Gauging the Ecological Capacity of Southern Appalachian Reserves: Does Wilderness Matter?

J. C. Haney
M. Wilbert
C. De Grood
D. S. Lee
J. Thomson

Abstract—A multi-unit wilderness system in the Southern Appalachians was evaluated for its long-term capacity to support biodiversity and provide other forms of "ecological insurance." Based on spatial thresholds for selected species, community and ecosystem level attributes, ecological capacity was found to be conditional, hierarchical and interactive. Existing reserves appear to have successfully maintained some ecological structure and processes for up to half-century. However, most reserves theoretically large enough to represent certain animal taxa were too small to sustain, in situ, all native habitats for these taxa. Designated wilderness did not represent all major forest types common to the bioregion. Additions to the network would enhance but not completely safeguard the ecological capacity of this wilderness system.

How large must wilderness be? Answers to this question depend on the specific region and goals outlined for a particular wilderness reserve. Size of wilderness can depend on either social preferences or the natural values to be preserved. If the goal is to provide solitude for recreationists, for example, wilderness size might depend on the number of visitors dispersed within a "viewscape,"a feature which in turn is dictated by the region's topography and proximity to anthropogenic structures.

The wilderness system is often promoted as a means to safeguard ecological attributes no longer found on, or at greater risk within, extensively managed lands. Although this expectation is easily framed, judging whether or not wilderness actually fulfills this role is far more complicated. Such judgement requires knowing whether a protected landscape is sufficiently large and representative to sustain desired ecological attributes over long time horizons.

Two principal approaches exist for testing these expectations. The first uses past trends to judge whether desired ecological values have in fact been maintained, at least up until the present. The second approach relies on projection of trends into the future to see how well ecological values are likely to be maintained given known rates of disturbance and other sources of natural or anthropogenic risk.

Selected spatial thresholds in ecological structure or function, including natural disturbance regimes, are used here to estimate adequacy in the size of wilderness and other protected landscapes in the Southern Appalachians. We employ both retrospective and futuristic perspectives in these analyses. We also review evidence for the ability of the designated wilderness reserve system in this region to protect certain elements of biodiversity over the last half century. Finally, we examine whether and how the addition of lands adjacent to this wilderness system might enhance long-term sustainability. Our analyses used a combination of existing wilderness areas, nearby public lands and other land units that have been proposed recently for protection.

Ecological Capacity Defined

For any particular landscape, a common goal of wilderness designation may be to protect both its ecological structure and the underlying functional processes that maintain that structure (ecological capacity). We employ the term ecological capacity instead of ecological integrity, since the latter relies mainly on measurement of biotic structure referenced to known benchmarks of endemic natural conditions (Angermeier and Karr 1994, Karr 1993). It is possible for an ecosystem to have low integrity (due to recent degradation) but high capacity so long as restoration is feasible. This situation is typical of Eastern wilderness areas, most of which consist of lands previously harvested, tilled or otherwise altered by human use.

Ecological capacity is therefore a measure of the relative ability of a reserve to adequately protect a suite of designated natural attributes. Ecological capacity is dependent on both the characteritics of the reserve itself and the surrounding landscape matrix. If either a single unit or the wilderness system as a whole is too small, protection of an ecological attribute is likely to be jeopardized. For example, a reserve may be too small to sustain viable populations of some sedentary animal, or too small to withstand fire or other disturbances that typically operate over spatial scales considerably larger than the area of the reserve.

In addition, wilderness might be expected to be sufficiently large or otherwise configured so as to contain all

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J. C. Haney and C. De Grood are Forest Ecologist and Research Analyst in the Ecology and Economics Research Department, The Wilderness Society, 900 17th Street, NW, Washington, DC 20006 U.S.A., e-mail: jchris_haney@tws.org. M. Wilbert and J. Thomson are GIS and Remote Sensing Analysts in the Center for Landscape Analysis, The Wilderness Society, 1424 Fourth Ave., Rm. 816, Seattle, WA 98101 U.S.A. D. S. Lee is Curator of Ornithology, North Carolina State Museum of Natural Sciences, P.O. Box 29555, Raleigh, NC 27626 U.S.A.

ecosystem structure, community types or species representative of the bioregion. Here too the size, shape and distribution of individual protected units and the wilderness system as a whole will dictate whether this ecological capacity is actually achieved.

Fortunately for planning purposes, not all spatial scales are equally relevant in understanding area requirements. Rather, there are critical thresholds in which abrupt shifts in ecological responses occur at certain key scales (Frelich and Reich 1998, With and Crist 1995, With and King 1999). Once identified, these can be used as screening criteria to judge whether land units meet and preferably exceed some minimum threshold in a defined area requirement (e.g., fire disturbance regimes: Heinselman 1973, Johnson and Van Wagner 1985).

A complete assessment of all critical thresholds significant to minimum area planning for wilderness is beyond the state of current knowledge. Nevertheless, a subset of these area requirements can be readily calculated with both empirical data and theoretical considerations. We use a selected suite of area requirements specific to the Southern Appalachian landscape in order to assess the ecological capacity of this wilderness system.

A Case Study: The Southern Appalachians

Study Area

Our study examined protected and other federally managed lands in a four-state region (Tennessee, North Carolina, South Carolina, Georgia). This portion of the Southern Appalachians contains extensive forest interior habitat bisected by no interstates and few major highways (fig. 1).

The region includes 217,000 acres of wilderness areas, more than 93% of which is forested, in 17 individually designated units scattered across four contiguous national forests: the Nantahala-Pisgah, Sumter, Cherokee and Chattahoochee. The largest single unit is the 36,800-acre Cohutta Wilderness Area; the smallest unit is the 2,600-acre Gee Creek Wilderness Area. Along with the 515,500-acre Great Smoky Mountains National Park (GSMNP), 93% of which is proposed and managed as wilderness, the de facto National Wilderness Preservation System in this region exceeds 730,000 acres.

