

Coweeta Regionalization Progress Report on NSF Grant DEB 96-32854, Entitled:

"Long-term studies of disturbances as they affect ecological processes in landscapes of the southern Appalachians."

EXECUTIVE SUMMARY

This report presents progress made from 1996 to the present in our integrated Regionalization studies, combining ecological and socio-economic studies in a ten-county southern Appalachian region. In addition, we present detailed plans for continuing and new research to be conducted over the remaining four years of the grant.

Our research is concerned with four linked components- 1) prehistoric, historic and contemporary patterns of disturbance and land use; 2) socioeconomic drivers of land use change; 3 and 4) effects of land use change on aquatic and terrestrial ecosystems. This research is focused on three main questions, summarized as: how does land use change interact with natural environmental gradients, and human decisions and actions, relating to aquatic and terrestrial ecosystem processes, and are there predictable relationships of the foregoing, carried out over several decades into the future?

We focus, in turn, on a delineation of current and future socioeconomic research, showing how human history and preferences inform and shape land and resource use in the southern Appalachians. Specific aspects of land use change on aquatic and terrestrial ecosystems are considered next, and how patterns of use in either one influences events in the other. This includes shifts between agricultural, forest, recreational and second-home development in the Little Tennessee and French Broad River basins. We then examine aspects of land use change as they affect regional C pools and fluxes, relating them to current and projected land use patterns and population growth out to the year 2030 and beyond. Throughout the document, we indicate where presentations and publications have been produced or are in press or submitted on this work.

With this document, including the Appendix material, we feel we have laid a solid foundation for performing relevant and important science within the mission of the LTER program.

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I. INTRODUCTION

The southern Appalachian region is characterized by steep environmental gradients in temperature, precipitation, and a suite of related biotic and abiotic factors that influence the structure and function of terrestrial and aquatic ecosystems. Superimposed on these naturally occurring gradients are complex patterns of historic (centuries to millennia) and contemporary (decades to centuries) disturbances. While natural disturbances (e.g., windthrow, flooding, landslides) occur in the region, humans have long been the primary cause of change in the southern Appalachians, beginning with fire and low intensity agriculture (pre-contact Cherokee), increasing with widespread logging and land clearing at the turn of the century, and becoming pervasive with large increases in population and attendant development over the past 20 years. These anthropogenic disturbances have greatly impacted ecosystems at local to regional scales during both historic and contemporary periods. Anthropogenic disturbances may be more important than natural gradients in structuring biological communities and determining biogeochemical cycles in the southern Appalachian region. In particular, forest tree, forb, and animal species composition and abundance may be more a factor of the land use history than non-anthropogenic environmental factors. Anthropogenic disturbances may also interact with natural environmental gradients. For example, long-term agriculture may be more frequent in mesic, fertile, streamside bottomlands, and intense fire may occur more often and be suppressed less frequently on dry ridges. This mix of historic and contemporary anthropogenic

disturbances, and their interaction with environmental gradients, has created a mosaic of land use patterns across the region. Our primary objectives are to understand the interactions among human decisions, land use patterns, environmental gradients, and terrestrial and aquatic ecosystem structure and function. Much of this work builds on our 60+ years of research on ecological processes in terrestrial and aquatic ecosystems in the Coweeta Basin. but the new work involves substantially larger spatial and temporal scales than previous studies. Moreover, it explicitly examines the social and economic determinants of human land use decisions, and the physical and biotic consequences of resultant land use patterns.

This document contains a description of research activities, progress, and findings stemming, from the regionalization project awarded to the Coweeta LTER site. We have two primary goals with this document: (1) to describe research progress during the first two years of this grant, including how research was modified in response to the review panel comments, and (2) to describe plans for the continuing and new research for the remaining four years of the grant. The main body of this document contains the descriptions of the first two years' progress and future work. Our most significant single response to reviewers was to add research on the socioeconomic and anthropological causes of anthropogenic disturbance, integrating Dr. Ted Gragson as a co-PI, and initiating a number of specific research projects, described below. In addition, we have added Dr. Ron Pulliam, to replace the deceased Joshua Laerm, to understand and model how climate and land use changes interact to determine current and future distributions of terrestrial plant and animal species. For the sake of clarity and narrative flow, specific responses to reviewer suggestions are included in [Appendix A](#).

Our research focuses on four fundamentally linked components ([Figure 1](#)): (1) prehistoric, historic and contemporary patterns of human activity and land use; (2) contemporary socioeconomic drivers of land use change; (3) effects of land use change on aquatic ecosystems; and (4) effects of land use change on terrestrial ecosystems, and has three main questions:

- 1. How does land use change interact with natural environmental gradients to control aquatic and terrestrial biological diversity and ecosystem processes in the southern Appalachians?*
- 2. How are human decisions regarding land use influenced by social, economic, and ecological factors within the region?*
- 3. Can we use our understanding of the linkages among socioeconomic factors, land use change, and ecosystem structure and function to predict future land use patterns and their ecological consequences?*

While we report two years of progress from studies focused on the ecological, historical and social conditions found in the southern Appalachians, we believe our results will have much broader implications.

