a large percentage of the area of the small patches but only a minor portion of large patches. Nevertheless, keeping plot size constant allowed a more direct comparison of the communities found in the two patch sizes by eliminating the need to correct for species area effects due to different sized plots (Palmer 1991). Moreover, the patch size distribution of this landscape was highly skewed. Ninety-three percent of the patches in this landscape (Figure 1) were small (<25 ha), and less than 2% were large (>200 ha). In light of the difficulties of comparing the vegetation of entire patches, we chose to consider the vegetation of study plots as the sampling unit of comparison for this study.

By limiting our study to closed-canopy, mesic, deciduous forest, we attempted to control for environmental characteristics that might affect herb populations. We defined mesic forest as a community located on a north-facing or sheltered slope with forest canopy dominants of more than one of the following species: *Liriodendron tulipifera*, *Acer saccharum*, *Tilia americana*, *Aesculus octandra*, *Carya cordiformis*, and *Betula lenta*. *Fagus grandifolia*, *Quercus rubra*, *Acer rubrum* were also often present. Extensive stands of *Rhododendron maximum* and *Tsuga canadensis* were avoided although small stands of both species were encountered. Only closed-canopy forests with trees >50 cm dbh were sampled. All plots were in second growth forest that had been disturbed before 1945 by logging and/or agriculture. We found no evidence that

any of the plots had been cultivated, but woodland grazing has been a common practice in this region (Owsley 1949). A detailed history of disturbance was not available for these patches; nevertheless, we attempted to control for disturbance history in the plot selection process by choosing sites with minimal evidence of recent anthropogenic disturbances. To assess the recent history (within 20 years) of anthropogenic disturbance, land owners were interviewed and physical evidence of disturbance (e.g., fences, stumps, road beds) were noted for each plot. Plots that had experienced recent timber harvest or intensive woodland grazing were rejected. It was impossible to locate plots in small patches with no evidence of disturbance. Therefore, plots were selected in large patches that roughly matched the level of disturbance observed in small patches. That is, we did not compare plots in small patches with plots in large patches of forest that could be classified as old-growth with minimal human disturbance.

### *Field Sampling*

The diversity and abundance of vascular plants were measured for each study plot. Each study plot was divided into four 1-ha subplots (four subplots per plot  $\times$  14 plots = 56 subplots). For each plot, herb and shrub diversity and abundance were measured using 40 0.5-m<sup>2</sup> quadrats. The herb/shrub quadrats were located using a stratified random sampling design with each 1-ha subplot receiving 10 quadrats (Figure 2). Quadrats were located at least 20 m from forest edges; however, our ability to avoid the forest edge was limited in small forest patches. Only a small fraction of a 5-ha patch was  $>100$  m from an edge. In the herb/shrub quadrats, the number of emergent stems for each species was recorded along with a visual estimate of each species' percent coverage within the quadrat. Coverage was estimated for foliage up to two m above the ground surface. The number of stems per quadrat for each species was used as an estimate of density.

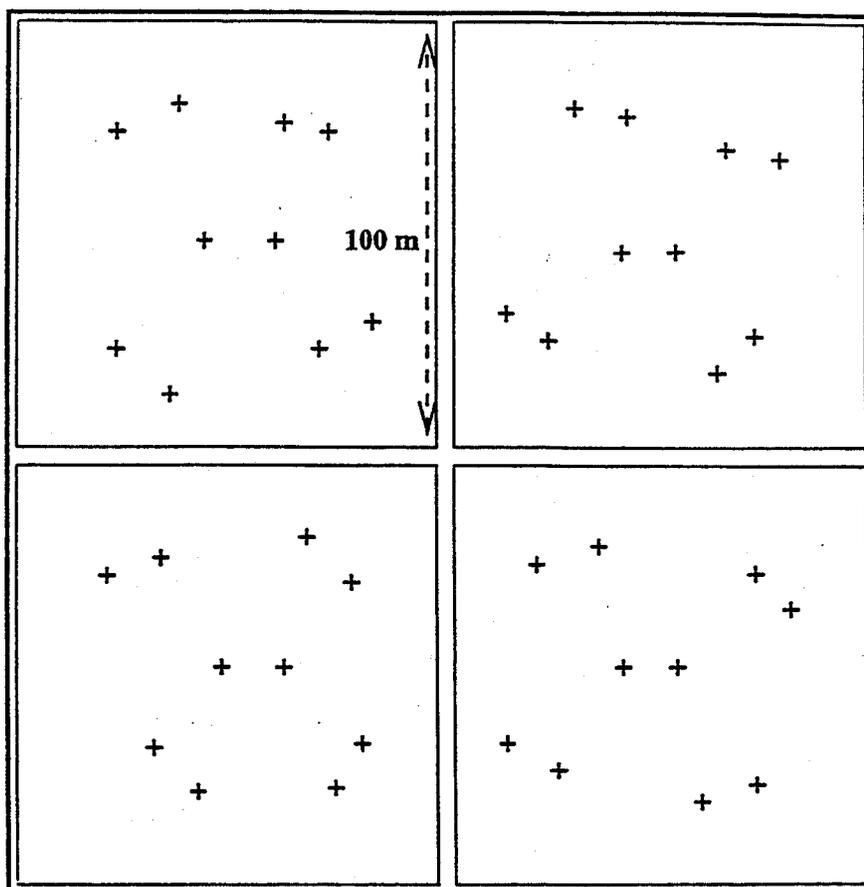
Soil samples were taken from each 1-ha subplot by collecting mineral soil to a depth of 15 cm. The soil was collected from a point adjacent to each of the 10 herb quadrats and combined to form a composite sample for the subplot. Samples were dried at 70°C for 48 hr and mailed for testing to the Soil Testing Laboratory of the North Carolina Department of Agriculture, Agronomic Division. This laboratory measured aspects of soil chemistry, texture, nutrient availability, and organic matter relevant to agricultural and forestry uses (see Tucker 1996 for soil lab methods). Table 2 lists the 15 soil metrics analyzed for this investigation.