Some of the region's individual wilderness areas are contiguous and therefore best analyzed in terms of their combined size. We considered wilderness units contiguous if their nearest points were <200 meters apart in the GIS data layer in the Southern Appalachian Assessment (SAMAB 1996). Contiguous wilderness units thus included the Big Frog and Cohutta Wilderness Areas (41,400 acres), Joyce Kilmer/Slickrock and Citico Creek Wilderness Areas (33,600 acres), and the Raven Cliffs and Mark Trail Wilderness Areas (27,500 acres). After combining these tracts, 15 individual land units were available for evaluating ecological capacity (14 on national forests and the GSMNP).

An additional 797,243 acres on nearby lands have been proposed for protection (fig. 1). This total includes all USDA Forest Service roadless areas (164,890 acres; 97.5% forested) and unroaded blocks designated as desirable for protection by a variety of non governmental groups, including

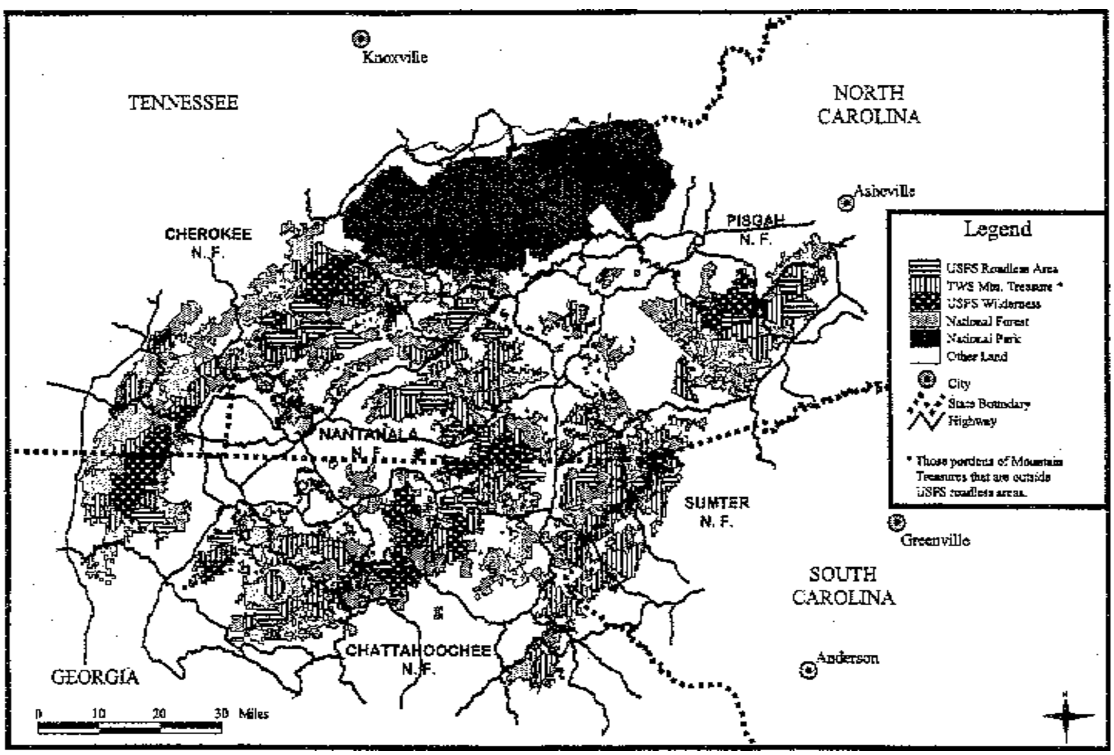

Figure 1—Study region used to evaluate the ecological capacity of existing wilderness, other protected lands, and proposed reserves in the Southern Appalachians.

a multi-state inventory sponsored by The Wilderness Society called the “Mountain Treasures”parcels (632,353 acres; 99% forested). The acreage of Mountain Treasures parcels included in our analyses is that fraction outside and additional to the USDA Forest Service’s roadless area inventory. Not all parcels proposed for protection are necessarily eligible for wilderness designation, although most have been recommended by public interest groups for some form of permanent protection in scenic, research natural and other administrative categories.

Forest Type Representation

Forests cover approximately 69% of the 37 million-acre Southern Appalachian region (SAMAB 1996). Eight major forest types are found: mixed mesophytic hardwoods, mixed pine-hardwoods, montane spruce-fir, northern hardwoods, oak, southern yellow pine, white pine-hemlock and bottomland hardwoods. We used the Forest Service’s CISC (Continuous Inventory of Stand Condition) data cross-walked to these eight major forest types, as summarized with FIA (Forest Inventory and Analysis) data, to figure acreages of each type within the existing wilderness system, as well as on lands proposed for protected status. We used only the forested acreages in these comparisons.

Representation of each forest type in existing wilderness and in areas proposed for permanent protection was then compared to the relative proportions of forest types characteristic of the Southern Appalachian Assessment region as a whole (SAMAB 1996). We used the regional proportions of forest types in log-linear models and calculated the standardized residuals (Wilkinson 1989) so that individual types over- or underrepresented in the reserve system could be identified. Absolute values of standardized residuals that summed to a minimal total were used to identify particular protection systems (both existing and proposed) that best represented the major forest types.

Disturbance Regimes and Minimum Dynamic Area

We surveyed major sources of disturbances in the Southern Appalachians (Bratton and Meier 1998, Greenberg and McNab 1998, Harrod and others 1998, SAMAB 1996), and used disturbance frequency and spatial extent to estimate minimum dynamic areas for quasi-equilibrium landscapes. Quasi-equilibrium landscapes consist of shifting mosaics made up of all forest age classes that persist in perpetuity, although the location and extent of each successional stage varies (Shugart 1984). The minimum dynamic area (MDA) is the smallest land area on which all successional stages (early, middle, late, old growth) are expected to be maintained at all times by natural disturbance (Frelich 1995). Maintenance of such structural diversity by natural means only is a common scenario if administrative or legal prescriptions preclude more interventionist management within the wilderness system.