For example, the relationships among land use changes, exotic species introduction, and biological diversity are major unknowns in ecology--we have established studies in both terrestrial (section V) and aquatic ecosystems (section IV) to identify these relationships. Work over the last 20 years has brought into question the assumption that most ecological processes are in dynamic equilibrium. Our studies have or will provide general conclusions regarding how disturbance frequency (section 11), life history, demography, and dispersal (section V) interact to determine how quickly ecosystems reach equilibrium. Global carbon pools and flux rates are a major uncertainty of widespread importance. Our paleo-, historic, and current records (section II) and rate measurements (section V) will significantly reduce this uncertainty in the region; in addition, we are developing and testing methods, models, and estimates which should be globally applicable.

II. PREHISTORIC, HISTORIC, AND CONTEMPORARY PATTERNS OF DISTURBANCE AND LAND USE

II.A. Work Accomplished and in Progress

Linking ecosystem function with land use change requires an accurate, quantitative record of the patterns of land use and land cover. Uncertainty regarding the legacies of past land use has limited our ability to explain the structure and function of present-day ecosystems. During the past two years, we developed a 50-yr record (hereafter, the "historic" record) of land cover change for our 70,000 km² study area, based on aerial photographs (1950s) and satellite data (1970s and 1990s) ([Figure 2](#)). This is a key integrating data set in many aspects of the regionalization research. These data have permitted coordinated study site selection for the terrestrial and aquatic field studies and thus are a critical link in the integration of our research program.

Initial analyses of the time series of land cover change revealed some surprises about the location, extent and shape of recent human activities on the landscape. Although logging peaked ca. 1915 and agricultural activities peaked in the 1930s, nearly 50% of the land area of some counties was still cleared in the 1950s. Forest cover and urban/suburban land covers have been replacing agriculture during the subsequent four decades, although the rate and extent of this change varies across the region (Bolstad et al., in preparation). When the pattern of all forest cover is examined, including those substantially forested areas with embedded housing, forest fragmentation has clearly decreased in the region. However, when only undisturbed forests are considered, forest fragmentation has increased in many areas. Urban/suburban development has more than kept pace with agricultural abandonment, leading to a net loss of continuous undisturbed forest (Wear and Bolstad 1998).

In addition to analysis of the historic record, we have extended our observations farther back in time based on sediment sampling. We have inferred cultural and climate effects on fire and vegetation over the last few millennia using sediment charcoal, ²¹⁰Pb, and pollen data from 10 sites in the southern Appalachians ([Figure 3](#)). Results show that fire and vegetation

are extremely variable across the range of elevation, topographic, and vegetation settings represented in our data set. Pollen and ^{210}Pb analyses are still in progress. When completed, these data will further refine prehistoric characterization of the southern Appalachian landscape. We are concurrently integrating our southern Appalachian results within a continental data set of past fire importance (Clark et al. 1996).

III. SOCIOECONOMIC RESEARCH

III.A. Work Accomplished

III.A.1. Land and Resource Use in the Southern Appalachians. Our time-series data clearly demonstrate that patterns of land cover have changed in the southern Appalachians during the past 40 yr, but explaining these changes requires new integrative approaches that include understanding derived from both the natural and social sciences (Turner et al. 1995, Turner et al. 1998). Physical attributes (e.g., vegetation, elevation, slope) and social variables (e.g., markets, cultural attitudes) all contribute to human land-use decisions and thus to landscape patterns, yet understanding how these many variables interact remains incomplete. We have developed new models that (1) address changes in land use rather than only land cover, as has been done previously (e.g., Turner et al. 1996, Wear et al. 1996); (2) incorporating market effects for agricultural and forest products on land-use decisions; and (3) examine a longer time frame (our 40 year "historic" period) than has previously been analyzed.

We used a number of modeling strategies to understand how the physical and biotic environment affect land use choices, and how these choices in turn affect ecosystems and biotic communities. Discrete land use choice models were developed for the Little Tennessee River Basin, which show that market factors have significantly influenced land use choices. Models also indicate that the relationships between market factors, site physical variables, and land use choices have shifted substantially since the 1950s (Chowdhury 1996; Wear et al. 1998). Expanding on these studies, more sophisticated economic-based land use models have been constructed for a number of counties (Wear and Bolstad 1998). These models extend definitions of land use by including a measure of human occupancy using building densities and by applying measures of forecast performance based on information theory. Results show that topography and road networks direct population diffusion and intensive land use toward riparian areas. This model also has been used to predict future land use 40 years hence ([Figure 4](#)). Current conditions are incorporated to develop site-specific probability maps for each possible land use. These predictions provide a spatially explicit estimate of future human disturbance, at an identifiable level of statistical confidence. Predictions may help (1) identify regions or areas most likely to receive greatest future impacts, (2) to model related impacts of future land use change (e.g., to model future regional carbon flux), or (3) to design sampling schemes for fieldwork to test related hypotheses regarding ecosystem and community function (section IV.B.1).