### *Data Analysis*

The soil analyses produced 15 measures of soil texture and chemistry for each 1-ha subplot. The covariance structure of these 15 metrics was analyzed using a factor analysis with a principal components solution and varimax rotation (PROC FACTOR, SAS 1989) in order to reduce the 15 soil metrics to five complex soil factors (Johnson and Wichern 1988). Based on the absolute value of the rotated factor loadings, specific soil metrics were associated with each factor. This data reduction effectively removed the covariance structure of the data set, producing uncorrelated factor scores. The factor scores for each subplot were used as independent variables to assess the effects of soil attributes on vegetation. A *t*-test for two samples with unequal variances was used to determine whether soils differed between plots located in large versus small patches (SAS 1989).

Seventeen herb species (Table 1) were selected as representative of cove-forest communities based on published descriptions of their habitat (e.g., Radford et al. 1968, Weakley 1995). For each species studied, the coverage and density estimates were summed for each 1-ha subplot to reduce the number of zero counts. Then, the coverage sums were arcsin-square root transformed and the density sums were square-root transformed to increase normality of the data (Sokal and Rohlf 1995). These values represent the coverage and abundance of herb species for each 1-ha subplot, the same scale as the soil measurements. Values for all 1-ha subplots ( $N = 56$ ) were used in tests for the effects of soil chemistry on plants because soil chemistry often varied among subplots within a plot. However, to test for an effect of patch size, the values for the four 1-ha subplots for each plot were averaged (by calculating a mean) to obtain a single value that represented the plot for each species (i.e.,  $N = 14$ ). We also tested for the

## Study Plot



——— 4-ha study plot  
 ——— 1-ha subplot  
 + sample quadrat

Figure 2. The arrangement of plot, subplots and quadrats employed in the field sampling. Pairs of quadrats were randomly positioned in the center and four quadrants of each 1-ha subplot. Quadrats were at least 7 m apart.

effects of patch size and soils on the *total coverage* and *total density* of all seventeen species by summing the coverage and density values for all species prior to transformation. Both total coverage and total density were then square-root transformed.

The effect of patch size was tested by comparing the mean coverage and density of plots from small versus large patches for each species. A *t*-test for two samples with unequal variances was used (PROC TTEST, SAS 1989). To determine whether populations were more variable among large and small patches, differences in variance of coverage and density were tested using an *F*-test. For each series of tests, *P*-values were adjusted using a Bonferroni correction. To determine whether patch size affected the presence/absence of the selected species, a  $2 \times 2$  contingency table was constructed for each species. The two factors in the contingency table were patch size (small or large)  $\times$  population (present or absent) for each plot ( $N = 14$ ). A Fisher exact test (PROC FREQ, SAS 1989) was used to test for a significant relationship between patch size and presence/absence.

Although the plot selection process controlled for general soil type, some fine-scale variation in soil chemistry was observed that may have affected species abundances. It was possible

**Table 1. Species chosen as characteristic of cove forests in southern Blue Ridge Mountains. Taxonomic nomenclature and authorities follow Kartesz (1994)**

Scientific Name	Common Name
<i>Adiantum pedatum</i> L.	Maidenhair fern
<i>Asarum canadense</i> L.	Wild ginger
<i>Astilbe biternata</i> (Vent.) Britt.	False goatsbeard
<i>Botrychium virginianum</i> (L.) Sw.	Rattlesnake fern
<i>Cardamine diphylla</i> (Michx.) Wood	Toothwort
<i>Carex plantaginea</i> Lam.	Sedge
<i>Caulophyllum thalictroides</i> (L.) Michx.	Blue cohosh
<i>Cimicifuga racemosa</i> (L.) Nutt.	Black cohosh
<i>Disporum lanuginosum</i> (Michx.) Nichols.	Yellow mandarin
<i>Disporum maculatum</i> (Buckl.) Britt.	Spotted mandarin
<i>Sanguinaria canadensis</i> L.	Bloodroot
<i>Solidago flexicaulis</i> L.	Broad-leaved goldenrod
<i>Stellaria pubera</i> Michx.	Hairy chickweed
<i>Tiarella cordifolia</i> L.	Foam flower
<i>Trillium rugelii</i> Rendle	Southern nodding trillium
<i>Uvularia grandiflora</i> Sm.	Bellwort
<i>Viola canadensis</i> L.	Canada violet

that some soil factors may have been correlated with patch size; therefore, we corrected the plant data for the effects of patch size before performing tests on the effects of soil factors. These corrections were accomplished by estimating a regression equation for the effects of patch size on measures of coverage and density for each plant species using a general linear model (PROC GLM, SAS 1989). The residuals from this regression represent variation in plant coverage and density, corrected for the effects of patch size. These residuals were then tested for the main effects of the five soil factors (see Table 2) using analysis of variance (PROC GLM, SAS 1989). Hypothesis tests were performed using the type III sums of squares (SAS 1989).