Two broad methods have been proposed for calculating MDAs. One approach is rule-based and identifies the MDA as either twice the size of the largest disturbance patch (Johnson and Van Wagner 1985) or 50 times the size of the average disturbance patch (Shugart 1984). A second approach consists of a stochastic model in which the statistical risk from stand-replacing disturbance is calculated as a function of land area. We used both methods in our analyses to compute MDAs for the Southern Appalachian region.

Large-scale disturbances include those arising singly or in combination from climatic, edaphic and biotic factors. Larger rather than small-scale disturbances are more important to MDA estimation because an area large enough to accommodate the most extreme disturbance will automatically accommodate smaller, less catastrophic ones. Thus, we searched the literature for broad categories of disturbance in order to identify the largest disturbance patches likely to occur in the Southern Appalachian region:

Fire—Fire is prevalent in oak, southern yellow pine and mixed pine-hardwood forests of the Southern Appalachians (Abrams 1992, Barden and Woods 1976, Delcourt and Delcourt 1997, Harmon 1982). An average of 6 to 16 lightning fires per million acres strike the region annually (Bratton and Meier 1998, SAMAB 1996). Under the assumption that fires result in at least some deaths of canopy trees, we plotted the probability of stand replacement as a function of hypothetical forest planning areas for 10-year intervals, the approximate time for closure of the canopy following extreme stand-replacing fires. A 10-year interval was chosen for the stochastic fire model because this disturbance frequency would result in perpetual maintenance of some early successional habitat on the planning area.

To figure the acreages actually burned by fires caused by lightning and other sources, we examined fire records from 1970 to 1993 for each of seven regional national forests (table 1). Fires in this region commonly orginate from both natural and anthropogenic sources, but because their origin makes little difference when figuring the largest disturbance patch, we sought mainly to identify the sizes of the average and largest fires.

Windthrow—A variety of meteorological and climatic factors cause trees to be windthrown in the Southern Appalachians, including microbursts, macrobursts, tropical storms (including hurricanes), tornadoes, and passage of severe weather fronts (e.g., Bratton and Meier 1998, Greenberg and McNab 1998, SAMAB 1996). Windthrows can lead to increased fuel loads and susceptibility to fire (Bratton and Meier 1998), so the potential for disturbance types to interact and potentially reinforce each other is high.

Table 1—Sizes of burns (in acres) on seven National Forests of the Southern Appalachians, 1970-1993 (SAMAB 1996).

Forest	Mean size	SD	Maximum[a]	Cause
Talladega	16.7	48.1	1055 (155)	incnd.
Chattahoochee	11.0	46.3	1050	ltng.
Cherokee	12.3	70.0	1699 (288)	incnd.
George Washington	20.3	174.6	4359 (550)	equip.
Nantahala-Pisgah	12.1	63.1	2215 (1300)	other
Sumter	20.4	190.3	2856 (87)	other
Jefferson	22.7	112.0	1850 (211)	other
All	14.3	87.4	4359 (1300)	equip.

[a]Largest fire from any cause; largest fire caused by lightning (if available) shown in parentheses.

We plotted probability of severe windthrow as a function of forest planning area for 10-year intervals, the approximate time for closure of the canopy following an extreme stand-replacing disturbance. Severe windthrow was defined as the statistical likelihood of F2-F5 tornadoes expressed per unit area. Annual likelihood of storms of this magnitude is 1.1 per 10,000 square miles for the five states of Alabama, Georgia, South and North Carolina and Tennessee (NOAA National Climatic Data Center). As in the stochastic fire model, a 10-year interval was chosen for the windthrow model because disturbances at this frequency would result in perpetual maintenance of some early successional habitat on the planning area.

Other Disturbances—Other types of disturbance common in the region include ice glazing and outbreaks of forest insects (SAMAB 1996). These disturbances rarely if ever cause complete canopy removal or stand replacement, however. Ice storms mainly prune over relatively small areas, often targeting conifers with shallow root systems (<175 acres, Bratton and Meier 1998). Although such disturbance may not immediately replace stands, it could contribute (along with drought) to fuel loads and thus susceptibility to a larger or more complete disturbance from fire.

We found no evidence that outbreaks of native insects routinely cause complete stand-replacement at scales larger than fire or windthrow in the forests of this region. Outbreaks of nonnative insects are another matter. Gypsy moth (*Lymantria dispar*) has not yet reached this study area, but hemlock woolly adelgid (*Adelges tsugae*) could eventually cause (Benzinger 1994), and the balsam woolly adelgid (*Adelges picea*) already has caused (Busing and Clebsch 1988), nearly complete removal of the canopy in white pine-hemlock and montane spruce-fir forest types, respectively. Still, it is not evident that disturbances by nonnative forest insects cause complete canopy turnover at spatial scales equivalent to or greater than those associated with fire and windthrow.

Historical Change, Representation and Productivity of Forest Wildlife Communities

In addition to the distinctiveness that diverse community types and large forest interiors bring in and of themselves to regional landscapes, forest ecosystems are also required habitats for many constituent species. Birds and large carnivores are among several taxa found to be particularly sensitive to forest conditions, including the amount of edge, fragmentation and interior area (e.g., Hawrot and Niemi 1996, Machtans and others 1996, Weinberg and Roth 1998, Wenny and others 1993). Due to “hostile conditions”now prevalent in anthropogenic landscapes (Askins 1995), wilderness areas and other large forest reserves are particularly important because these refugial “sources” promote elevated densities, pairing success and productivity of forest-interior wildlife that subsidize the “sink” habitats in more disturbed landscapes (Clark and Pelton 1999, Robinson and others 1995a, Van Horn and others 1995).

