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Source: The American Midland Naturalist, 162(1):148-168.
Published By: University of Notre Dame
DOI: http://dx.doi.org/10.1674/0003-0031-162.1.148
URL: http://www.bioone.org/doi/full/10.1674/0003-0031-162.1.148

Am. Midl. Nat. 162:148–168

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ABSTRACT.—Large ungulates are an important driver of plant community composition and structure. In eastern North America, white-tailed deer (*Odocoileus virginianus*) thrive in agricultural mosaics and fragmented forested landscapes, at times reaching unprecedented densities. Nevertheless, few long-term data sets are available that allow an assessment of the long-term consequences of chronic herbivory. We quantified herbaceous-layer change over a 26 y period in Cades Cove, Great Smoky Mountains National Park, USA. Cades Cove has a long and well-documented history of deer overabundance, with densities reaching 43 deer km^{-2} during the late 1970s. Over the 26 y sampling interval, mean coverage of herbaceous species declined significantly ($P < 0.001$) in the forests bordering Cades Cove. Although most plots only lost 1–2 species during the interval, 46 herbaceous species recorded on plots during the 1970s were wholly absent in 2004 (63% of which were forest species). Additionally, the herbaceous layer has become significantly more homogeneous over time. In contrast, species richness and cover on reference plots increased by 106 and 183%, respectively, over a similar time interval. Whereas some compositional changes were associated with forest succession, proximity to the Cove's edge environments was the most informative environmental gradient, lending support to the hypothesis that deer foraging behavior results in a biotic edge effect in fragmented landscapes. Chronic herbivory may result in impoverishment and simplification of herbaceous layers in forests otherwise protected from habitat degradation and loss.

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INTRODUCTION

Globally, protected areas are important elements of plant and animal conservation strategies (Brooks *et al.*, 2004). However, even within protected areas, species loss and ecosystem simplification resulting from altered or suppressed disturbance regimes have been documented (Fauzi and Buchary, 2002; Rooney *et al.*, 2004), suggesting traditional conservation efforts focused primarily on habitat protection may not be completely successful.

Many protected areas are managed with a ''natural regulation'' ethic, which limits direct human interference with biological processes (Soukup *et al.*, 1999). However, due to historic and contemporary anthropogenic alterations of protected areas and their environs, biological systems in these protected areas often require management beyond natural regulation to ensure ecosystem integrity (Porter and Underwood, 1999; Weisberg and Coughenour, 2003; Ervin, 2004; Turner and Beazley, 2004). For example, in the eastern and midwestern United States, forest fragmentation, row crop agriculture and the extirpation of large predators have facilitated the expansion of white-tailed deer (*Odocoileus virginianus*) populations to unprecedented levels (Alverson *et al.*, 1988; Anderson, 1997; Augustine and deCalesta, 2003). Consequently, intense herbivory associated with locally overabundant deer populations poses a major threat to native plant communities, especially where hunting is limited to conservative buck-only harvesting or prohibited entirely (Rooney and Dress, 1997; Horsley *et al.*, 2003; Campbell *et al.*, 2004; Rossell *et al.*, 2005; Barrett and Stiling, 2006; Tremblay *et al.*, 2007).

Leopold (1933) was among the fist to articulate the importance of edge habitats for species such as the white-tailed deer. Edges between mature and successional forests or between forest and field are often areas of enhanced biological diversity, but an increasing awareness has emerged in recent years that edge effects are not inherently positive (Saunders *et al.*, 1991; Guthery, 1997; Lidicker, 1999). For example, forest edges in landscapes dominated by agricultural row crops may concentrate mammalian predators, which constitute an ecological trap for nesting songbirds in these habitats (Heske *et al.*, 1999). Similarly, herbivores that use edges may profoundly modify the structure and composition of these habitats (Cadenasso and Pickett, 2000). Highly mobile ungulates, such as white-tailed deer whose populations respond positively to fragmented landscapes (Anderson, 1997), may alter woody plant communities distal from recognizable edges (Alverson *et al.*, 1988; Cadenasso and Pickett, 2000). Nevertheless, little is known about the potential consequences of herbivore-mediated edge effects on the long-term stability of herbaceous plant communities.

We examined long-term changes in the composition and structure of understory vegetation within and around Cades Cove, Great Smoky Mountains National Park (GSMNP), USA. In the 1930s, all property in Cades Cove was acquired for inclusion in GSMNP, which was dedicated in 1940 (Campbell, 1994). At that time, the Cove was a mosaic of small fields, pastures and woodlots surrounded by continuous secondary forest. Following acquisition, many old fields were planted with non-native grasses (*e.g.*, *Lolium pratense* (Huds.) S.J. Darbyshire), while others were allowed to succeed to forest. Woodlots and succeeding fields have not been managed or grazed by livestock since acquisition. Combined with the absence of hunting and large predators, this habitat mosaic provided ideal habitat for white-tailed deer. Consequently, Cades Cove has a long and well-documented history of deer overabundance, and at times has contained some of the highest reported deer densities in the Southeast (Wathen and New, 1989). A recent study in Cades Cove identified pronounced changes in the spring flora attributable to foraging by the eruptive deer population, which reached a peak density of 43 deer km^{-2} during the late 1970s (Webster *et al.*, 2005a). Recent exclosure studies in Cades Cove have shown that contemporary deer densities, while lower than peak levels, are sufficient to inhibit the regeneration of most tree species (Fig. 1; Griggs *et al.*, 2006; Webster *et al.*, 2008) and reduce the stature and fecundity of early-blooming, liliaceous species (Webster *et al.*, 2005a; Jenkins *et al.*, 2007).

We reinventoried 30 long-term monitoring plots that were established in western Great Smoky Mountains National Park between 1977–1979. Nineteen of these plots were located in the woodlots and surrounding secondary forests of Cades Cove. These plots were the dominant focus of this study and received the most in-depth analysis. The remaining 11 plots served as a reference to assess whether broad changes in composition observed on the Cades Cove plots were occurring in areas of similar vegetation but without a history of chronic herbivory.

This well-chronicled history of deer abundance in conjunction with long-term permanent plot data (26 y interval) from the 19 plots in Cades Cove provided a unique opportunity to examine the long-term consequences of deer overabundance and chronic herbivory on forest plant communities recovering from past agricultural use and settlement. Additionally, the geographic isolation of the Cove (surrounded by mountains and embedded within a large forested matrix) helped reduce the influence of other potential park boundary effects.

METHODS

STUDY AREA

Nineteen of our study plots were located in western Great Smoky Mountains National Park (GSMNP), in Cades Cove, TN, a broad valley managed as a cultural landscape (*i.e.*, 19th Century agrarian settlement). Cades Cove covers approximately 2700 ha and is surrounded by mountainous parkland, which protects the Cove from boundary effects between protected natural areas and other ownerships. Although Cades Cove was incorporated into GSMNP in 1940, some fields were leased for crops and grazing until the early 1990s. Cattle were prevented from grazing in woodlots through an extensive network of fences. The contemporary landscape of Cades Cove consists of woodlots interspersed within old-fields that are mowed and burned to represent a 19th Century agrarian settlement. Presently, Cades Cove is surrounded on all sides by closed-canopy forest.