III.A.2. Social and Institutional Context. In January 1997 we began research into the root social processes which drive patterns of land and resource use.

We have looked at what defines southern Appalachia as a distinct separate region, with, ". . . a historically evolved, contiguous territorial society that possesses a physical environment, a socioeconomic, political, and cultural milieu, and a spatial structure distinct from other regions... " (Markusen 1987). In comparison with other U.S. counties matched for size and infrastructure development, the southern Appalachians have increased significantly over a 22-year period in personal income, population, manufacturing, retail, and service employment, although these changes have been unevenly distributed throughout the region. Employment gives strong evidence for a segmented economy, further supported by the spatial distribution of residents. In 1990, the region was predominantly rural-non-farm and suburban: < 3% of all households were rural farm households and < 2% of the population derived income from agriculture.

Non-metro counties in the southern Appalachians apparently have undergone the same human desertion phenomenon recorded across the United States between 1940 and 1970. A general migration within the region from remote rural locations to rural locations on the fringe of urban areas. The migration source for many contemporary rural-non-farm households is a core of poverty-stricken counties running through the middle of the project area. These rural deserters typically find it easier to obtain employment in service and retail occupations (where most change has occurred) than in specialized occupations. The large proportion of rural-non-farm households may have negative ecological consequences since members of these households drive longer distances to work and live beyond the influence of city ordinances and city services, such as sewer and water systems, perhaps resulting in more significant impacts on terrestrial and aquatic ecosystems.

Critical to recent change in southern Appalachian society is a substantial influx of retirees to the region: North Carolina, Virginia and Georgia currently rank nationally as the 5th, 9th and 10th destination for retirees based on population movement. Individuals over 65 years of age are concentrated in certain areas, e.g., the Franklin-Highlands-Cashiers Area, and the Asheville Area; in some counties, > 20% of the resident population is > 65 years of age. Individuals in this age group tend to locate near amenities, most notably good hospital care, cultural events, and recreational opportunities. These and other factors provide essential context for understanding how people have interacted with land and resources and the potential for change in these interactions.

III.B. New Research

III.B.1. Land and Resource Use in the Southern Appalachians. To date, our analysis of land use has focused on mechanistic and descriptive models of land use choices that link observed behavior to physical and locational attributes of specific sites. We will extend our analysis to previously unaddressed issues regarding the formation of land values ([Table 5](#)). The utility or value derived from land in various uses has remained an unobserved or latent variable. We will examine how land values are determined by the interaction of buyers and sellers in markets for land with various productive and aesthetic attributes. This component provides a

direct linkage with terrestrial (sections V.A.1 and V.A.2) and aquatic (section V.B.3) research on the impacts of land use pattern on species diversity, composition, and structure (e.g., are there certain vegetation types or species [e.g., trout streams] which impact land value?). Observations on land transactions, coupled with interviews with buyers and sellers, will be used to fit hedonic market models that account for the influence of location, land productivity, and aesthetic qualities on the values of land (Palmquist 1989; Bockstael 1996). To address the importance of aquatic ecosystems to land values., we are focussing on the importance of trout stream habitat on land use decisions and land values ([Appendix B](#)) This provides an important connection between socio-economic and aquatic research components of the Coweeta LTER. As the study region increasingly becomes a recreational retreat for citizens from surrounding metropolitan areas and recently retired in-migrants, the demand for recreational opportunities such as trout fishing supplants formerly important productive activities (e.g., forestry). Given the high proportion of public lands and waterways within the region, this transition in demand is leading to changes in settlement patterns and land valuation. Through a structured survey design, we will elicit those actions that landowners have either taken or not taken in maintaining or creating trout habitat. We predict such factors as proximity to public lands and amount of stream frontage influence both segmentation of the land into parcels and its resulting value and transaction potential. The resulting fragmentation of the land can then be linked to observed changes in the physical and biotic properties of waterways in the region. Both of these studies will initially be conducted in the North Georgia portion of the study area and extended into the whole region in subsequent years.