The Southern Appalachians contain the largest block of protected forested landscape in the eastern U.S. (Simons and others 1999). Long-term changes in the composition and relative population levels of forest birds and other wildlife in the Southern Appalachians were investigated by inspection of the literature (Kendeigh and Fawver 1981, Simons and others 1999, Wilcove 1988), as well as by conducting one new analysis on a 50-year data set from the Unicoi Mountains just south of the Park (Ganier and Clebsch 1944, 1946, Haney and others 1998, McConnell and McConnell 1983).

For birds, actual population levels were available for the Park whereas only data on relative abundance and composition were available from the Unicoi Mountains. Change in composition of the bird community of the Unicoi Mountains was compared via a Friedman’s test on the ranked abundances of all bird species recorded across three time spans: 1944-1946, 1981-1982, and 1996-1998. This test is not sensitive to the relative abundance of individual species, but rather assesses major compositional changes in the community as a whole.

To estimate the minimum area required to represent a regional bird community typical of landscapes in and near the wilderness system, we modeled the species accumulation rate as the function of area sampled in two national forests, the Nantahala-Pisgah in North Carolina and the Cherokee in Tennessee. In 1996 and 1997, 65 transects (11.1 acres each) were conducted during the breeding season and total individuals for each species tallied. Areas both inside and outside existing wilderness were sampled. Habitat types sampled for this landscape-level area curve (Flather 1996) included grass and heath balds, roadsides, clearcuts and other harvested units, and a variety of forest types, including white pine-hemlock, mixed mesophytic, northern hardwoods, oak and mixed pine-hardwoods.

The asymptote to the species area curve for these data was calculated with a maximum likelihood estimator (Raaijmakers 1987) and the minimum area corresponding to this asymptote interpolated along the curve’s horizontal axis. Asymmetric confidence limits (CI) for the asymptote and interpolated survey effort were calculated with n = 20,000 Monte Carlo iterations of the curve in 20 separate trials (Henderson and Seaby 1997).

Forest birds are primarily open-cup nesters and thus particularly susceptible to parasitism by the brown-headed cowbird (*Molothrus ater*), normally an occupant of open landscapes (Robinson and others 1995b). Since forested wilderness might be planned to mitigate such reproductive losses in more degraded habitat, we figured the minimum area necessary to offer forest birds at least some absolute protection from nest parasitism. We used a radius of ~23,000 feet to figure the most area- and edge-minimizing patch shape (circle) given the maximum distances traveled by cowbirds during daily commutes from roosting areas (Rothstein and others 1974, Thompson 1994). A major assumption of this minimum area requirement for avian productivity is that the reserved forest block is separate from but still accessible to cowbird feeding sites (Robinson and others 1995b).

Understory Diversity and Forest Regeneration

Overbrowsing by high populations of white-tail deer (*Odocoileus virginianus)* can cause severe impacts to forest regeneration, understory diversity and wildlife habitat (Anderson and Loucks 1979, Frelich and Lorimer 1985, McShea and Rappole 1992). These disruptions of Eastern forest ecosystems occur typically at threshold densities of ~21-47 deer per square mile (deCalesta 1994). We calculated a minimum area requirement based on the average travel distance of deer that would halve deer density and thereby mitigate negative impacts of browsing at the center of the forest block. This standard is similar to that used in some USDA Forest Service management plans (for example, Alverson and others 1988).

Ecological Capacity of Southern Appalachian Wilderness: A Report Card

Community Representation and Change

Forest Types—Forest Service wilderness areas and the GSMNP jointly contain seven of the eight major regional forest types (fig. 2). Currently, there is no bottomland hardwood forest protected in this portion of the National Wilderness Preservation System. Over-represented forest types in the system as a whole include mixed mesophytic, montane spruce-fir, northern hardwood and white pine-hemlock, all types commonly associated with middle and upper elevations. Mixed pine-hardwood, oak and southern yellow pine, all types more prevalent at middle and lower elevations, are disproportionately uncommon in this wilderness system.

In GSMNP, mixed pine-hardwood (standardized residual = -132) and montane spruce-fir forest (standardized residual = 742) were the most under- and overrepresented types, respectively. In all Forest Service wilderness areas combined, southern yellow pine (standardized residual = -69) and mixed mesophytic (standardized residual = 126) were the most under- and overrepresented types, respectively. In the combined wilderness system, mixed pine hardwood (standardized residual = -142) and montane spruce-fir forest (668) were the most under- and overrepresented types, respectively (fig. 2).

The much smaller acreage of Forest Service wilderness areas actually better approximated the mix of forest types typical of the region than did the GSMNP, an area more than twice as large (total of standardized residual absolute values = 562 versus 1,700, respectively). The existing wilderness system as a whole was no more efficient in its representation of major forest types than was the GSMNP alone (both standardized residuals total = 1,700).

Areas proposed for protection include all eight major types common to the region (fig. 3), although the amount of bottomland hardwoods is still quite small (720 acres total; 199 acres in Forest Service roadless, 521 acres in Mountain Treasures). Areas proposed for protection tend to be overrepresented with white pine-hemlock (standardized residual = 306) and underrepresented with southern yellow pine (standardized residual = -127). As measured by total absolute values of standardized residuals in the log-linear models, lands proposed for protection were more efficient in representing forest types in proportion to their regional occurrence than GSMNP or the wilderness system as a whole, but not as efficient as existing Forest Service wilderness areas (total of standardized residual absolute values = 940).