**Table 2. Rotated factor pattern for the soil metrics. Factor loadings shown in bold indicate the associations between soil metrics and factors**

Descriptive Label Soil Metric	pH-Cations Factor 1	Zn-Na Factor 2	C-Cu Factor 3	Mn-S Factor 4	Mg Factor 5
Humic Matter	-0.1062	0.0917	<b>0.8747</b>	0.0670	-0.2919
Weight: Volume	-0.0126	-0.1320	-0.2164	<b>-0.7641</b>	0.0991
Cation Exchange Capacity	<b>0.8334</b>	0.3205	0.0323	0.0740	-0.1746
Base Saturation	<b>0.9508</b>	0.1004	-0.0330	0.0272	0.1123
Acidity	<b>-0.7781</b>	0.0938	0.2020	0.0622	-0.2266
pH	<b>0.9580</b>	0.1180	0.0598	0.0286	0.0344
P	<b>0.4880</b>	0.1414	-0.5843	-0.2232	-0.4491
K	<b>0.6811</b>	0.1156	-0.3343	0.0568	0.1435
Ca	<b>0.9347</b>	0.1562	0.0179	0.0439	-0.1872
Mg	0.0889	-0.0806	-0.0542	-0.0283	<b>0.9297</b>
Mn	0.3260	0.0641	0.1433	<b>0.7215</b>	0.2663
Zn	0.0793	<b>0.9113</b>	-0.0114	0.2613	-0.1189
Cu	0.0263	0.0468	<b>0.9050</b>	0.1912	0.1483
S	-0.5369	0.1894	-0.0616	<b>0.6323</b>	-0.1843
Na	0.2490	<b>0.6638</b>	0.1185	-0.1887	0.0924
Percent variance explained	39.9	18.2	16.7	13.7	11.4

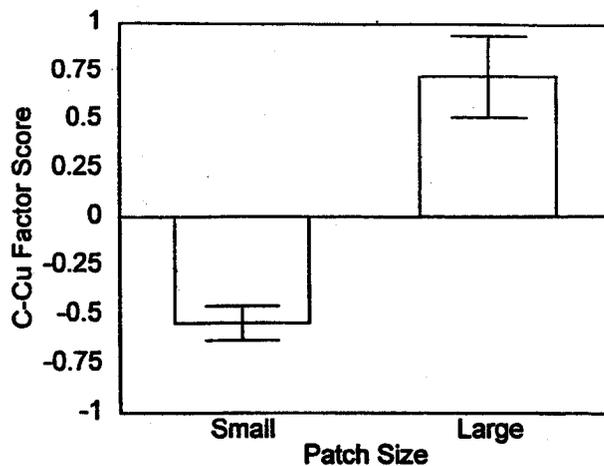


Figure 3. Soil organic matter is positively related to patch size. Mean and standard error of the C-Cu factor scores are plotted.

## RESULTS

### Soil Metrics

The factor analysis reduced the soil metrics to five soil factors (Table 2). The first factor (pH-cations) described variation in soil pH and the abundance of cations and anions. This factor accounted for most of the variation in the soil data and was negatively related to soil acidity. Factor 2 (Zn-Na) reflected the availability of zinc and sodium. Factor 3 (C-Cu) described the amount of humic matter (interpreted as stored carbon) and availability of copper. Factor 4 (Mn-S) reflected the availability of manganese and sulfur, and factor 5 (Mg) described the availability of magnesium. Hereafter, these soil factors will be referred to by the descriptive labels listed in Table 2.

A t-test revealed that only the C-Cu soil factor was significantly correlated with patch size ( $T = 5.99$ , d.f. = 34,  $P < 0.001$ ). The C-Cu factor scores for large patches were significantly greater than the score for small patches (Figure 3). There were no significant differences due to patch size in the other soil factors (all  $T < 1.6$ ,  $P > 0.13$ ).

### Cove-forest Herbs

Larger patches of forest tended to have a greater coverage and greater density of cove-forest herbs than small patches (Table 3). Eight of the 17 species were more abundant in plots in large patches. One species, *Stellaria pubera*, was more abundant in plots in small patches. In general, trends in percent coverage were matched by trends in plant density. Plots with higher coverage for a particular species tended to have greater density of individuals of that species. Three of the four liliaceous species (*Disporum lanuginosum*, *Disporum maculatum*, and *Uvularia grandiflora*) were less abundant in small patches; *Trillium rugelii* was the exception. *Trillium rugelii* tended to be more abundant in the large patches, but the trend was not statistically significant. There were no individuals of *D. maculatum* and *U. grandiflora* found in the small patches. *Stellaria pubera* was more abundant in small patches. *Caulophyllum thalictroides* tended to have greater coverage and density in large patches (Table 4); however, this species had a patchy distribution resulting in a great deal of variability among samples.