Following incorporation of GSMNP, white-tailed deer numbers in Cades Cove increased dramatically in the absence of large predators, harsh winters and hunting. Pre-settlement deer densities in mountainous regions of the southeastern United States have been estimated at between 3–4 deer km^{-2} (Knox, 1997), but were probably even lower during the settlement period due to heavy hunting and habitat destruction (Dunn, 1988). However, by the late 1970s, it was estimated that deer densities in Cades Cove were 43 deer km^{-2} (Kiningham, 1980; Wathen and New, 1989). Eruptive population growth during the 1970s was punctuated by a crash due to a disease outbreak, but spotlight surveys conducted during the early and mid-1980s indicated that the population had rebounded and stabilized at a relatively high density [Wathen and New, 1989; *see* Griggs *et al.* (2006) for a detailed chronology of deer abundance in Cades Cove].

The remaining 11 plots were located in areas of similar vegetation, but without a history of chronic herbivory. All reference plots were at least 3 km linear distance from Cades Cove and physically separated by mountainous terrain. These plots were likewise located in stands with a history of human disturbance including logging of varying intensity, ground fires and livestock grazing (Pyle, 1988). Reference plots exhibited a wider range of elevations (500–

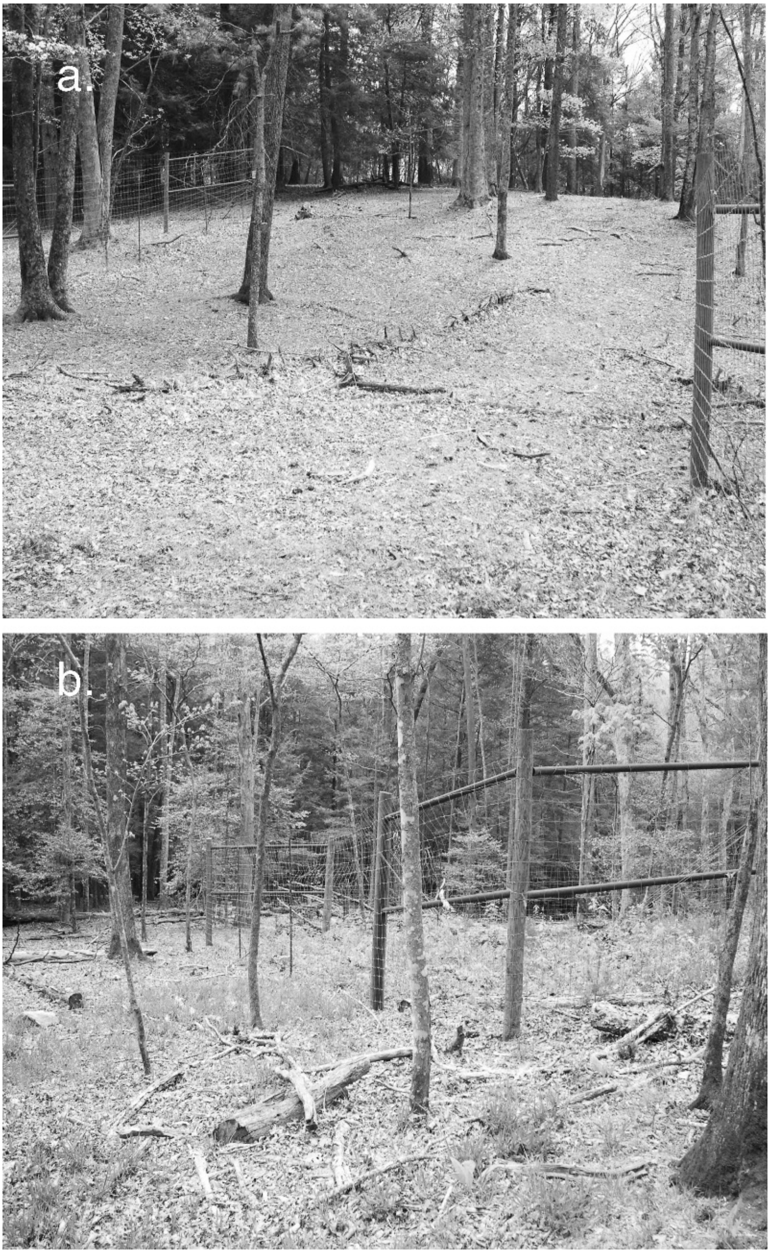

FIG. 1.—Mixed conifer-hardwood woodlots in Cades Cove, Great Smoky Mountains National Park, USA. Note complete absence of woody regeneration outside of deer exclosures [*see* Webster, Jenkins & Rock (2005a), Griggs *et al.* (2006) and Webster *et al.* (2008) for recent exclosure study results for Cades Cove]. Photos taken on 16 April 2003 at Hyatt Lane site (a) and 20 April 2004 at the John Oliver site (b) by C.R. Webster

1180 m) than the Cades Cove plots (520–680 m). Soils underlying both Cades Cove and reference plots were largely derived from metasedimentary rock such as metasandstone and phylite (Natural Resources Conservation Service, 2007). In Cades Cove, soils were formed from metasandstone derived from debris fans of varying thickness overlying carbonite bedrock (Southworth *et al.*, 2003). Soils on the reference plots were formed from metasedimentary bedrock (Southworth *et al.*, 2005).

Detailed vegetation data were collected from the 30 plots during the summers of 1977–1979 as part of a larger vegetation study by GSMNP (White and Busing, 1993). The nineteen permanent plots, randomly located in woodlots and forests in and around the Cove, encompassed three forest community associations as defined by NatureServe (White *et al.*, 2003):

(1) *Liriodendron tulipifera – Betula lenta – Tsuga canadensis / Rhododendron maximum* Forest (hereafter ''acid cove'') stands are generally located along upland streams at the edge of the Cove. Contemporary overstories of these stands are dominated by *T. canadensis* L. Carr. and *L. tulipifera* L. (Webster *et al.*, 2005b). *R. maximum* L. typically dominates the understory. We sampled four plots in this association.

(2) *Pinus strobus – Quercus alba (Carya alba) / Gaylussacia ursina* Forest (hereafter ''mixed conifer-hardwood'') is typically located along the edge of the Cove and on slopes and low ridges within the interior woodlots. Contemporary overstories of these stands are dominated by *Quercus* species, *P. strobus* L. and *T. canadensis* (Webster *et al.*, 2005b). We sampled seven plots in this association.

(3) *Pinus virginiana* Successional Forest (hereafter ''successional pine'') stands are generally located on gentle slopes between older forest and pasturelands. Contemporary overstories are dominated by *P. virginiana* Mill. (a short-lived pioneer species), *Oxydendrum arboreum* (L.) DC. and *P. strobus.* We sampled eight plots in this association.

Based on aerial photo interpretation, acid coves and mixed conifer-hardwood stands were forested prior to National Park Service acquisition, and successional pine stands were abandoned agricultural fields (Webster *et al.*, 2005b). Six of the reference plots were classified as acid cove forests and five were classified as mixed conifer hardwood forests. No reference plots were available within successional pine forests.

Because heavy cover of subcanopy, evergreen ericaceous shrubs (*e.g.*, *Rhododendron maximum*) and conifers (*i.e.*, *Tsuga canadensis*) can reduce herbaceous-layer cover and diversity (Baker and Van Lear, 1998), we tested for differences in the density of this group of species between mixed conifer-hardwood and acid cove plots in Cades Cove and reference areas. While reference plots contained greater density of these species than the Cades Cove plots (1642 ± 494 vs. 698 ± 298 stems ha^{-1}), the difference was not significant (one-way ANOVA, $F_{1,\ 22} = 3.08$, $P = 0.094$) due to high variability among plots.