Bird Community—Minimum areas capable of representing all species typical of bird communities in forested landscapes of the Southern Appalachians averaged about 600 acres (fig. 4; 568 acres, lower 95% CI; 734 acres, upper 95% CI). This is merely the smallest land area on which there exists a reasonable expectation that all native, woodland species would be represented; it is not equivalent to a

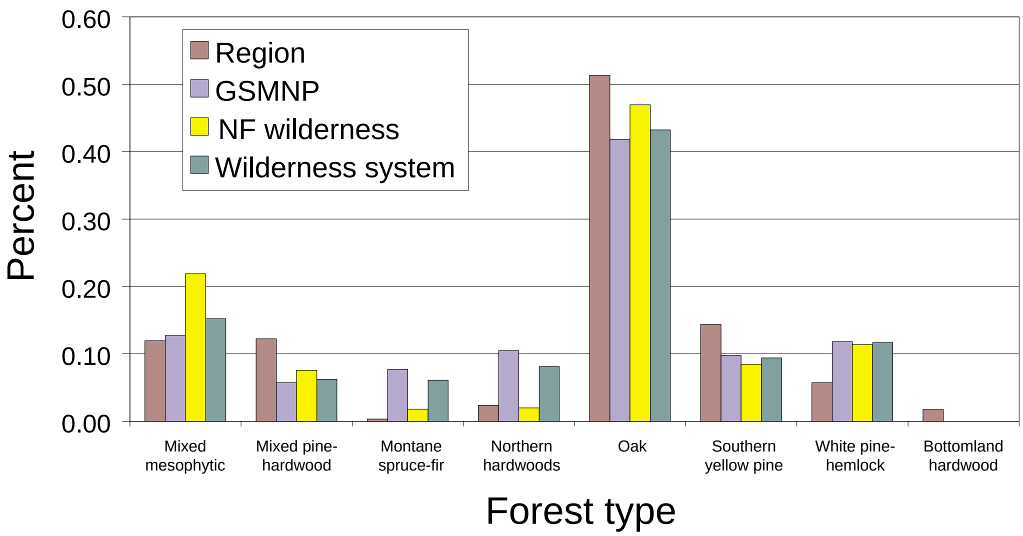

Figure 2—Representation of eight major forest community types in the Great Smoky Mountains National Park (GSMNP; MacKenzie and White 1998), on National Forest wilderness areas (USDA Forest Service data), and in the combined wilderness system compared to forest types found throughout the entire Southern Appalachian Assessment region (SAMAB 1996). Mixed pine-hardwood, oak, southern yellow pine, and bottomland hardwood forest types are more common at lower elevations.

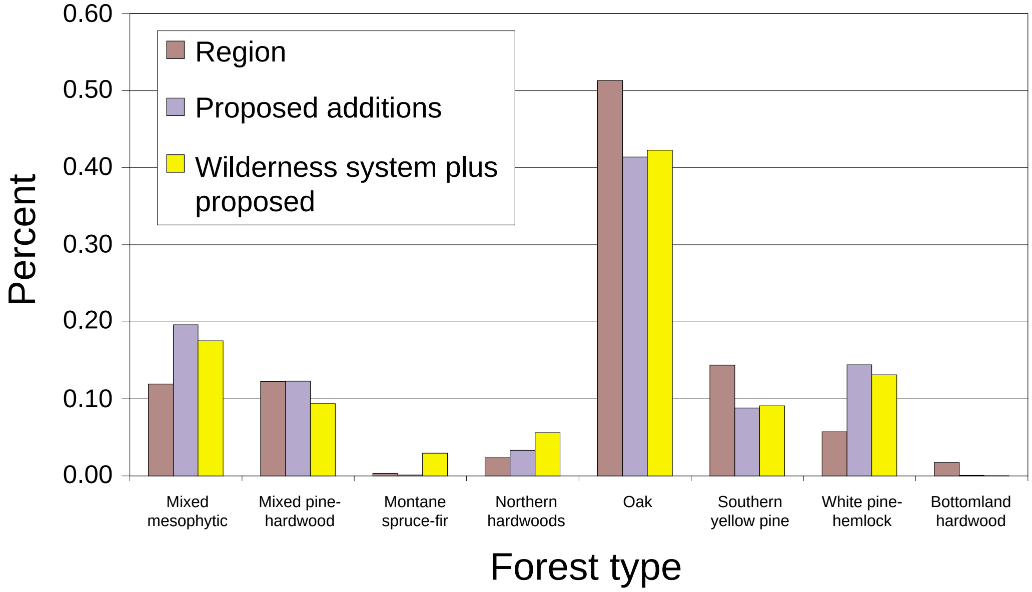

Figure 3—Representation of eight major forest community types in areas proposed for protection (USDA Forest Service roadless areas and the Wilderness Society's® Mountain Treasures inventory), and in the existing wilderness system plus these proposed areas, relative to forest types found throughout the entire Southern Appalachian Assessment region (SAMAB 1996).

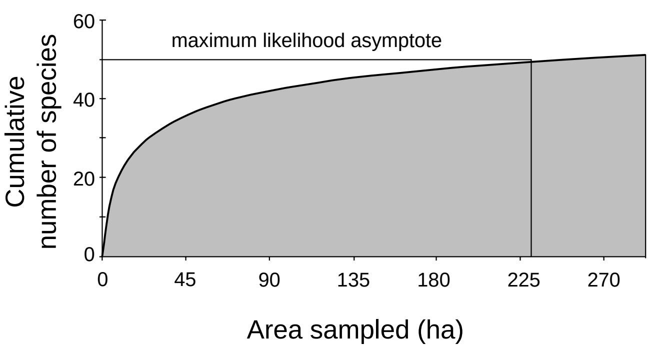

Figure 4—Species accumulation curve for complete representation of the bird community characteristic of the upper Unicoi Mountains, Nantahala-Pisgah and Cherokee National Forests, North Carolina and Tennessee, respectively. Asymptote of the curve was figured with a maximum likelihood estimator (Raaijmakers 1987). The point on the horizontal axis (~600 acres) which corresponds to this asymptote represents the minimum area required to represent all species typically present in the region.

minimum area required for population viability (either for a single or all species). All of the individual wilderness units and thus 100% of the combined acreage in the entire existing wilderness system in the Southern Appalachians exceed this minimum area.