Patch size also affected the variance in species' density among patches. At the 4-ha scale, variances in coverage and density estimates for *Adiantum pedatum*, *Botrychium virginianum*, *Carex plantaginea*, *Stellaria pubera*, and *Solidago flexicaulis* were greater for plots located in small patches than for plots in large patches (Table 4; F-test, all  $P < 0.05$ ). For species that were more abundant in large patches, variances in coverage and density tended to be greater for patch sizes with the greater mean (Tables 3, 4).

Patch size affected the probability that a given species occurred in a study plot (Table 5). *Asarum canadense*, *Astilbe biternata*, *C. thalictroides*, *Cardamine diphylla*, *D. maculatum*, and

Table 3. Effects of patch size and soil factors on the mean coverage and density of cove-forest species. Empty cells indicate that effects were not significant. A sign indicates the direction of effect and significance at the  $P < 0.05$  level

Species	Coverage							Density						
	Patch Size	pH, Cations	Zn, Na	C, Cu	Mn, S	Mg		Patch Size	pH, Cations	Zn, Na	C, Cu	Mn, S	Mg	
<i>Adiantum pedatum</i>	+	+						+	+					
<i>Asarum canadense</i>	+		+	+				+		+				
<i>Astilbe biternata</i>					+	+					+		+	
<i>Botrychium virginianum</i>	+							+						
<i>Cardamine diphylla</i>														
<i>Carex plantaginifolia</i>					-									
<i>Caulophyllum thalictroides</i>			+	+						+				
<i>Cimicifuga racemosa</i>		+		+					+					
<i>Disporum lanuginosum</i>	+			+				+			+			
<i>Disporum maculatum</i>	+			+				+			+			
<i>Sanguinaria canadensis</i>	+			+				+			+			
<i>Solidago flexicaulis</i>														
<i>Stellaria pubera</i>	-			+				-			+			
<i>Tiarella cordifolia</i>	+			+				+			+			
<i>Trillium rugelii</i>				+							+			
<i>Uvularia grandiflora</i>	+			+				+			+			
<i>Viola canadensis</i>				+							+			
Total (Sum of individual species)	+	+		+	-			+	+		+		+	

**Table 4. Mean and standard error (SE) of coverage and density by patch size measured at 1-ha scale. Coverage was arcsine-square root transformed, and density was square-root transformed. Units are the summed percent coverage and density for ten 0.5 m<sup>2</sup> quadrats in a 1-ha plot. See Table 3 for effects of patch size on means**

Species	Patch Size	Coverage (Mean ± SE)		Density (Mean ± SE)		Variance Test <sup>1</sup>
		Small	Large	Small	Large	
<i>Adiantum pedatum</i>		0.20 ± 0.06	0.08 ± 0.02	3.36 ± 0.95	1.42 ± 0.40	S
<i>Asarum canadense</i>		0.04 ± 0.02	0.21 ± 0.07	0.53 ± 0.35	3.25 ± 1.06	L
<i>Astilbe biternata</i>		0.01 ± 0.01	0.17 ± 0.04	0.18 ± 0.11	6.42 ± 1.36	L
<i>Botrychium virginianum</i>		0.18 ± 0.04	0.11 ± 0.03	2.02 ± 0.50	1.58 ± 0.52	S
<i>Cardamine diphylla</i>		0.01 ± 0.01	0.10 ± 0.04	0.04 ± 0.04	0.89 ± 0.34	L
<i>Carex plantaginea</i>		0.04 ± 0.02	0.03 ± 0.01	0.71 ± 0.36	0.64 ± 0.26	S
<i>Caulophyllum thalictroides</i>		0.08 ± 0.07	0.19 ± 0.07	0.63 ± 0.48	1.82 ± 0.64	-
<i>Cimicifuga racemosa</i>		0.20 ± 0.04	0.19 ± 0.05	6.92 ± 1.53	6.46 ± 1.48	-
<i>Disporum lanuginosum</i>		0.03 ± 0.01	0.20 ± 0.06	0.89 ± 0.43	4.41 ± 1.29	L
<i>Disporum maculatum</i>		0.00 ± 0.00	0.08 ± 0.04	0.00 ± 0.00	0.79 ± 0.40	na
<i>Sanguinaria canadensis</i>		0.09 ± 0.03	0.57 ± 0.12	1.20 ± 0.40	7.81 ± 1.76	L
<i>Solidago flexicaulis</i>		0.16 ± 0.09	0.08 ± 0.05	2.11 ± 1.12	1.24 ± 0.76	S
<i>Stellaria pubera</i>		0.36 ± 0.07	0.08 ± 0.02	3.46 ± 0.67	1.06 ± 0.27	S
<i>Tiarella cordifolia</i>		0.02 ± 0.01	0.24 ± 0.08	0.19 ± 0.11	2.71 ± 0.88	L
<i>Trillium rugelii</i>		0.19 ± 0.07	0.30 ± 0.11	1.89 ± 0.71	2.90 ± 1.02	-
<i>Uvularia grandiflora</i>		0.00 ± 0.00	0.06 ± 0.02	0.00 ± 0.00	1.10 ± 0.48	na
<i>Viola canadensis</i>		0.09 ± 0.05	0.24 ± 0.05	0.88 ± 0.49	2.65 ± 0.60	-
<b>Total</b>		<b>17.8 ± 2.38</b>	<b>30.71 ± 2.46</b>	<b>18.33 ± 2.51</b>	<b>31.66 ± 2.53</b>	<b>-</b>

<sup>1</sup> The last column shows the results of an F-test (significant at P < 0.05) to determine whether patch size had a significant effect on variance in coverage and density. The results for coverage and density variances were similar. The symbols mean: S, small patches have significantly greater variance; L, large patches have greater variance; -, no significant difference; na, not applicable because mean and variance equal zero for small patches.