FIELD TECHNIQUES

Within each of the thirty 20 × 50 m permanent plots, a grid of ten 10 × 10 m subplots was established and permanently marked with steel rod (White and Busing, 1993). Within every-other subplot ($n = 5$), a diagonal transect (14.14 m) was established at a random corner along which five 1 × 1 m herbaceous cover plots were established. A total of 25 herbaceous cover subplots (25 m^2 total) were sampled in each plot (White and Busing, 1993). During the 1977–1979 sampling period, all woody stems ≥ 1 cm dbh (1.37 m) were measured on the 20 × 50 m plot and percent cover was estimated for each herbaceous species on each of the 25 subplots.

Percent cover was estimated ocularly into 10 cover-abundance scale classes (Peet *et al.*, 1998; class midpoints were used for analysis). All herbaceous species occurring on the 20 × 50 m plot were identified and recorded for determination of species richness.

Overstory vegetation on the Cades Cove plots was reassessed between 1995 and 2002 (Webster *et al.*, 2005b). We reinventoried herbaceous vegetation on each subplot in 2004 using the same methods as the original inventory conducted in 1977–1979 (described above). Overstory and herbaceous vegetation on the reference plots were reinventoried between 1995 and 2001 using the same methods as the original 1977–1979 survey. To avoid seasonal variation in species coverage/representation, plots were reinventoried as close as possible to the initial sampling date. Mean absolute and relative percent cover (cover of species *i* / total coverage of all species) of individual species were calculated by plot. Species nomenclature follows Kartesz (1999).

DATA ANALYSIS

To evaluate compositional differences through time along environmental gradients in Cades Cove, we used non-metric multidimensional scaling (NMS; Kruskal, 1964; Mather, 1976) as implemented in PC-ORD version 4.24 (McCune and Mefford, 1999). Compositional dissimilarity was assessed using a square root transformed and 'zero-adjusted' Sørensen's (Bray-Curtis) coefficient. Zero-adjusted Sørensen's is appropriate for denuded assemblages where impoverishment is likely due to a common cause and not simply a consequence of sampling error that accompanies inadequate sample sizes (Clarke *et al.*, 2006). The zero-adjustment has the advantage that it has little effect on dissimilarities between non-denuded samples, but has a desirable homogenizing effect on dissimilarities between blank or near-blank samples that would otherwise be undefined or demonstrate erratic behavior. A square-root transformation reduces the influences of samples with high cover or abundance which otherwise dominate dissimilarity values (Field *et al.*, 1982). For the NMS, we used PC-ORD's autopilot mode, with default settings of 0.00001 for the stability criterion, 40 real runs and 50 randomized runs of 500 iterations each for each dimensionality (or 50 continuous iterations within the stability criterion), and a starting dimensionality of six (McCune and Grace, 2002). Autopilot uses a random starting configuration and selects appropriate dimensionality for the ordination by (1) minimizing stress (a measure of lack of fit; Kruskal, 1964; Mather, 1976) for each dimensionality, (2) considering additional dimensions only if they substantially reduced stress and (3) performing Monte Carlo tests, whereby the final stress for each dimensionality must be lower than that for 95% of randomized runs, thus assuring that additional dimensions capture new information. We assessed the role of underlying environmental gradients by joint-plotting environmental variables and species scores in sample unit space. Correlations of environmental variables to ordination axes were calculated with Pearson's r, and environmental vectors were scaled to the maximum absolute value obtained by the axes in the ordination plot.

Because the NMS vector plot suggested an increase in similarity among plots since 1977–1979, we used the program PERMDISP (Anderson, 2004; Anderson *et al.*, 2006) to test the null hypothesis of no differences in β diversity between sampling periods. PERMDISP tests for homogeneity in multivariate dispersions by doing permutational ANOVA on average distances to group centroids, as defined in the principle coordinate space of an appropriate dissimilarity measure. Significant decreases in average distances to group centroids between time periods would strongly suggest biotic homogenization. Alternatively, we could simply compare average dissimilarities between all pairs of samples, but this approach does not permit statistical evaluation due to partial dependencies of individual dissimilarity values (Anderson *et al.*, 2006).

For comparisons of species richness and total percent cover between time periods, we used a paired *t*-test. This test is appropriate for dependant observations, such as time series data (Zar, 1999). Means are reported plus or minus one standard error. Pearson correlation analysis was used to examine relationships between environmental and stand structure variables (Zar, 1999). To help identify species characteristics related to changes in community composition, we evaluated changes in the representation of various life history traits (USDA PLANTS Database, 2004). Growth forms were selected to characterize browse susceptibility and impact (low-growing: low susceptibility; bunch: high susceptibility, low impact; single-crown: high susceptibility, high impact; multiple crowns: high susceptibility, low impact). Shade tolerance was examined to help isolate the effects of forest succession and stand development from herbivory. Distance measures (distance from plot edge to road and forest/field edge) were determined with Arcview (version 3.2). A one-way ANOVA with a Tukey's pairwise comparison was used to compare the mean distance from edge among plots in the three forest types located around Cades Cove.

Since they were resampled 4–9 y prior to the reinventory of the Cove plots, span a greater range of elevations and were not a formal control, reference plot data were not compared statistically to the data from Cades Cove. As a point of reference, we summarized species loss and changes in percent cover on reference plots and compared the fates of woodland species lost from the Cades Cove plots over the sampling interval. Using the procedures outlined above we also evaluated differences in β diversity between sampling periods. Simple linear regression was used to test the influence of elevation on percent cover and species richness since the greater range of elevation across reference plots could influence these attributes.

RESULTS

SPECIES LOSS AND ABUNDANCE WITHIN THE CADES COVE SETTLEMENT AREA

Overall in Cades Cove, 46 herbaceous species recorded on plots during the 1970s were absent in 2004, and 10 species not recorded during the 1970s were recorded in 2004 (Table 1). Mean coverage of herbaceous species declined significantly (from 18.4 ± 7.9% to 6.8 ± 3.8%, $P < 0.001$). Declines within forest types ranged from 57.2% in mixed conifer-hardwoods to 85.1% in successional pine stands. Both successional pine and mixed conifer-hardwood forests contained exotic species during both sampling intervals. The mean coverage of these species also declined (from 7.6 ± 5.2% to 3.9 ± 3.5%). In fact, five exotic species were lost, whereas only one exotic was gained (Table 1). The exotics that were lost included both shade-tolerant and shade-intolerant species.

Absolute coverage of almost all individual species life forms declined between the sampling intervals (1977–1979 and 2004; Table 2). The only increase observed was in the coverage of annual plants, which is associated with an increase in the coverage of the exotic grass *Microstegium vimineum* (Trin.) A. Camus. The greatest declines were observed for species with single crowns and bunch growth forms. The decline in species with bunch growth forms (mostly graminoids) was associated with a general decline in species less tolerant of shade. Correspondingly, an increase in relative coverage of shade-tolerant species was observed; however, absolute coverage declined by 49% (Table 2). Low-growing species also increased in relative coverage while declining in absolute coverage (Table 2).