During the last half-century, we found no evidence of major structural changes in the bird community in a portion of the Southern Appalachians that possesses extensive interior forest habitat, including several wilderness areas (Friedman χ_r^2 corrected for ties = 1.19, df = 2, P = 0.55; table 2). No species present during the survey conducted 50 years ago in the Unicoi Mountains had disappeared from the regional avifauna. The four dominant bird species remained identical during this half-century: dark-eyed junco (*Junco hyemalis*), chesnut-sided warbler (*Dendroica pensylvanica*), black-throated blue warbler (*Dendroica caerulescens*), and veery (*Catharus fuscescens*).

Other evidence also points to relative stability and high ecological capacity for forest birds in the Southern Appalachians. Although many of the same species have been decreasing elsewhere in the eastern U.S., Wilcove (1988) found no evidence of significant declines in bird populations studied in the GSMNP after 35 years. His comparison included a variety of forest types, including oak, mixed mesophytic, white pine-hemlock and northern hardwood. Bird populations also experience relatively high productivity in or near at least some of the large wilderness areas of this region (Simons and others 1999) despite opposite trends in the same species elsewhere (Robinson and others 1995a).

Table 2—Changes in the composition of the avian community in the Unicoi Mountains, Tennessee and North Carolina, in the Southern Appalachians across three time spans during the last 50 years.

Survey interval	Ý ranks	Mean rank
1944-1946	116.5	2.04
1981-1982	107.5	1.89
1996-1998	118.0	2.07

Other Minimum Area Estimates

Minimum Dynamic Areas—Rule-based models gave varied estimates for MDAs in the Southern Appalachian region. Rule-based approaches using disturbance patch sizes caused by fire gave MDAs of 715 and 8,700 acres, based on mean and maximum fire size, respectively (table 1). Rule-based approaches using disturbance patch sizes caused by wind gave an MDA of 1,200 acres, based on maximum size of windthrow (a 1994 tornado near Tullulah Gorge; Bratton and Meier 1998). We could find no published estimates of the average size of disturbance patches caused by wind in this region.

Using these rule-based estimates, about 13% of the individual wilderness units and 76% of the combined acreage in the entire wilderness system in the Southern Appalachians exceed the largest MDA estimated with fire statistics. All of the individual wilderness units and thus 100% of the combined acreage in the entire wilderness system in the Southern Appalachians exceed the largest MDA estimated with windthrow statistics.

MDAs calculated with stochastic models were generally larger than those estimated with rule-based approaches. An MDA in which there exists a high likelihood (95-100%) of fire occurring often enough to create early successional habitat at least once every 10 years is equivalent to about 7,000 acres (fig. 5). An MDA in which there exists a similarly high likelihood of severe windthrow occurring often enough to create early successional habitat at least once every 10 years is equivalent to about 650,000 acres (fig. 5).

Using these figures, about 87% of the individual wilderness units and 99% of the combined acreage in the entire wilderness system in the Southern Appalachians exceed the largest MDA estimated with stochastic fire models. Not a single individual wilderness unit in the entire Southern Appalachian wilderness system exceeds the largest (and thus most stringent) MDA estimated with the stochastic windthrow model. However, at 515,519 acres, the GSMNP comes close to achieving this measure of landscape equilibrium. A reasonably high probability (88%) still exists that stand-replacing windthrow will create early successional habitat on this National Park at least once every 10 years.

Mitigation of Nest Parasitism—The minimum area necessary to offer forest birds some absolute protection from nest parasitism was estimated to be 38,000 acres. Distances used in this calculation have been found to truly mitigate nest parasitism in an Eastern national forest with regional cowbird abundance similar to that found in the Southern Appalachians (Coker and Capen 1995, Robinson and others 1995). About 13% of the individual wilderness units and 76% of the combined acreage in the entire wilderness system in the Southern Appalachians exceed this minimum area requirement. Supporting this theoretical assessment, cowbirds have been essentially absent in and near the largest wilderness areas of this region during the past 50 years (e.g., Ganier and Clebsch 1946, Haney and others 1998, Wilcove 1988).

Mitigation of Understory Degradation—A minimum area that offers some enhanced protection from overbrowsing by deer was figured as 49,662 acres. Only 7% of the individual wilderness units and 70% of the combined acreage in the entire wilderness system in the Southern Appalachians consist of areas that exceed this minimum. Actual size of blocks for mitigating deer overbrowsing would vary, depending upon the surrounding landscape matrix; the minimum area for any given level of mitigation would increase if early successional habitat were created deliberately (Alverson and others 1988: 355). Notably, very little of the study area (fig. 1) has severe problems associated with the kinds of overbrowsing common in the highly fragmented Mid-Atlantic states (e.g., deCalesta 1994, McShea and Rappole 1992). Only in a few situations is there significant impact to the understory from overbrowsing, such as at Cades Cove, GSMNP, where no hunting, few natural predators and a landscape matrix consisting of both agriculture and woodland combine to promote locally high deer densities.