III.B.2. Social and Institutional Context. Research on changes in major social and institutional factors will continue using surveys, detailed personal interviews, and archival searches. The survey of land buyers and sellers described above will also be used to gauge changing attitudes of local populations. We are completing a survey of county distinctiveness and types of change administered to all chambers of commerce in the study region. In addition, we identified 15 cooperative informants. local residents with multi-generation family histories of residence in the region, and in-migrants with 10-20 year histories of residence. Interviews were conducted to assess the underlying rationality for their actions over time (life histories) and to establish a local chronology of change for the area. Biotic research described herein has indicated that terrestrial and aquatic ecosystem structure, biodiversity, and integrity are strongly influenced by the long-term history of land and resource use. Unfortunately, most readily available physical and economic data for the study region only extend back to 1950 and many of the forces driving the observed changes acted before this date. We will continue to reconstruct the human population size and the nature and extent of their disturbance of the landscape for Macon County since first white settlement (1819). Early census information, agricultural schedules, and land fide maps will allow us to define nearly the entire post-European land use history, although at a coarser resolution than the recent historic (40 year) data, and will further support research on the effects of land use legacies on ecosystems.

III.B.3. Interdisciplinary Collaborations. We are collaborating with the

terrestrial and aquatic research groups to tie the socioeconomic factors to land use change ([Appendix B](#)). Forecasts of land use change (Wear and Bolstad 1998) will be used as the basis for generating land use change hazard maps. By overlaying boundaries of stream catchments we will identify which drainages may be most susceptible to change and those which should remain relatively stable over the next several years. These catchment hazard ratings will be used by the aquatic group to augment their stream sampling so that the effects of changes in landscape condition on stream quality can be monitored. The forecasts of land use change will also be used to (1) examine the effects of increasing residential development on landscape fragmentation and connectivity, and (2) examine the potential effects of land use changes on carbon storage conditions in the region.

IV. EFFECTS OF LAND USE CHANGE ON AQUATIC ECOSYSTEMS

IV. A. Work Accomplished and in Progress

Both the historical record and socioeconomic analyses identify the greatest human impacts in riparian and other near-stream areas, where farming was more profitable, infrastructure developed, and access easier. However, few studies have linked these changes in land use to their impacts on stream ecosystems, particularly over broad spatial and long temporal scales. In the Little Tennessee (LT) and French Broad (FB) rivers, we are investigating (1) the influences of differing past (50 year) and present land use practices on fishes and invertebrates, and their trophic interactions across a continuum of forest - agriculture - urban landscapes; and (2) how past and current land use affect the future of aquatic ecosystems ([Figure 5](#)).

IV.A.1. Responses of stream fauna to current and past land use. Several previous studies at Coweeta and elsewhere have established the links between current stream environments and biotic diversity, structure, and abundance. However, no studies have explicitly identified the relationships between these variables and the legacy of past and present land use. We monitored fish and invertebrate diversity, abundance, and functional groups and characterized physical habitat in FB and LT streams ([Table 1](#)). Using GIS, we correlated faunal characteristics with current land use patterns and with available information from land use ca. 50 years ago. We found significant impacts of Current land use practices, but just as significant impacts of past watershed and riparian land use on present-day species biodiversity (Harding et al. 1998, Helfman et al. 1998).

Agricultural vs. forested streams differed significantly in diversity and species composition. Invertebrate species richness was significantly greater in forested streams, whereas fish diversity and abundance were significantly greater in agricultural streams ([Table 2](#)). Higher sediment loads in agricultural streams were associated with a decrease in crevice spawners and increase in pebble-pile nesters; trout were limited to forested systems and were correlated with reduced diversity in non-trout taxa (Helfman et al., 1998). Reduction of forests caused shifts in composition and function, with fewer sensitive, diverse southern Appalachian taxa (mayflies, stoneflies, caddisflies, darters), and reduced trout abundance.

Our findings also indicate that in some watersheds historic land use is a more useful indicator than present land use in predicting species diversity ([Table 3](#)), and the magnitude and length of human agricultural disturbance in a watershed limit the recovery of stream biodiversity for many decades (Harding et al., 1998). Forested and agricultural streams clearly differed in assemblage composition, with the exception of two streams ([Figure 6](#)). Both these forested streams drain watersheds that were nearly half agricultural in 1950 and over 90% forested in 1990. Invertebrate and fish assemblages and substrate of these two atypical "forested" streams most closely resemble those observed in agricultural catchments ([Figure 6](#)). Reforestation has not resulted in recovery of stream fauna, possibly due to the observed persistence of finer sediments associated with previous farming.

Sampling of LT and FB drainages also include urbanized streams ([Table 1](#)). Preliminary analyses of fish and invertebrates show lower overall diversity and density in urban and suburban streams than in either forested or agricultural streams, higher species diversity and density at suburban than at urban sites, and greater occurrence of introduced fish species at urban sites. This sampling effort will continue through another year and will consider building density ([Figure 7](#)), because Wear and Bolstad (1998) found that building density is a strong correlate of the impact of human activities on Appalachian landscapes. As building density increases, invertebrate species richness declines ([Figure 8](#)). Information from the resulting analyses will be incorporated into forecasts of land use and economic impacts of faunal change discussed in section III.B.3.