COMPOSITIONAL CHANGE ALONG ENVIRONMENTAL GRADIENTS WITHIN THE CADES COVE SETTLEMENT AREA

A three dimensional NMS solution (final stress = 12.81, normalized and scaled from 0–100; P-value for Monte Carlo test = 0.0196) provided the best ordination of the multidimensional species data. The three NMS axes combined accounted for 75% of the variance in species data (r^2 for axes 1, 2 and 3 were 0.22, 0.11, and 0.42, respectively). Of the environmental gradients examined (Table 3), distance to edge had the strongest overall correlation to the NMS ordination (Table 4). Stem density, Δ in basal area, and tree age had moderate correlations to ordination axes 1 and 2, suggesting that these axes, in part, describe successional gradients, whereas axis 3 describes edge effects. Distance variables were not correlated ($P > 0.05$) with overstory attributes (Table 5). Similarly, while acid cove plots were more distal from edges than either mixed conifer-hardwood or successional pine plots ($P = 0.011$ and 0.003, respectively), there was no significant difference in the proximity of plots in the latter two forest types to field edges ($P = 0.782$).

Life forms sensitive to deer browsing (*i.e.*, lilies and orchids) displayed a positive association with distance whereas more browse tolerant species (*i.e.*, ferns, graminoids and legumes) displayed a negative association with distance (Fig. 2). Exotic species were also associated with shorter distances from the Cove and its edges (Fig. 2). The percent cover of this group, however, declined by approximately 50% over the course of the study.

UNDERSTORY HOMOGENIZATION WITHIN THE CADES COVE SETTLEMENT AREA

Visual interpretation of the NMS vector plot of samples through time in species-space (Fig. 3) revealed that compositional change was greatest along axis-3 and that plots have become more homogeneous in composition. For all plots considered together and for the mixed conifer-hardwoods habitat type, PERMDISP results showed that average distances to group centroids significantly declined over time (Table 6). The composition of successional pine plots also became more similar between sampling intervals, but this result was not statistically significant ($P = 0.18$). Acid cove plots, on the other hand, showed no trend towards increasing similarity.

Plots close to forest/field edges showed the greatest reduction in heterogeneity based on differences in distance to group centroids between sampling periods (Fig. 4). Ninety one percent of the plots that were within 200 m of an edge declined in heterogeneity. At greater distances, the distribution of increases and decreases was more evenly divided, but sample sizes were too low to identify a threshold distance for edge-mediated homogenization.

PLANT COMMUNITY CHANGE ON REFERENCE PLOTS

In general, reference plots accumulated woodland species over the course of the sampling interval and mean species richness increased by 106 ± 28% (Table 7). Only one plot exhibited a net loss of species—the majority of which were early successional (*e.g.*, *Dichanthelium commutatum* (J.A. Schultes) Gould, *Lespedeza hirta* (L.) Hornem. and *Schizachyrium scoparium* (Michx.) Nash). Across both forest types, percent cover increased by 183 ± 76% (Table 7). While four plots exhibited declines in percent cover over the sampling interval, none experienced a net loss of species, and three of the four experienced an increased in species richness. For all reference plots considered together and for the acid cove habitat type, PERMDISP results showed that average distances to group centroids did not decline significantly over time (Table 6). Mixed conifer-hardwood plots did, however, increase in similarity, but in contrast to the Cades Cove plots this increase in similarity was associated with an increase in species richness (mean increase, 68 ± 36%). Species gained on reference plots were typically interior woodland species such as *Goodyera repens* (L.) R. Br. ex Ait. f., *Prosartes lanuginosa* (Michx.) D. Don, *Dioscorea quaternata* J.F. Gmel., *Polygonatum biflorum* (Walt.) Ell., *Lilium michauxii* Poir. and *Trillium undulatum* Willd. In other words, homogenization on mixed conifer-hardwood reference plots was driven by species gain rather than loss. While the reference plots spanned a greater range of elevations than the

TABLE 1.—Herbaceous species lost from Cades Cove sample plots between 1977/79 and 2004 as well as species that were first recorded in 2004 (gained). Non-native species are indicated by an asterisk

Scientific name	Common name	Lost	Gained	Shade-tolerance rank[‡]
Amorpha glabra Desf. ex Poir.	mountain false indigo	x		Intermediate
Andropogon virginicus L.	broom sedge	x		Intolerant
Arnoglossum atriplicifolium (L.) H.E. Robins.	pale Indian plantain	x		Intolerant
Asplenium platyneuron (L.) B.S.P.	ebony spleenwort	x		Tolerant
Bidens frondosa L.	devil's pitchfork	x		Intermediate
Brachyelytrum erectum (Schreb. ex Spreng.) Beauv.	bearded shorthusk		x	Tolerant
Calamagrostis coarctata (Torr.) Eat.	Nuttall's reed grass	x		Intolerant
Campanulastrum americanum (L.) Small	American bellflower		x	Tolerant
Cerastium fontanum Baumg.*	mouse-eared chickweed	x		Intolerant
Chaerophyllum tainturieri Hook.	hairyfruit chervil		x	Intolerant
Chamaecrista nictitans (L.) Moench	partridge pea	x		Intolerant
Chrysopsis mariana (L.) Ell.	Maryland golden aster	x		Intolerant
Chrysosplenium americanum Schwein. ex Hook.	American golden saxifrage	x		Tolerant
Danthonia compressa Austin ex Peck	flattened wild oat grass	x		Tolerant
Dichanthelium boscii (Poir.) Gould & C.A. Clark	Bosc's rosette grass	x		Intermediate
Dichanthelium dichotomum (L.) Gould	cypress witchgrass	x		Tolerant
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	hemlock rosette grass	x		Intermediate
Prosartes lanuginosa (Michx.) D. Don	yellow fairybells	x		Tolerant
Eleocharis obtusa (Willd.) J.A. Schultes	blunt spike rush	x		Intolerant
Euphorbia corollata L.	flowering spurge	x		Intermediate
Eurybia surculosa (Michx.) Nesom	creeping aster	x		Intolerant
Geum canadense Jacq.	white avens	x		Tolerant
Hieracium venosum L.	rattlesnake weed	x		Intermediate
Houstonia purpurea L.	Large bluet		x	Intermediate
Hypericum hypericoides (L.) Crantz	St. Andrew's cross	x		Intermediate
Juncus tenuis Willd.	poverty rush	x		Intermediate
Leersia virginica Willd.	cut grass	x		Tolerant
Lindernia dubia (L.) Pennell	yellow-seed false pimpernil	x		Intermediate
Lobelia puberula Michx.	downy lobelia	x		Intermediate
Melilotus officinalis (L.) Lam. *	yellow sweet clover	x		Intolerant
Mentha × *piperita* L. (pro sp.) [*aquatica* × *spicata*]*	peppermint	x		Intolerant
Muhlenbergia schreberi J.F. Gmel.	nimblewill	x		Tolerant
Oxalis montana Raf.	mountain woodsorrel		x	Tolerant
Oxalis stricta L.	yellow wood sorrel	x		Tolerant
Panicum anceps Michx.	beaked panicgrass	x		Intermediate
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper		x	Tolerant
Paspalum laeve Michx.	field crown grass	x		Intolerant
Phytolacca americana L.	American pokeweed		x	Tolerant
Platanthera clavellata (Michx.) Luer	small green wood orchid	x		Tolerant
Polygonatum pubescens (Willd.) Pursh	hairy Solomon's seal		x	Tolerant
Polygonum caespitosum Blume*	Oriental lady's thumb		x	Tolerant
Prunella vulgaris L.*	selfheal	x		Intermediate