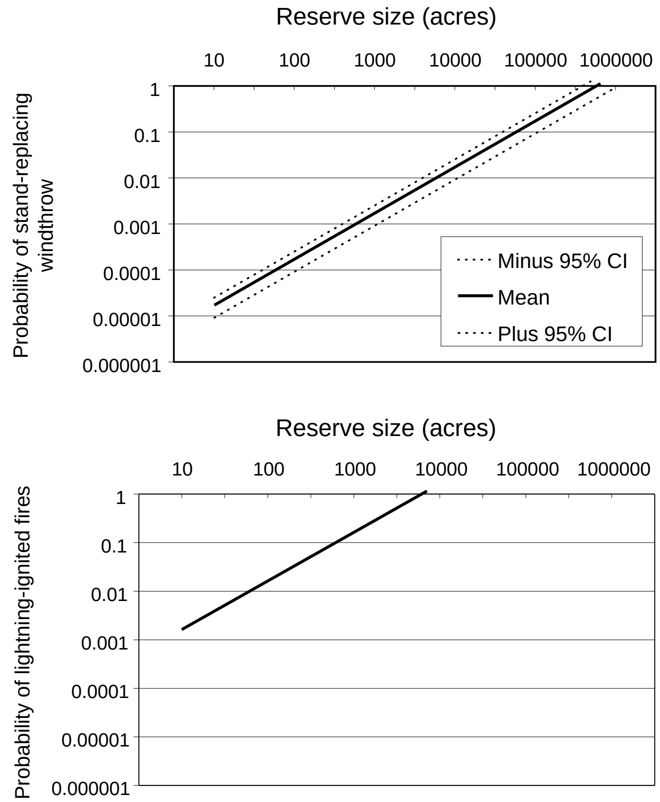

Figure 5—Planning sizes and rates of extreme stand-replacing disturbance for forest reserves in the Southern Appalachian states. Note log scale used for probabilities on vertical axis. Mean and 95% confidence limits for windthrow were figured using intra-regional differences in the frequencies of F2-F5 storms 10 years^{-1} across a five-state region (Tennessee, North Carolina, South Carolina, Georgia, Alabama).

Implications for Ecological Capacity in the Southern Appalachians ____

Our analyses provide encouraging evidence that some aspects of ecological capacity are well-maintained in the Southern Appalachian wilderness system. Wilderness protects the majority of forest types (fig. 2), the system as a whole does a superior job of protecting four of the region's seven scarcest forest community types (mixed mesophytic, montane spruce-fir, northern hardwoods, white pine-hemlock), and one individual unit (GSMNP) approaches landscape equilibrium and thus likely conforms to the most stringent requirement of a minimum dynamic area. Over much of this region, regeneration of understory plants is unimpeded by overbrowsing. The largest remaining and most area-sensitive carnivore, the black bear (*Ursus americanus)*, has stable or increasing populations in the core of the wilderness system (Clark and Pelton 1999).

Under the scenario modeled by stochastic disturbance regimes (fig. 5), where distinctions between single and combined units for landscape equilibrium are not necesssary, the existing wilderness system as a whole is larger (730,000 acres) than the largest estimate of a minimum dynamic area (650,000 acres). One inference that can be drawn from this finding is that even under a management regime of active fire suppression (Buckner and Turrill 1999), frequency of windthrow is statistically sufficient to ensure a high probability of some early successional habitat in perpetuity for the forests in this regional landscape. (Disturbance intervals in this region are much longer than required for development of old-growth characteristics [Lorimer 1980, White and others 1985]).

Additional evidence of relative stability was obtained in the composition of the regional biota based on historical comparisons of avian communities (table 2). Since establishment of GSMNP and the protection afforded other previously degraded lands acquired earlier this century, bird populations and composition have remained largely unchanged at some locations in the region. Long-term absence of nest parasites (Wilcove 1988) and high productivity of bird populations (Simons and others 1999) also suggest that this wilderness system may be achieving some of its ancillary goals of fostering hiqh-quality forest interior habitat for wildlife.

Several deficiencies in ecological capacity were nevertheless revealed. Single units of the wilderness system are apparently not sufficiently large to serve as effective repatriation sites for large species of extirpated carnivores (Lucash and others 1999). The wilderness system offers no protection for the bottomland hardwoods (fig. 2), although adding some of the proposed areas to the protected system could enhance representation of this forest type (fig. 3). Measured against various minimum dynamic areas, additions of protected areas would enhance the viability of individual units and the wilderness system as a whole (table 3, fig. 6). Even with these additions, however, the wilderness system of the Southern Appalachians would continue to underrepresent forest types more prevalent at lower elevations (fig. 3).

Implications for Wilderness Planning

Ecological capacity in wilderness is conditional, interactive and hierarchical. These three general principles are likely to dictate management and area planning for any wilderness system. Minimum area requirements are conditional, in that their estimation depends on explicitly framing the desired condition for which the planning is aimed. Disturbance frequency and representation each allowed calculation of specific minimum planning areas as long as empirical data were available and assumptions used were valid (for example, disturbance rates do not change markedly over time). It is important to note that we examined only a few of all possible minimum area requirements for regional ecosystems, and not necessarily those that could be most critical to wilderness design.

A second principle that arises from our evaluations is that use of minimum area requirements for wilderness planning necessitates considerations of multiple interactions. For example, if wilderness reserves are designed to promote metapopulation dispersal in forest interior birds and thus maintain balanced source-sink dynamics (Pulliam 1988), such planning must simultaneously ensure adequate species representation (fig. 4), buffer from excessive nest parasitism and maintain structural habitat diversity (including successional age classes) in all of the regional forest types (figs. 2 and 3). Failure in any one of these (or other) area requirements will compromise a goal of the wilderness system to sustain a regional avifauna.

Similarly, although we analyzed the effects of fire and windthrow separately (fig. 5), the two disturbances clearly interact with each other (Bratton and Meier 1998), as well as with other sources of disturbance. Although a metric that combined cumulative rates of disturbance would be quite useful for wilderness planning, each disturbance in isolation may be more relevant to landscapes that are dominated by a particular forest type (xeric versus mesic) or management regime (such as fire suppression).