**Table 5. Proportion of plots supporting extant populations of cove-forest species. The influence of patch size on the frequency of extant populations was tested with a contingency table analysis. Significance values (P) are reported for a Fisher exact test**

Species	Patch Size		P <sup>1</sup>
	Small	Large	
<i>Adiantum pedatum</i>	0.62	0.50	ns
<i>Asarum canadense</i>	0.25	0.83	0.05
<i>Astilbe biternata</i>	0.38	1.00	0.03
<i>Botrychium virginianum</i>	1.00	0.83	ns
<i>Cardamine diphylla</i>	0.12	0.67	0.06
<i>Carex plantaginea</i>	0.38	0.50	ns
<i>Caulophyllum thalictroides</i>	0.12	0.83	0.01
<i>Cimicifuga racemosa</i>	0.75	0.83	ns
<i>Disporum lanuginosum</i>	0.38	0.67	ns
<i>Disporum maculatum</i>	0.00	0.67	0.01
<i>Sanguinaria canadensis</i>	0.62	0.67	ns
<i>Solidago flexicaulis</i>	0.38	0.33	ns
<i>Stellaria pubera</i>	0.88	0.83	ns
<i>Tiarella cordifolia</i>	0.38	0.83	ns
<i>Trillium rugelii</i>	0.38	0.67	ns
<i>Uvularia grandiflora</i>	0.00	0.67	0.01
<i>Viola canadensis</i>	0.38	0.83	ns

<sup>1</sup> ns = not significant; P > 0.10.

*U. grandiflora* were all more likely to be present in large patches than in small patches. *Disporum lanuginosum*, *Tiarella cordifolia*, *T. rugelii*, and *Viola canadensis* tended to be more frequent in large patches, but these trends were not statistically significant (Table 5). No species were more likely to be found in small patches than in large patches. Although *S. pubera* was more abundant in small patches, it was equally likely to be found in plots in both patch sizes. Note that the same number and arrangements of quadrats were employed for plots in both small and large patches of forest. Therefore, these results were not due differences in sampling effort.

The relationships between soil factors and species coverage and density were mixed. The C-Cu factor affected 11 of 17 individual species and the total coverage of all cove-forest herbs (Table 3). All these species were more abundant at plots having greater amounts of soil humic matter. Soil pH-cations were positively associated with *A. canadense*, *C. racemosa*, *Sanguinaria canadensis*, and the total coverage and density of cove-forest herbs. The availability of Zn-Na was positively correlated with *A. biternata*, *C. racemosa*, and *S. canadensis*. Both the availability of Mn-S and Mg was positively related to populations of *B. virginianum*. In contrast, Mn-S was negatively correlated to *C. plantaginea*, *C. racemosa*, *S. canadensis*, and the total coverage of all species. Thus, most species were positively related to higher levels of soil humic matter and nutrients with the exception of *C. racemosa*. This species showed a positive correlation with pH and Zn-Na, a negative response to Mn-S. At plots with more C-Cu, it had greater coverage but no differences in density.

## DISCUSSION

Cove-forest herbs were, in general, more abundant in larger patches of mesic forest. The reduction in coverage and density of these species could have been produced by several mechanisms. The following mechanisms might explain this pattern: (a) effect of habitat fragmentation on population dynamics, (b) habitat differences influenced by patch size, and (c) differences in the past disturbance regime among patch sizes.

### *Habitat Fragmentation and Population Dynamics*

Small patches harbored smaller populations of herbs that were demographically isolated from other populations; therefore, herb populations in small patches may have experienced higher probabilities of local extinction. Small populations suffer higher rates of extinction for many species (e.g., Berger 1990, Dennis et al. 1991), and the geographic isolation inhibits the arrival of propagules from other populations that could rescue a given population from extinction (Brown and Kodric-Brown 1977, Kadmon and Pulliam 1993). In this study, presence/absence data shows that several species were more likely to be present in larger patches (Table 5). Of these species, *A. canadense*, *A. biternata*, *D. maculatum*, *U. grandiflora*, *T. cordifolia* and *V. canadensis* have limited dispersal capabilities that may prevent them from reaching some isolated patches. For example, *A. biternata* and *T. cordifolia* produce numerous small seeds that fall a short distance from the parent plant while *A. canadense*, *D. maculatum*, *U. grandiflora*, *T. cordifolia* and *V. canadensis* are dispersed by ants (Beattie and Culver 1982, Smith et al. 1989). Moreover, species that disperse well were not affected by patch size. These species included the ferns, *A. pedatum* and *B. virginianum*, and the composite, *Solidago flexicaulis*; which are wind dispersed and should be able to recolonize isolated patches. Matlack (1994a) found that disjunct stands of successional forest had reduced numbers and abundances of forest herbs. Moreover, the probability of recolonization and migration rate by herb species was negatively related to distance to a source population and positively related to seed dispersal ability. Thus, dispersal-limited species may be more likely to go extinct in small, isolated forest patches.