Fish diversity and abundance reported above were obviously affected by degree of forestation in riparian regions regardless of non-riparian land use. In an additional study we chose a series of sites differing primarily in degree of riparian deforestation and tested for relationships between this gradient and (1) the distribution and diversity of habitat types, (2) fine sediment deposition, and (3) fish density and diversity. We sampled sites downstream from deforested riparian patches 0 - 5.6 km long (Jones et al. 1998) ([Table 1](#)). Fish abundance decreased with forest cover, with the largest reductions in benthic-dependent, riffle-dwelling species and largest increases in water column or pool-dwelling, species. Habitat diversity and the abundance of shallow pools decreased, moderate to deep pools were more abundant, and riffles were filled with fine sediments. Riparian deforestation also appears to favor invasion by exotics and leads to a decrease in fish species that are dependent on swift, shallow water flowing over sediment free substrates or that do not guard hidden eggs; deforestation leads to an increase in fishes that live in slower, deeper water, or that guard their young ([Figure 9](#)). Physical features of the stream responded proportionally to gradients of disruption (i.e., increasing deforestation = decreasing habitat diversity), whereas fishes showed apparent thresholds of response to deforestation ([Figure 9](#)). Even if the overall watershed remains primarily forested, fish biodiversity and abundance declines rapidly when disruption of much more than 1 km of upstream riparian zone.

Agricultural streams with forested headwaters may differ structurally and functionally from similar streams that are cleared to the headwaters

(Vannote et al. 1980). We compared benthic invertebrate assemblages and physico-chemical characteristics along the headwaters to downstream gradients in agricultural streams with forested and deforested headwaters ([Table 1](#)). Initial results show large upstream but small downstream differences in species composition, richness, functional feeding group biomass, and density. We will continue this detailed characterization to reveal the magnitude of headwater effects on downstream physical conditions and biotic processes.

Logging in the southern Appalachians between 1900 and 1920 left few areas untouched, but one large area (the Joyce Kilmer Memorial Forest) escaped cutting and provides "baseline" conditions. We sampled habitat characteristics and species diversity of aquatic insects in streams that drain forests of different ages ([Table 1](#)). Forest recovery has been tracked using GIS layers constructed from historical records, aerial photographs, and remote sensing data. Results show stream invertebrate biodiversity is still recovering 70 years after disturbance, although these streams are more similar to uncut forests than to 20-year-old cuts ([Table 4](#)).

IV.A.2. Influence of Land Use on Stream Trophic Dynamics. We are investigating the role of stream macroconsumers (fishes and crayfishes) in trophic dynamics and the interacting effects of sediments in southern Appalachian streams draining watersheds differing in land use. This work relates to the above studies, in that it seeks to identify the mechanisms and processes by which the higher trophic levels respond to the proximal impacts of land use change (e.g., sediments, loss of shading, trout introduction). Our experimental studies of macrobiotic effects at Coweeta are directly comparable to similar studies conducted at sites in both Puerto Rico and Costa Rica (Pringle and Hamazaki 1997, 1998). Intersite comparisons address: (1) the extent to which stream macrobiota structure stream benthic communities, (2) the role of macroconsumers in structuring benthic environments and communities in tropical versus temperate streams, and (3) possible legacies of extirpated macroconsumers (e.g., fishes, crayfishes) in disturbed temperate streams (Schofield et al., in prep.; see also IV.B.3).

Few studies have experimentally examined sedimentation effects on benthic assemblages in situ. In addition to documenting bedload movement in streams with differing land use in the watershed, we are testing two hypotheses: (1) Fishes and/or crayfishes play key roles in controlling the benthic community; their exclusion will result in a trophic cascade leading to enhanced abundance of herbivorous benthic insect prey and corresponding decreases in algal standing crop. (2) Interactions among stream macrobiota, sediments, and algae will be influenced by changes in land use via changes in light and sediment delivery. Increased sedimentation will swamp out potential trophic cascades, so that exclusion of macrobiota will have less impact on herbivorous benthic insects in streams with a higher sediment load.

We tested these hypotheses ([Table 1](#)) using electric fences to manipulate the presence and absence of macrobiota while avoiding cage artifacts (Pringle and Blake 1994). Exclusion of fishes and crayfish resulted in higher

abundances of large (> 4 mm) insect larvae and increased standing crop of chlorophyll and AFDM. Macrobiota appear to influence the structure of southern Appalachian benthic communities by decreasing the amount of organic matter available for other consumers and by preferentially preying on certain taxa and size classes of insects.