Table 3—Increase in ecological capacity for three selected minimum area requirements as a consequence of adding lands proposed for protection to the existing wilderness system in the Southern Appalachians.

Minimum area requirement (size)	Existing system[a]		Existing plus proposed[b]	
	No. units (%)	Area in acres (%)	No. units (%)	Area in acres (%)
Mitigation of nest parasitism (38,000 acres)	2 (13)	556,973 (76)	7 (30)	1,228,801 (87)
Mitigation of overbrowsing (49,662 acres)	1 (7)	515,519 (70)	6 (26)	1,183,540 (84)
Largest disturbance patch caused by fire (8,700 acres)	9 (53)	694,190 (95)	14 (61)	1,350,349 (96)

[a]*n* = 15 individual, non-contiguous land units (732,500 acres total) already designated in or proposed for the National Wilderness Preservation System in the Southern Appalachians (fig. 1).
[b]*n* = 23 individual, non-contiguous "patches" consisting of existing wilderness plus contiguous lands proposed for protection (1,402,000 acres total) in the Southern Appalachians (fig. 6).

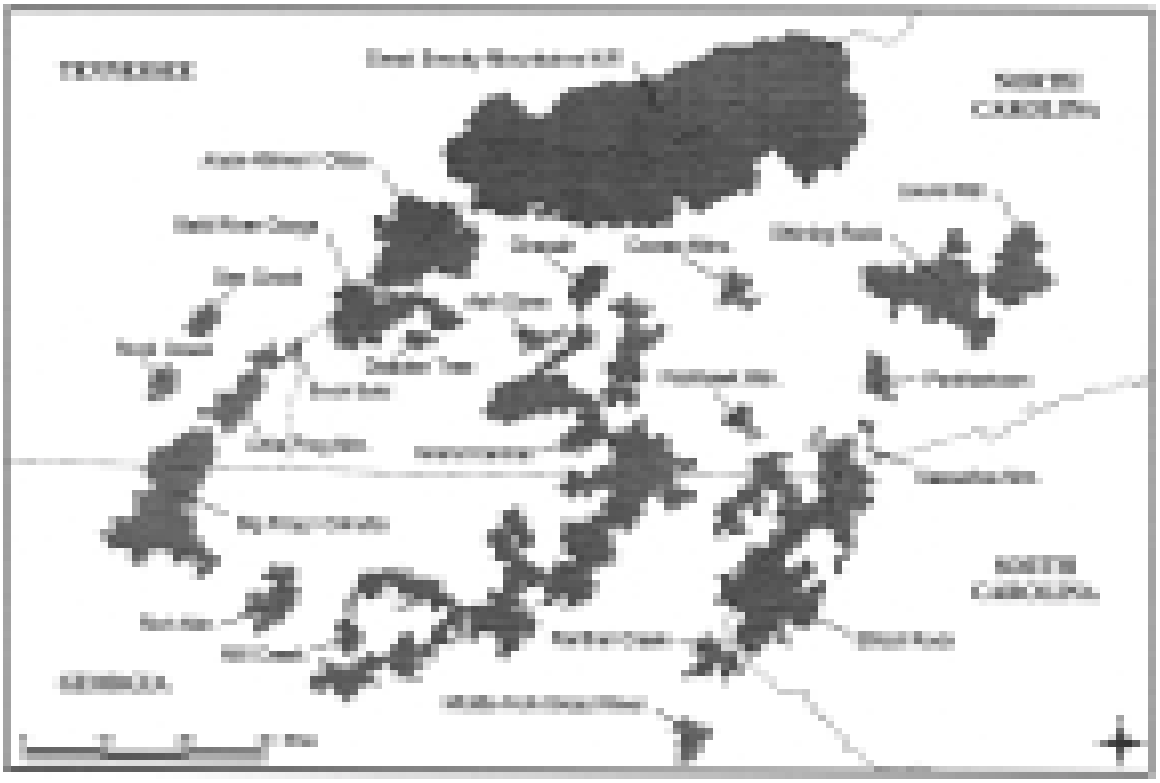

Figure 6—Twenty-three contiguous patches resulting from combining existing units of the National Wilderness Preservation System in the Southern Appalachians with adjacent lands proposed for protection by public interest groups. Contiguity was defined as intersection of adjacent polygons along at least two points within a distance of 656 feet (200 m).

Finally, our analyses underscore the hiearchical nature of factors that combine to influence ecological capacity in wilderness areas. Both spatial and temporal hierarchies can impact such planning. For example, the minimum area requirements that we calculated are insufficient to mitigate impacts to ecological capacity from sources outside wilderness area boundaries. In the Southern Appalachians, these exogenous factors include exotic wildlife and insects (Busing and Clebsch 1988, Peine and Lancia 1999, Schlarbaum and others 1999), atmospheric pollution (Nicholas and others 1999), and regional declines in individual neotropical migrant bird species from habitat degradation on their wintering grounds (James and others 1996, Rappole and McDonald 1994). Such impacts may confound the best planning for and management of the wilderness system itself.

In a temporal sense, planning that is adequate for current levels of natural disturbance may be insufficient in the face of significant long-term changes, including those attributable to global climate. Major shifts in disturbance rates are virtually certain to either increase or decrease the size of minimum planning areas (fig. 5). Restoration of endemic fire regimes in this region, now suppressed for at least 70-90 years (Buckner and Turrill 1999), would likely direct forest succession on a trajectory toward younger age classes and greater representation of the more fire-tolerant forest types (Harrod and Harmon 1998). Such management, coupled with an increasing variety and magnitude of other disturbance agents facilitated by humans, would all act to reduce the size of MDAs in the Southern Appalachians. Under any scenario that effectively reduces MDAs, the wilderness system should continue to sustain much of the ecological capacity it now provides.

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