TABLE 1.—Continued

Scientific name	Common name	Lost	Gained	Shade-tolerance rank‡
Pycnanthemum muticum (Michx.) Pers.	mountain mint	x		Tolerant
Rumex acetosella L.*	common sheep sorrel	x		Intolerant
Sanguinaria canadensis L.	bloodroot		x	Tolerant
Sanicula marilandica L.	Maryland black snakeroot	x		Tolerant
Sanicula smallii Bickn.	small's black snakeroot	x		Tolerant
Schizachyrium scoparium (Michx.) Nash	little bluestem	x		Intolerant
Sericocarpus asteroides (L.) B.S.P.	toothed white-topped aster	x		Tolerant
Solanum carolinense L.	Carolina horse nettle	x		Intolerant
Solidago curtisii Torr. & Gray	Curtis' goldenrod	x		Tolerant
Solidago puberula Nutt.	downy goldenrod	x		Intolerant
Solidago rugosa P. Mill.	wrinkle-leaf goldenrod	x		Intermediate
Sorghastrum nutans (L.) Nash	Indian grass	x		Intolerant
Stylosanthes biflora (L.) B.S.P.	side-beak pencil flower	x		Tolerant
Symphyotrichum lateriflorum (L.) A.& D. Löve	calico aster	x		Intermediate

‡ Shade-tolerance rank as reported in the USDA PLANTS Database (2004). If this trait was not listed in the database, then rank was based on the habitat description in an applicable field guide (*e.g.*, Carman 2001) as follows: Tolerant = woodland or forest; Intermediate = open woods; Intolerant = old field, waste places, or prairie

Cove plots, no significant trends between richness or cover and elevation were observed within this elevation range (P = 0.561 and P = 0.390, respectively).

DISCUSSION

Our results suggest that over the last 26 y the understory plant communities across three distinct forest types within Cades Cove have become increasingly impoverished. In 2004, the

TABLE 2.—Absolute and relative percent cover of understory species on sample plots in Cades Cove grouped by life history traits (mean ± 1 SE)

	Absolute cover (%)		Relative cover (% of total)	
	1977/79	2004	1977/79	2004
Growth form				
Low-growing‡	2.6 ± 1.2	2.1 ± 1.0	50.2 ± 7.8	74.7 ± 7.0
Bunch¶	11.6 ± 6.2	4.2 ± 3.5	23.7 ± 7.0	17.6 ± 6.8
Single crown§	2.5 ± 1.3	0.5 ± 0.3	19.5 ± 4.6	6.8 ± 2.1
Multiple crowns£	0.2 ± 0.1	0.1 ± 0.04	6.6 ± 3.5	0.9 ± 0.4
Shade tolerance				
Intolerant	3.6 ± 2.1	0.2 ± 0.1	14.3 ± 4.4	5.06 ± 2.2
Intermediate	1.5 ± 0.9	0.5 ± 0.2	20.2 ± 3.8	15.2 ± 4.0
Tolerant	11.8 ± 6.6	6.0 ± 3.6	65.5 ± 5.9	79.8 ± 4.6

‡ Low-growing includes: ''prostrate,'' ''creeping,'' and plants that have low basal leaves at maturity (*e.g. Viola* spp.)

¶ Bunch species were mostly graminoids

§ Single crown includes plants with a single apical meristem/crown

£ Multiple crowns refer to plants with more than one apical meristem, shrub-like

TABLE 3.—Attributes of Cades Cove (n = 19) and reference plots (n = 11)

Variable	Mean (± 1 SE)	Median	Min	Max
Cades Cove				
Mean overstory tree age (yr)	83.5 ± 5.6	71.0	53.0	135.0
Distance from field edge (m)	279.1 ± 66.1	144.0	33.0	894.0
Distance from road (m)	312.4 ± 67.6	208.0	42.0	995.0
Basal area 1977/79 (m^2 ha^{-1})	32.5 ± 2.4	34.62	6.21	55.4
Basal area 2000* (m^2 ha^{-1})	37.7 ± 2.3	37.8	10.2	53.0
Stem density 1977/79 (trees ha^{-1})	617.9 ± 43.5	590.0	300.0	1040.0
Stem density 2000 (trees ha^{-1})	617.4 ± 48.7	600.0	340.0	1030.0
Reference				
Distance from field edge (m)†	6113 ± 1195	4400	1090	13,302
Basal area 1977/79 (m^2 ha^{-1})	35.2 ± 2.2	34.2	24.3	50.2
Basal area 2000 (m^2 ha^{-1})	35.3 ± 2.2	35.4	22.8	46.2
Stem density 1977/79 (trees ha^{-1})	707 ± 119	670	170	1670
Stem density 2000 (trees ha^{-1})	696 ± 102	720	120	1440

Note: Overstory attributes are for trees ≥10 cm diameter at breast height (1.37 m)

* Overstory data were collected between 1995 and 2002

† All plots were >3000 m from the edge of a field in Cades Cove; shorter distances were associated with other clearings distal from the Cove

herbaceous layer on the sample plots contained an average of nine species, which had a total cover of less than 7%. However, during the 1970s inventory these same plots contained an average of 11 species and had a total percent cover of over 18%. These results are in contrast to those observed on reference plots; where species richness increased, understory plant communities on different forest types did not become more similar and within forest type homogenization was predominately associated with species gain rather than loss. At the time of the 1970s survey, Cades Cove contained one of the highest documented deer densities in the southeast at 43 deer km^{-2} (Kiningham, 1980; Wathen and New, 1989).

TABLE 4.—Pearson correlations between NMS ordination axes and environmental and stand structure variables for sample plots in Cades Cove

	NMS axis: 1		2		3	
Variable	r	r^2	r	r^2	r	r^2
Tree age	0.325	0.106	0.045	0.002	−0.169	0.029
Basal area 1977/79	0.074	0.005	0.073	0.005	−0.153	0.023
Density 1977/79	−0.097	0.009	0.349	0.122	−0.344	0.118
Basal area 2000*	−0.308	0.095	−0.303	0.092	−0.046	0.002
Density 2000	−0.402	0.162	−0.027	0.001	−0.245	0.060
Change in basal area	−0.375	0.141	−0.370	0.137	0.107	0.011
Change in density	−0.278	0.078	−0.299	0.090	0.055	0.003
Distance to edge	0.386	0.149	−0.132	0.017	−0.420	0.177
Distance to road	0.199	0.040	−0.143	0.021	−0.400	0.160

* Overstory data were collected between 1995 and 2002

TABLE 5.—Pearson correlation matrix of environmental and stand structure variables (correlation coefficient followed by P-value) for Cades Cove sample plots

	Distance from			Basal area			Stem density	
	Mean overstory tree age (yr)	Field edge	Road	1977/79	2000*	Δ	1977/79	2000
Distance from field edge (m)	0.287							
	0.233							
Distance from road (m)	0.210	0.942						
	0.388	0.000						
Basal area 1977/78 (m^{2} ha^{-1})	−0.079	−0.037	−0.094					
	0.749	0.881	0.701					
Basal area 2000 (m^{2} ha^{-1})	0.045	0.212	0.255	0.487				
	0.854	0.384	0.291	0.034				
Δ Basal area (m^{2} ha^{-1})	0.123	0.244	0.344	−0.518	0.494			
	0.617	0.313	0.149	0.023	0.031			
Stem density 1977/78 (trees ha^{-1})	−0.378	−0.028	0.033	0.478	0.052	−0.425		
	0.111	0.911	0.892	0.038	0.833	0.070		
Stem density 2000 (trees ha^{-1})	−0.348	0.232	0.425	−0.212	0.280	0.485	0.289	
	0.145	0.340	0.070	0.383	0.246	0.035	0.230	
Δ Stem density (trees ha^{-1})	−0.009	0.226	0.349	−0.565	0.206	0.764	−0.534	0.655
	0.972	0.352	0.144	0.012	0.397	0.000	0.019	0.002

* Overstory data were collected between 1995 and 2002

Since that time, deer densities have declined, but remain much higher than those found elsewhere in GSMNP (Griggs *et al.*, 2006). Vegetation surveys conducted in the Cove during the 1970s documented significant reductions in herbaceous coverage and species richness due to intense deer herbivory (Bratton, 1979). Our results suggest that the chronic, but presumably less intense, herbivory associated with the contemporary deer herd has been sufficient to inhibit plant community recovery and further homogenize the woodland flora of the Cove.