Sedimentation alters this interaction. Greater numbers of large insect larvae were found when macrobiota were excluded in an agricultural watershed with large sediment bedloads; yet the difference in standing crop of organic matter and chlorophyll was less dramatic when compared to a forested stream. There was a similar masking of biotic interactions when we experimentally added sediments to electric exclusion manipulations in the forested stream.

Several conclusions arise from these analyses. We have found no evidence of a trophic cascade in response to the macrobiota. exclusion, perhaps a consequence of an abundance of omnivorous species, as has been found in tropical streams (e.g. Flecker 1996, Pringle and Hamazaki 1997). In addition, macrobiota do not play as important a role in removing sediments, nor do they have dramatic effects on trophic dynamics as has been observed in tropical streams (Pringle and Hamazaki 1997, Pringle and Hamazaki 1998, Pringle and Blake 1994, Pringle et al. 1998). Experiments planned for summer 1998 will examine these interactions along the urbanization gradient described above (IV.A.1).

IV.B. New Research

IV.B.1. Legacies of Land Use Past and Future. Land use from 1880 - 1940 caused large soil inputs to southern Appalachian streams. Since then farms have been abandoned, forests have regrown, and there is currently rapid population growth, yet legacies of past land use remain. Two-year results plus detailed land use trajectories in the GIS data will allow us to identify the causes and processes by which land use affects stream communities. We will continue our current studies, described above, plus initiate new sampling to precisely define the interaction of agricultural patch size and recovery time on invertebrate and fish diversity in streams ([Appendix B](#)). We will sample organisms and substrate characteristics in streams with different land use trajectories ([Table 1](#)) and determine the relative importance of patch size, land use pattern, and temporal sequence on recovery.

Similar sampling will be combined with transition "hazard" maps predicting future land use (Wear and Bolstad 1998). These models indicate that land use change is most probable near the riparian zone at the urban edge. We will map the transition "hazard" index based on these models and identify forested 3rd- or 4th-order streams, four each with low and high probability of change. Due to resource limitations and to slow rates of land cover change, we will sample for physical and biotic characteristics ([Table 1](#)) once every three years for the next several decades. The socioeconomic forecasting model presents us with a unique opportunity to document the effects of land use changes on aquatic ecosystems as they are occurring;

the proposed sampling regime is designed to utilize that opportunity.

We are tracing changes in land use over time to determine if changing land use is correlated with changing fish and crayfish assemblage characteristics. We are searching historical museum records for species composition, relative abundance, and habitat characteristics, which are being linked to historical aerial photographs and topographical maps that show land cover types and past building densities ([Table 1](#)). Assemblage attributes will be regressed against land use characteristics. This information will then be included in the forecasting exercise described in section IV.B.2. Shifts in faunal characteristics between past and present will be used to estimate the accuracy of forecasts of change in the biota in the future.

IV.B.2. Scaling Watershed Observations to Present and Future Landscapes.

The analyses described in previous sections relate fish and invertebrate assemblages observed at a site to the characteristics of the watershed and riparian zone above that site. To improve statistical inference and future site selection, we developed automated techniques to extract land use information for first- through fifth-order watersheds in the LT basin (Gardiner, E.P. and P.V. Bolstad. 1998. Landscape stratification for stream ecology. ESA/ASLO meeting, St. Louis, MO, [Figure 7](#)). We will perform similar analyses for the FB basin using 1990 spatial data and for land use maps predicted for 2030 by socioeconomic models (Wear and Bolstad 1998). Integrating socioeconomic modeling with our spatial data of land use, we will analyze changes in the frequency distribution of watershed characteristics in streams of different size ([Appendix B](#)). We will augment our data from sampling along the human disturbance gradient with analyses of museum records to develop past, present, and alternative future scenarios for the aquatic biota. The trajectory of change in the FB is accelerated compared to LT (T. Gragson, pers. comm.). Using alternative projections of development provided by the socioeconomic models, our data on faunal changes in similar habitats in the two river systems can be used to predict alternative potential states of aquatic systems under different human population and development scenarios

IV.B.3. Stream Trophic Dynamics.

Top predators can structure communities at lower trophic levels, and observed land use changes may directly or indirectly affect the abundance of these macroconsumers in streams. Considerable efforts have been directed at sampling native fish populations. However, despite the prevalence and diversity of crayfishes in the Southeast, the important role they play in structuring benthic communities (Charlebois and Lamberti 1996, Parkyn et al. 1998), and their high degree of imperilment throughout the U.S., little is known about their distribution, abundance, or significance in the trophic dynamics of southern Appalachian streams. We propose an initial electroshocking survey that documents the species and relative abundances of crayfishes in forested, agricultural, and urban streams sampled previously for fishes and aquatic insects (IV.A.1-2). We will then conduct a series of crayfish enclosure experiments in which crayfish species and/or densities will be manipulated in streams with varying land use ([Appendix B](#)). The experiments will be designed to determine direct and indirect effects of crayfish on the stream benthos and whether those

effects vary with land use type.