### *Habitat Differences*

Small patches may have different physical habitats than large patches thereby affecting the occurrence and abundance of herb species. The analysis of soil measurements indicated that both patch sizes were similar with respect to the availability of soil nutrients, with the exception of soil humic matter and copper. The plot selection process also ensured that habitat

factors such as overstory condition, geological parent material, and topography were similar between patch sizes. We did not directly measure microclimatic variation in air temperature and water availability. These habitat parameters can be affected by patch size and could be important to the germination, growth, and survival of these species. Small patches are likely to experience strong "edge effects" due to their high perimeter-to-area ratio (Saunders et al. 1991). In the eastern United States, microclimatic parameters, such as temperature, litter moisture, humidity, and light, show that edge effects may extend at least 50 m from the edge into the forest interior although these effects are moderated on north-facing slopes (Matlack 1993). Populations of forest herbs may be correlated with distance to edge (Matlack 1994b). While we avoided sampling the immediate edge of these forest patches, effects that extended >100 m from the forest edge would have affected all regions within a small patch. Such alterations of the forest microclimate may have reduced habitat suitability for species adapted to mesic, forest-interior conditions.

Our data show that soil humic matter, as measured by soil factor C-Cu, was positively correlated with patch size (Figure 3), and humic matter affected the coverage and density of many species. Humic matter was the only habitat characteristic measured that varied between patch sizes, but it was also the factor most strongly related to species abundances. Soils with increased organic matter tend to have increased water retention, improved aeration and tilth, and have enhanced supplies of plant nutrients (Coleman and Crossley 1996). The organic matter also supports the growth of decomposers and symbiotic microbes which supply nutrients to growing plants and may even provide protection from pathogens (e.g., Chanway et al. 1991). Thus, if the ecology and history of a small patch influences the organic matter of its soils, that patch's ability to support populations of forest herbs will likewise be affected.

### *Disturbance*

The disturbance regimes of small patches may have been different from large patches. Anthropogenic disturbance can affect herb populations by directly killing individuals and degrading habitat (Meier et al. 1995). Catastrophic disturbances such as clearcutting may extirpate a population or dramatically reduce coverage and abundances. Recovery after an intense disturbance may take a long time (Duffy and Meier 1992). Long-term, chronic disturbances, such as grazing, may interfere directly with the reproduction and survival of herb species (Lubbers and Lechowicz 1989, Anderson 1994, McIntyre et al. 1995).

Despite our efforts to control for disturbance history, the correlation between soil humic matter and patch size suggests that small patches have been disturbed more frequently and/or more intensely in the past. Land uses such as grazing and logging can result in the loss of stored C in soils and can promote erosion (e.g., Black and Harden 1995). All of the plots studied had been logged during the early part of the century and were second growth timber. Timber management can affect the diversity and abundance of forest herbs (Meier et al. 1995), and the diversity of the herb layer is connected to the diversity and condition of the overstory (Gilliam et al. 1995). A full recovery of the herb community depends on the development of ecosystem characteristics associated with old, mature forests (Halpern and Spies 1995).

Agricultural uses of forests could be an important source of anthropogenic disturbance. There is no evidence that any of our study plots had been cultivated during the last 75 years. However, small patches were often adjacent to land presently or formerly in agricultural use. A woodlot on the property of a farm family is more likely to have been used for grazing and for a source of forest products than a plot nested within a larger landscape dominated by forest. Woodlots were often burned, either intentionally or accidentally, for a variety of reasons. We frequently observed the remnants of barbed wire fences in the small patches, and a number of potential study plots in the landscape were rejected because they were being actively grazed or the landowner informed us that the woodlot had been used for grazing within the past two decades. There are several ways grazing could reduce soil C. Soil is disturbed by cattle walking on slopes, resulting in losses of organic matter due to erosion and enhanced decay. Livestock also actively crop and browse living biomass thereby intercepting organic matter that would normally end up in the soil. Cattle regularly graze on herbs, particularly liliaceous species.

Therefore, it is plausible that these small patches have experienced more anthropogenic disturbance.

Disturbance can interact with habitat fragmentation to decimate or reduce populations. Once a disturbance destroys a population in a isolated patch, opportunities for recolonization would be reduced due to patch isolation for species with limited dispersal capabilities. Disturbances that degrade habitat may convert patches from self-sustaining source populations to sink populations in which local reproduction does not keep up with mortality (Pulliam 1988). Then, patch isolation would interfere with immigration necessary to maintain sink populations. Many of the species studied here are long-lived, and the demise of a sink population might take decades. Thus, there may be more than one mechanism affecting the herb communities in these forest patches. It is likely that some interaction between habitat fragmentation, habitat quality, and anthropogenic disturbance was responsible for the patterns observed in these data.