Over the course of the last 26 y, 46 species disappeared from our sample plots while only 10 new species were gained. During this interval, the stands examined were either in the understory reinitiation phase of stand development or beginning their transition out of the stem exclusion stage into the understory reinitiation phase (Webster *et al.*, 2005b). The understory reinitiation phase is typically associated with an increase in the coverage and diversity of understory plant species as growing space is released through the death of canopy trees and changes in crown morphology (Peet and Christensen, 1988; Oliver and Larson, 1996). Therefore, we expected an increase in the diversity and cover of late-seral woodland herbs. However, the cover of this guild declined by nearly 50% (shade-tolerant herbs, Table 2), and several common woodland species (16 shade-tolerant and 13 intermediate tolerant species) were lost from the plots over the 26-year interval [*e.g.*, *Stylosanthes biflora* (L.) BSP, *Platanthera clavellata* (Michaux) Luer and *Prosartes lanuginosa* (Michx.) D. Don]. We did not observe a similar loss of common woodland herbs in the mixed-conifer hardwood and acid cove reference plots, where mean plot species richness and percent cover have increased by nearly one- and two-fold, respectively since the 1970s. For example, *Prosartes lanuginose*, which was lost from the Cove plots, doubled in frequency

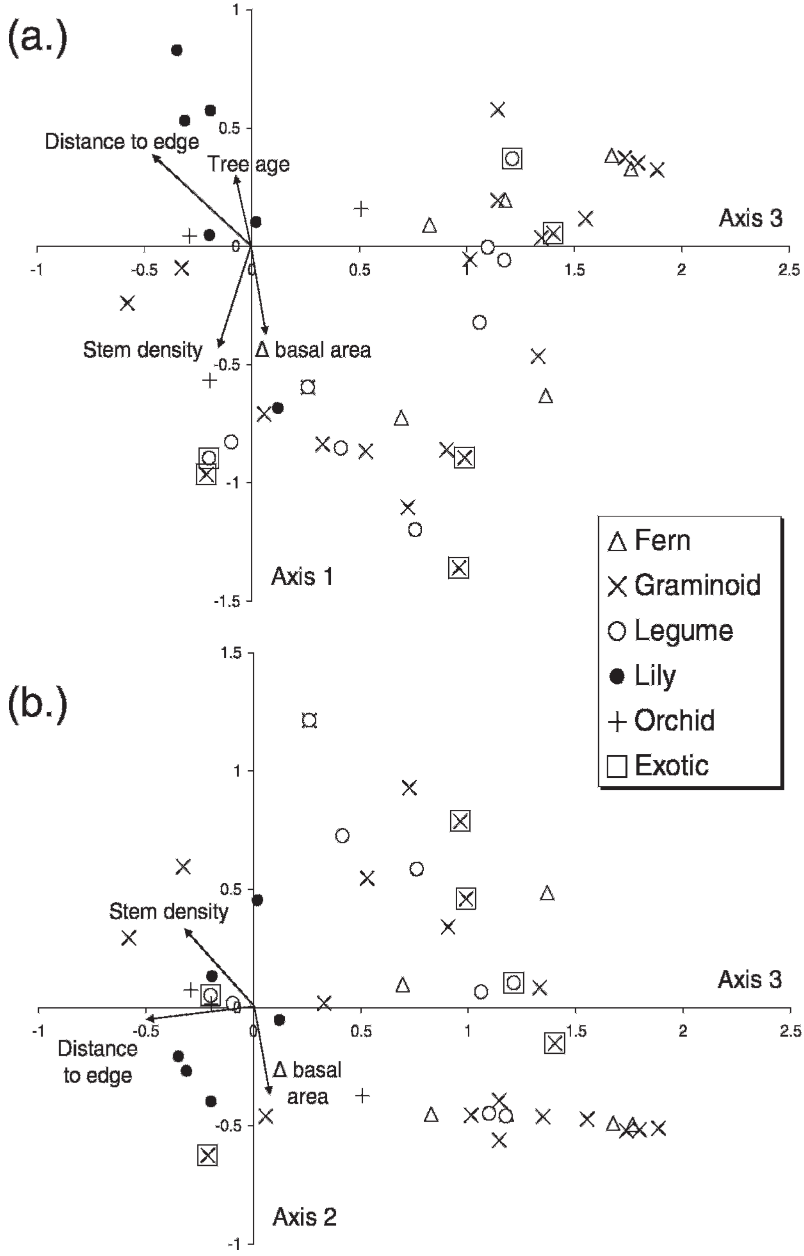

FIG. 2.—Nonmetric multidimensional scaling (NMS) joint plots of selected taxa and functional groups on Cades Cove plots in sample unit space versus environmental gradients. Species points represent typical positions for each species in sample space, while ignoring the breadth of their distributions. Units for environmental variables are given in Table 3; in (a) stem density is for the 2004 sampling period; in (b) stem density is for the 1977–1979 sampling period