As recreational/retirement development proceeds in the southern Appalachians, pressure will increase for continued and expanded trout introductions. LTER social scientists will address the extent to which proximity to a trout stream relate to land values (III.B.1), one of the drivers for trout introductions. We have documented (IV.A.1) alteration of native fish assemblages by brown and rainbow trout, but less impact on invertebrates; however, we do not know the food web consequences of this introduction. Hence we propose electric exclusion experiments in forested streams with and without populations of brown and rainbow trout to examine the impact of these species on trophic dynamics (Table 1). We will also examine the interaction of macrobiota and nutrients on benthic insects and algal communities in both agricultural and urban landscapes (Table 1), where the macrobiota exclusion technique will be used in combination with nutrient-diffusing substrata (Pringle and Triska 1996).

IV.B.4. Agricultural and Urban Development in the Watershed: Thresholds and Riparian Function. Research to date (IV.A.1) underscores a gap in our understanding of the interaction between riparian and upland regions. Intact riparian zones are widely employed as a mitigation tactic against destructive activities in upslope regions (e.g., Doppelt et al. 1993, Harper and Ferguson 1995). However, our findings indicate that the riparian zone can withstand disturbance up to a point, after which the fauna undergoes functional shifts. Our work (IV.A.1) dealt with riparian zones downslope from watersheds that were at least 80% forested. Work in intensive agriculture systems indicates that extensive upland disturbance can override the effects of an intact riparian zone, e.g., when agricultural land use exceeds 50% (in Wisconsin, Wang et al. 1997); similar impacts have been observed when 10 - 20% of the watershed is urban (Scott et al. 1986, Limburg and Schmidt 1990, Weaver and Garman 1994, Wang et al. 1997). Where does the balance lie between riparian buffering and upland disturbance? We will use GIS to locate 3rd to 5th order streams in the FB basin that have intact riparian zones in watersheds with defined ranges of agricultural and urban land use. We will sample fish and invertebrate assemblages and make habitat measurements, using our previous studies to generate expected conditions for relatively disturbed and undisturbed streams. Results should help us determine if a similar threshold of urbanization applies in the southern Appalachians and which types of urban land use show the greatest biological response. These studies will indicate the degree of development that occurs in a watershed before the buffering, capacity of the riparian zone will be overcome, or how much land needs to be converted from agriculture to forest before a stream can potentially recover within historical constraints (IV.A.1).

V. EFFECTS OF LAND USE CHANGE ON TERRESTRIAL ECOSYSTEMS

V.A. Work Accomplished and In Progress

Our work in terrestrial ecosystems focuses on the interactions among environmental gradients, disturbance, and land use patterns, and how these interactions influence the diversity and population dynamics of terrestrial

species and ecosystem C cycling ([Figure 10](#)). Understanding effects of land use on terrestrial animal and plant populations is highly relevant in the southern Appalachians, as the region supports some of the highest biological diversity in North America and is undergoing significant changes in land use patterns. Similarly, our focus on ecosystem C balance in a diverse and changing landscape will elucidate the significance of forests for C storage, and whether historical, present, and future land use patterns (driven by socioeconomic and environmental factors) will increase or decrease C storage in the region.

V.A.1. Effects of Disturbance History and Patch Structure on Vascular Plants, Vertebrates, and Macroarthropods. Land use change often results in habitat loss and fragmentation (Turner et al. 1994, Sinclair et al. 1995), with numerous habitat patches that are isolated and reduced in size. In addition, even after human land use ceases (e.g., cropland is abandoned) and succession again increases habitat connectivity, past land use effects on vegetation and soils may persist for decades (e.g., Foster et al. 1992). We have completed several studies on how land use and habitat fragmentation affect herbaceous species diversity and abundance in cove forests (mid-elevation mesic). We are currently extending these analyses to macroarthropods and herpetofauna.

One study tested for the effects of patch size on the abundance of cove-forest herbs in small (< 25 ha) and large (> 200 ha) forest patches in the French Broad (FB) River basin. Large forest patches had greater coverage and density of cove-forest herbs than did small patches, and some species (e.g., the lileaceous species *Disporum maculatum* and *Uvularia grandiflora*) were absent from small patches (Pearson et al. 1998 b). Large patches also had significantly more soil C than small patches, indicating a linkage between ecosystem C cycling (section V.A.2) and herbaceous diversity. These data and others have shown a positive relationship between soil organic matter and diversity of cove-forest herbs ([Figure 11](#)).