### *Soil Factors and Vegetation*

Of the soil characteristics studied, soil C-Cu had the greatest impact on these herb species. In our data, the pH-cations factor was positively correlated with the coverage and density of several species and the total coverage and density of all species combined (Table 3). This factor serves as a good indicator of the overall site fertility. Two species, *C. thalictroides* and *S. canadensis*, were correlated with several soil factors suggesting that these species respond to differences in nutrient availability measured at the 1-ha scale. Soil pH-cations has been identified as an important factor in other studies of plant communities in this region. McLeod (1988) demonstrated that pH and soil nutrients were associated with gradients in moisture and elevation that affect the geographic location of community types in the Black and Craggy Mountains in the southern Blue Ridge. Other authors (e.g., Cole and Ware 1997) have shown the effect of edaphic factors on successional dynamics and climax vegetation. Most studies analyze data taken from a wide range of community types or from across physiographic regions. However, this study, by selecting plots according to criteria designed to control for edaphic variation, collected data from a very restricted range of natural variation. Therefore, the effects of soil nutrients on the herbs we studied were not consistently important between species. The soil sampling technique used for this study provides a estimate of the average soil conditions at the scale of 1 ha. Thus, this sampling was appropriate for testing for an effect of patch size. However, this spatial resolution may have been too coarse to capture variation in soils relevant to herb populations with variations at finer spatial scales (Palmer 1991). Sampling at the scale of 0.05–0.10 ha would be more appropriate for discovering finer scale relationships.

### *Conclusion*

These data show that forest patch size is correlated with populations of cove-forest herbs in the French Broad River basin. These herb species had lower density and coverages in small patches of mesic forest as compared to large patches. Of the soil characteristics tested, humic matter was positively correlated with the abundance of most species and with patch size. These soil results suggest that small patches may have been more disturbed than large patches of forest. The land use history of this landscape is complex. Present-day communities are likely affected by the current and historical patterns of habitat availability and habitat quality. We hypothesize that past disturbances could have affected herb populations directly by increasing mortality rates and by degrading habitat. Moreover, these habitat changes could have been confounded by the small size and isolation of small forest patches. Land uses have affected the spatial pattern and quality of habitats in the French Broad River Basin. Patterns of forest fragmentation and the land use history of forest patches have likely affected the abundance and community composition of cove-forest herbs inhabiting patches of mesic forest in this landscape.

### ACKNOWLEDGMENTS

This study would not have been possible without the cooperation of private landowners in Madison and Buncombe counties and the Toecane Ranger District, Pisgah National Forest. K. Heafner, D. E. Williams Call, J. Meador, and J. B. Drake provided essential assistance with

the field work. J.D. Pittillo and three anonymous reviewers made suggestions for improving earlier drafts of this paper. P. Bolstad provided spatial data that was useful in selecting study sites. This research was supported by grants from the National Science Foundation DEB 9011661 and 9416803.

#### LITERATURE CITED

- ANDERSON, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Applications* 4:104-109.
- BEATTIE, A.J. and D.C. CULVER. 1982. Inhumation: how ants and other invertebrates help seeds. *Nature* 297:627.
- BERGER, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conserv. Biol.* 4:91-98.
- BLACK, T.A. and J.W. HARDEN. 1995. Effect of timber harvest on soil carbon storage at Blodgett Experimental Forest, California. *Can. J. Forest Res.* 25:1385-1396.
- BROWN, J.H. and A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* 58:445-449.
- CHANWAY, C.P., R. TURKINGTON, and F.B. HOLT. 1991. Ecological implications of specificity between plants and rhizosphere micro-organisms. p. 121-169. *In: Begon, M., A.H. Fitter, and A. MacFayden (eds.). Advances in ecological research, Volume 21. Academic Press, San Diego, California.*
- COLE, A.M. and S.A. WARE. 1997. Forest vegetation, edaphic factors, and successional direction in the Central Piedmont of Virginia. *Castanea* 62:100-111.
- COLEMAN, D.C. and D.A. CROSSLEY, JR. 1996. *Fundamentals of soil ecology.* Academic Press, San Diego, California.
- COOPER, S.R. 1995. Chesapeake Bay watershed historical land use: impact on water quality and diatom communities. *Ecol. Applications* 5:703-723.
- DALE, V.H., S.M. PEARSON, H.L. OFFERMAN, and R.V. O'NEILL. 1994. Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conserv. Biol.* 8:1027-1036.
- DEBINSKI, D.M. and P.R. BRUSSARD. 1994. Using biodiversity data to assess species-habitat relationships in Glacier National Park, Montana. *Ecol. Applications* 4:833-843.
- DENNIS, B., P.L. MONHOLLAND, and J.M. SCOTT. 1991. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* 61:115-144.
- DUFFY, D.C. and A.J. MEIER. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conserv. Biol.* 6:196-201.
- ELLER, R.D. 1982. *Miners, millhands, and mountaineers: industrialization of the Appalachian South, 1880-1930.* University of Tennessee Press, Knoxville.
- FLATHER, C.H., S.J. BRADY, and D.B. INKLEY. 1992. Regional habitat appraisals of wildlife communities: a landscape-level evaluation of a resource planning model using avian distribution data. *Landsc. Ecol.* 7:137-147.
- FRANKLIN, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecol. Applications* 3:202-205.
- FRANKLIN, J.F. 1994. Response to Tracy and Brussard. *Ecol. Applications* 4:208-209.
- GILLIAM, F.S., N.L. TURRILL, and M.B. ADAMS. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. *Ecol. Applications* 5:947-955.
- HALPERN, C.B. and T.A. SPIES. 1995. Plant diversity in natural and managed forests of the Pacific Northwest. *Ecol. Applications* 5:913-934.
- HANSEN, A.J., S.L. GARMAN, J.F. WEIGAND, G.L. URBAN, W.C. MCCOMB, and M.G. RAPHAEL. 1995. Alternative silvacultural regimes in the Pacific Northwest: simulations of ecological and economic effects. *Ecol. Applications* 5:535-554.
- JOHNSON, R.A. and D.W. WICHERN. 1988. *Applied multivariate statistical analysis.* Prentice Hall, Englewood Cliffs, New Jersey.
- KADMON, R. and H.R. PULLIAM. 1993. Island biogeography: effect of geographical isolation on species composition. *Ecology* 74:977-981.
- KARTESZ, J.T. 1994. *A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, 2nd ed.* Timber Press, Portland, Oregon.
- KREMEN, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Applications* 2:203-217.
- KREMEN, C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecol. Applications* 4:407-422.