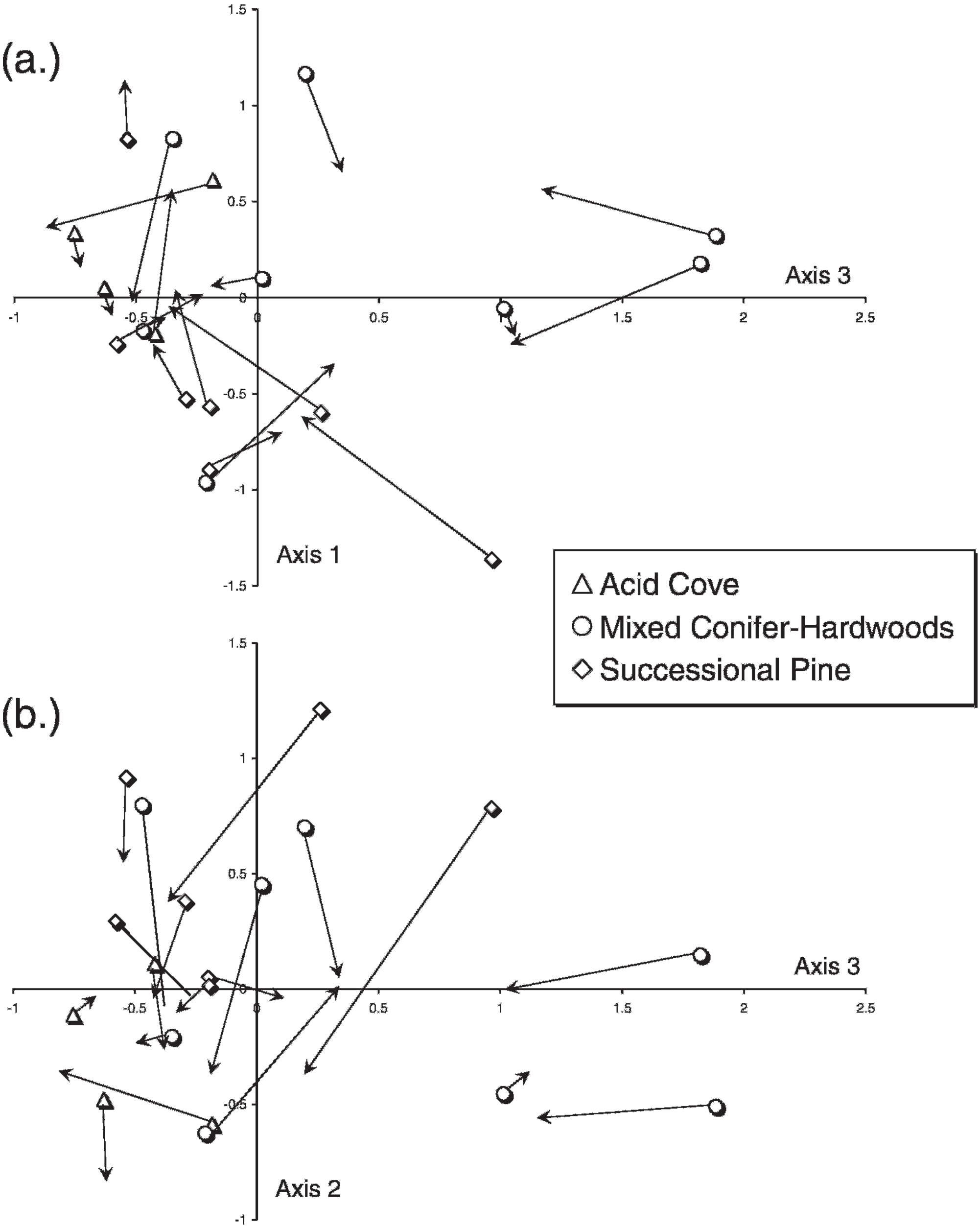

FIG. 3.—Nonmetric multidimensional scaling (NMS) vector plots for Cades Cove plots, with sample scores for axis 1 (a) and axis 2 (b) plotted against axis 3. Vectors, originating from the 1977–1979 sample plot locations, indicate direction and magnitude of sample plot movement in NMS space between sampling periods

TABLE 6.—Average distance to centroid (± 1 SE), based on square-root transformed Bray-Curtis dissimilarity values, for each habitat type and sampling interval (1977–1979 and 2004)

	Distance to centroid				
	1970s	2004*	n	F†	P
Cades Cove					
All Plots	59.06 ± 1.76	50.74 ± 2.79	19	6.352	0.02
Acid Cove	38.43 ± 3.14	39.73 ± 5.43	4	0.043	0.87
Successional Pine	53.14 ± 3.55	43.63 ± 5.57	7	2.075	0.18
Mixed Conifer-Hardwoods	58.81 ± 1.44	50.80 ± 2.04	8	10.248	0.01
Reference					
All Plots	50.42 ± 1.79	47.87 ± 2.74	11	0.605	0.44
Acid Cove	48.32 ± 1.52	50.46 ± 1.62	6	0.926	0.35
Mixed Conifer-Hardwoods	43.36 ± 3.28	34.56 ± 2.76	5	4.227	0.07

* Reference plots were resampled between 1995 and 2001

† F statistic for permutational ANOVA on PCoA scores

on reference plots between the 1970s and 1995–2002 inventories. Similarly, *Medeola virginiana* L. which was recorded on three Cove plots during the 1970s, but was found only on one plot during the reinventory, increased in frequency from 36% to 45% on reference plots over approximately the same interval.

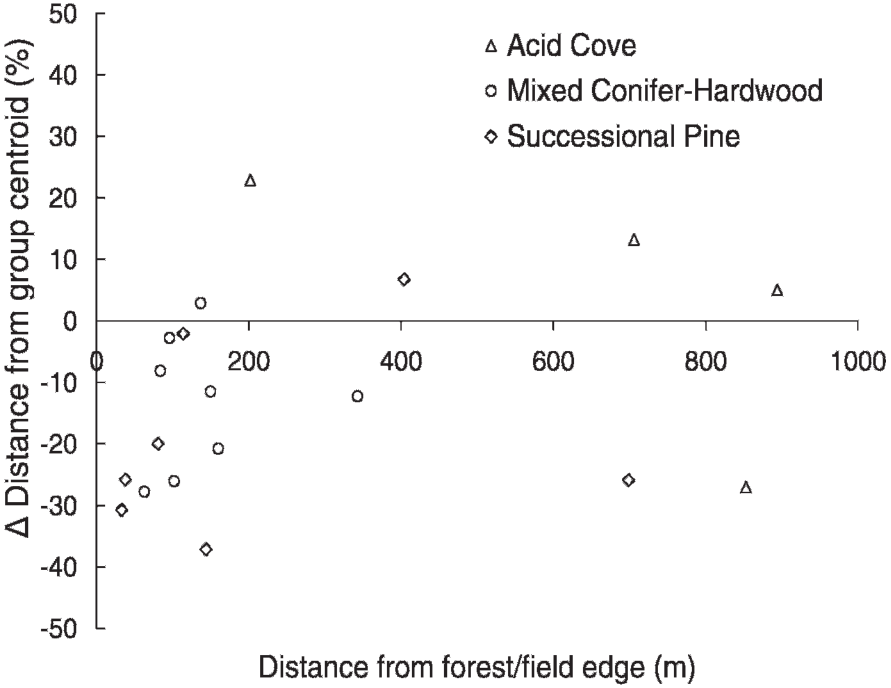

FIG. 4.—Change in distance from group centroid between sampling periods (1977–1979 vs. 2004) for Cades Cove plots as a function of plot distance from the closest forest/field edge. Negative values indicate a reduction in heterogeneity, which is interpreted as homogenization

TABLE 7.—Herbaceous-layer attributes of reference plots (n = 11)

Variable	Mean (± 1 SE)	Median	Min	Max
% Cover (1977/79)	7.0 ± 2.5	4.3	0.08	23.8
% Cover (1995/2000)	11.5 ± 6.1	5.2	0.43	68.2
Δ % Cover (%)	183 ± 76	41	−45‡	688
Richness (1977/79)	14.7 ± 3.3	13	1	36
Richness (1995/2000)	24.6 ± 5.1	24	4	52
Δ Richness (%)	106 ± 28	85	−27¶	300

‡ Four plots declined in percent cover (mean decline = 32%); however, none of those plots exhibited a net loss of species, three of which experienced net a gain in species richness

¶ Only one plot displayed a net loss of species, the majority of which were early successional

Forest herbs that disappeared from the Cades Cove plots typically were from families that contain preferred browse species and/or are disproportionately impacted by browsing (*e.g.*, Liliaceae and Orchidaceae; Anderson, 1994; Augustine and Frelich, 1998; Fletcher *et al.*, 2001; Webster *et al.*, 2005a; Wiegmann and Waller, 2006). Several late blooming woodland aster species, as well as some shade-tolerant grasses, which typically are not browse sensitive (Wiegmann and Waller, 2006), also disappeared. While some later-seral species were gained, they tended to be on plots distal from the Cove and were usually only represented by a few specimens (*e.g.*, *Sanguinaria canadensis* L. was found on only one plot, which was 343 m from the field/forest edge, where it had < 1% cover). Early-successional and old-field species that had persisted from earlier successional stages declined as expected.