- LUBBERS, A.E. and M.J. LECHOWICZ. 1989. Effects of leaf removal on reproduction vs. belowground storage in *Trillium grandiflorum*. *Ecology* 70:85-96.
- MATLACK, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conservation* 66:185-194.
- MATLACK, G.R. 1994a. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75:1491-1502.
- MATLACK, G.R. 1994b. Vegetation dynamics of the forest edge-trends in space and successional time. *J. Ecol.* 82:113-123.
- MCLEOD, D.E. 1988. Vegetation patterns, floristics, and environmental relationships in the Black and Craggy Mountains of North Carolina. Ph.D. dissertation. University of North Carolina, Chapel Hill.
- MCINTYRE, S., S. LAVOREL, and R.M. TREMONT. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 83:31-44.
- MEIER, A.J., S.P. BRATTON, and D.C. DUFFY. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Applications* 5:935-946.
- MEYER, W.B. and B.L. TURNER, II. 1992. Human population growth and global land-use/cover change. *Annual Rev. Ecol. Syst.* 23:39-61.
- OWSLEY, F.L. 1949. Plain folk of the Old South. Louisiana State University Press, Baton Rouge.
- PALMER, M.W. 1991. Patterns of species richness among North Carolina hardwood forests: test of two hypotheses. *J. Veg. Sci.* 2:361-366.
- PEARSON, S.M., M.G. TURNER, R.H. GARDNER, and R.V. O'NEILL. 1996. An organism-based perspective of habitat fragmentation. p. 77-95. *In: Szaro, R.C. and D.W. Johnston (eds.). Biodiversity in managed landscapes: theory and practice.* Oxford University Press, New York.
- PULLIAM, H.R. 1988. Sources, sinks, and population regulation. *Amer. Naturalist* 132:652-661.
- RADFORD, A.E., H.E. AHLES, and C.R. BELL. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill.
- REINERS, W.A., A.F. BOUWMAN, W.F.J. PARSONS, and M. KELLER. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecol. Applications* 4:363-377.
- ROBERTS, M.R. and F.S. GILLIAM. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecol. Applications* 5:969-977.
- SAMAB (SOUTHERN APPALACHIAN MAN AND THE BIOSPHERE). 1996. The Southern Appalachian assessment terrestrial technical report. Report 5 of 5. U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, Georgia.
- SAS INSTITUTE. 1989. SAS/STAT user's guide, ver. 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SAUNDERS, D.A., R.J. HOBBS, and C.R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5:18-32.
- SINCLAIR, A.R.E., D.S. HIK, O.J. SCHMITZ, G.G.E. SCUDDER, D.H. TURPIN, and N.C. LARTER. 1995. Biodiversity and the need for habitat renewal. *Ecol. Applications* 5:579-587.
- SKOLE, D.L., W.H. CHOMENTOWSKI, W.A. SALAS, and A.D. NOBRE. 1994. Physical and human dimensions of deforestation in Amazonia. *BioScience* 44:314-322.
- SMITH, B.H., C.E. DERIVERA, C.L. BRIDGMAN, and J.J. WOIDA. 1989. Frequency-dependent seed dispersal by ants of two deciduous forest herbs. *Ecology* 70:1645-1648.
- SOKAL, R.R. and J.F. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd ed. W. H. Freeman and Company, New York.
- TERBORGH, J. 1992. Maintenance of diversity in tropical forest. *Biotropica* 24:283-292.
- TRACY, C.R. and P.R. BRUSSARD. 1994. Preserving biodiversity: species in landscapes. *Ecol. Applications* 4:205-207.
- TUCKER, M.R. 1996. Soil test methods used by NCDA Agronomic Division. North Carolina Department of Agriculture, 4300 Reedy Creek Road, Raleigh North Carolina 27607-6465.
- TURNER, B.L. III, W.B. MEYER, and D.L. SKOLE. 1994. Global land use/land cover change: toward an integrated program of study. *Ambio* 23:91-95.
- TURNER, M.G., S.R. CARPENTER, E.J. GUSTAFSON, R.J. NAIMAN, and S.M. PEARSON. 1997. Land use. *In: Mac, M.J., P.A. Opler, P. Doran, C. Haecker, and L. Huckaby Stroh (eds.). Status and trends of our nation's biological resources.* Volume 1, Chapter 2. National Biological Service, Washington, D.C.
- WALKER, B.H. 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6:18-23.
- WEAKLEY, A.S. 1995. Flora of the Carolinas and Virginia. February, 1995 (working draft). The Nature Conservancy, Southeast Regional Office, 101 Conner Drive, Chapel Hill, North Carolina 27514.
- WEAR, D.N. and P. BOLSTAD. 1998. Land use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. submitted to *Ecosystems*.