A surprising result of our investigation was the decline in the number and cover of invasive exotic plants, such as *Lonicera japonica* Thunb. Over the sampling interval, the coverage of exotic plants declined by 50% and five species recorded during the 1970s were absent in 2004. Numerous studies have implicated invasive exotic plants in the simplification of native plant communities (Gordon, 1998; Levine *et al.*, 2003; Qian and Ricklefs, 2006). The only exotic species to increase in coverage was the invasive grass *Microstegium vimineum*, which does not appear to be consumed by deer (Griggs *et al.*, 2006). This species has been linked to changes in soil microbial communities and competitive exclusion of native species (Kourtev *et al.*, 2002; Cole and Weltzin, 2004). While highly abundant in some Cove woodlots (Griggs *et al.*, 2006; Webster *et al.*, 2008), *Microstegium vimineum* was a minor species on our sample plots, and the aggregate cover of exotic species during the 2004 inventory was ~4%. Consequently, exotic species do not appear to be driving species loss and homogenization on the sample plots examined in this study.

Our results are consistent with Rooney *et al.* (2004) who observed compositional erosion and floristic impoverishment of the herbaceous layer in areas of high deer abundance, that were otherwise protected from habitat degradation and loss. Herbaceous layer recovery from agricultural abandonment in the Cades Cove stands we examined has been largely arrested since stands have lost rather than gained late-seral species as they enter the understory reinitiation phase of stand development. Over the course of 26 y, the herbaceous layer in Cades Cove has become increasingly homogeneous, with three distinct forest types decreasing significantly in compositional dissimilarity. Conversely, reference plots across two distinct forest types have not decreased significantly in compositional dissimilarity. In both the Cades Cove and reference mixed conifer-hardwood plots, we observed significant declines in dissimilarity; however, the decline in Cades Cove was associated with species loss whereas the decline on reference plots was associated with species gain. Consequently, measures of homogenization should be viewed in light of other changes in the plant community, and some level of homogenization, especially if associated with the accrual of native late-seral species, may indicate recovery from past disturbance.

Across the three forest types examined, plant community composition was strongly associated with proximity to the Cove's edge environments. This relationship appears to represent a biotic edge effect, attributable, at least in part, to the foraging behavior of the Cove's resident deer population. Our evidence for this conclusion is as follows. First, all of these sample plots were within the bounds of the Cades Cove settlement area and were equally subjected to relatively intense anthropogenic disturbance prior to acquisition (Pyle, 1988). Second, none of the distance measures were significantly correlated with stand structure (Table 5), which has been shaped by past landuse (Webster *et al.*, 2005b). Third, all sample plots were at least 30 m from the forest edge (Table 3), reducing the influence of abiotic edge effects. Consequently, within the range of distances examined, distance was not a proxy for anthropogenic disturbance intensity. Finally, similar patterns of species loss and cover decline were not observed on reference plots >3000 m from the edge of a Cove field. The magnitude of this effect and our ability to establish a threshold distance for it, however, were likely compromised by the fact that the Cove contained a substantial deer herd during the 1970s when the plots were established. Research conducted around that time documented that intense deer herbivory by the resident herd had already led to drastic reductions in the cover of many species (Bratton, 1979).

While the spatial dependence in plant community change may be attributable, at least in part, to a deer behavioral response to forest edges, given the spatial extent of the Cades Cove study area it is unlikely that plant community change was influenced by variation in deer density. The mean summer home-range of adult female white-tailed deer in the southern Appalachians ranges from 378 to 1100 m in diameter (McShea and Schwede, 1993; Campbell *et al.*, 2004). Consequently, all of the distances examined in the Cades Cove plots (maximum distance from field edge, 894 m) could be nested within a single home-range. Reference plots, on the other hand, were well beyond the influence of the Cove's resident deer herd [>3 km; *see* also Bratton (1979)]. Deer are known to shift their activity patterns within their home-range in response to seasonally available pulses of forage (*e.g.*, acorns and agricultural crops; Nixon *et al.*, 1970; Murphy *et al.*, 1985; Nixon *et al.*, 1991; McShea and Schwede, 1993), hiding cover (Murphy *et al.*, 1985) or changes in hunting pressure or predation risk (Martin and Baltzinger, 2002). In agricultural mosaics, habitat use generally shifts from woodlands in the fall and winter to fields and open habitats in the spring (Murphy *et al.*, 1985). Consequently, forest herb populations near field edges would be expected to be more heavily utilized than those distal from edges.

Biotic edge effects associated with herbivore foraging behavior may result in either subtle or dramatic changes in vegetation. For example, meadow vole (*Microtus pennsylvanicus*) foraging along forest/field edges inhibits recruitment of some tree species within 30–40 m of an edge (Cadenasso and Pickett, 2000). Conversely, deer browsing may be more spatially variable along forest edges (Cadenasso and Pickett, 2000; Campbell *et al.*, 2006) since deer favor edge environments (Montgomery, 1963), but use them in a rather coarse grained manner (VerCauteren and Hygnstrom, 1998). Edge effects associated with deer foraging have been proposed for forested regions in the Northern Lake States, with the implication that large contiguous blocks of forest are less susceptible to deer mediated tree regeneration failures (Alverson *et al.*, 1988). However, as Augustine and deCalesta (2003) point out, large forested reserves in regions that lack large predators and harsh winters may be especially susceptible to severe deer browsing since natural mortality may be low in the absence of hunting. Consequently, the influence of forest fragmentation on deer abundance and impact may vary both locally and regionally (Milne *et al.*, 1989; Campbell *et al.*, 2006) with contrasting effects on local protected areas.

Long-term assessment of plant community composition provides valuable insights into the ecological consequences of chronic herbivory in forested ecosystems. As Morellet *et al.* (2007) point out, ungulate management across wide spatial scales requires a synthetic assessment of the ecological status of the ungulate-habitat system. Therefore, the contemporary health of a free-ranging ungulate population cannot be assessed in isolation of its habitat.

Acknowledgments.—We thank the National Park Service and the research staff at Great Smoky Mountains National Park, especially Keith Langdon, Kristine Johnson and Bill Stiver. Susan Bratton was integral in developing baseline studies in the 1970s. Hanni Muerdter, Jon Harrod, Mark Whited, Paul Allyn, Travis Martin, Art vonLehe, Meryl Rose, Heather MacCulloch and Catherine Harney assisted with field work and data entry, and Michael Kunze reformatted the 1977–1979 dataset. Mark Ford, Robert Scheller, Becky Nichols, Keith Langdon, Nancy Finley and two anonymous reviewers provided helpful comments on earlier drafts of the manuscript. Support for this project was provided by the School of Forest Resources and Environmental Science at Michigan Technological University. Internships for seasonal volunteers were provided through the Student Conservation Association.

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SUBMITTED 4 JANUARY 2008 ACCEPTED 30 SEPTEMBER 2008