We used field studies, modeling, and experiments to explain the responses we observed. For example, to disentangle the effects of patch size and past land use on the cove-forest herbaceous plant community, field studies were designed to address two questions: (1) In forest patches that were subjected to prior human land use (cropping, pasture, or intensive grazing), is there a detectable effect of patch size? and (2) In large forest patches, is there a detectable effect of past land use? Data obtained from 12 patches of mature cove forest revealed that past land use negatively affected species richness, total cover, and the cover of old-growth, mesophytic, and lileaceous species. Given prior disturbance, patch size affected species richness, total cover and coverage of weedy species and lillies, but had no effect on old-growth or mesophytic species (Turner et al. 1998).

Herbaceous species absence might result from relatively poor dispersal abilities or from changes that render patches unsuitable for the species. We began a series of reciprocal transplant experiments to examine the "habitat suitability" mechanism. A spatial model was developed to explore the "dispersal and patch isolation" mechanism (Ives et al. 1998, Pearson et al. 1998 c). Simulation results revealed that all populations persisted on

landscapes that were not fragmented (e.g., a suitable habitat occurred on > 35% of the landscape). However, species with low survival or fecundity were likely to become extinct in highly fragmented landscapes; increased dispersal capability was insufficient to compensate for low fecundity and survival, although it did increase persistence time. These results reveal complex interactions between life-history parameters and landscape pattern and highlight the potential for lengthy time lags in the responses of populations characterized by low dispersal and high longevity (such as many perennial forest herbs) to habitat fragmentation (Pearson et al. 1998 a). Collectively, our field and modeling studies suggest that cove-forest herbaceous plant communities are not in equilibrium in the southern Appalachians.

V.A.2 Tree demographics and dispersal. Experiments and monitoring studies have led to a stand model elucidating how tree species life histories determine stand composition, and how this varies along the elevational gradient and in response to disturbance and regional environmental change. Life history stages under analysis include seed production and dispersal, seed banks, and seedling and tree demography. Seed production and dispersal are now well-understood. We have several papers in press and in review demonstrating seed production variability, patterns of seed movement, and the extent to which recruitment limitation impacts dynamics of all major canopy species (Clark et al. 1998 b, c). The methods developed here have been applied across sites in order to compare patterns of fecundity and dispersal in other temperate and tropical sites (Clark et al. 1998 a). Dispersal patterns are also the basis for analyses of dispersal limitations on potential migration rates in the early Holocene (Clark et al. 1998 b, Clark, 1998 a), allowing assessment of the relative importance of diffusion from patch edges vs. long distance dispersal for reforestation of fragmented landscapes and migration into new areas.

The modeling and field studies described above suggest that dispersal also plays an important role in determining the distribution patterns of a variety of other terrestrial organisms besides trees. For example many of the understory forbs, salamanders, and shrews have very particular habitat requirements, and patches of suitable habitat are often very isolated from each other. We have begun field studies similar to those used with trees to estimate species-specific seed production and dispersal parameters for forbs, and we are evaluating similar techniques for small mammals.

V.A.3. Environmental gradients and land use effects on ecosystem C pools and fluxes. One of our first objectives was to understand variation in C pools and associated driving variables across the environmental gradient. We measured ecosystem C pools and environmental driving variables at >200 forested plots across the region and found significant differences in C pools among community types and across environmental gradients. For example, soil C increased significantly with elevation and as terrain became more concave, and these differences were significant across different soil types and bedrock geologies (Bolstad et al. 1998 a). Overstory biomass, composition, and structure responded significantly to terrain shape and elevation, but these were complex and highly variable relationships. Belowground components, including fine-root and total biomass, changed

with elevation and terrain shape, with significantly higher root biomass per unit stem biomass on ridges as opposed to coves, particularly when adjusted for understory density (Bolstad et al. in prep; Bolstad et al. in review). In addition, a suite of canopy variables changed with elevation, most importantly leaf nitrogen content, which increased from low to high elevations.

To determine the effects of land use, we established plots across a range of land uses and disturbance histories (old-growth, mid-successional forest, early successional forest, and pasture), forest types, and topographic positions to develop predictive relationships among environmental gradients, land use patterns, and ecosystem C balance across the region. Initial work has focused on measuring soil and vegetation C pool sizes, flux rates, and driving variables across the gradient ([Table 5](#)) to parameterize the simplified model shown in [Figure 12](#). Our ultimate objective is to link the results described below with paleo, historic, contemporary, and future land use (from socioeconomic models) to determine impacts on C cycling (V.B.3, V.B.4).

Soil CO₂ flux varied considerably among land use types, with nearly twofold greater rates of growing-season soil CO₂ flux in pasture than in forested ecosystems (9 vs 4.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for pasture and forest, respectively), while differences among early-successional, mid-successional, and old-growth forests were small ([Figure 12d](#)). Significant driving variables ($p < 0.05$) include soil temperature, fine root mass, litter mass, and soil C and N (Vose and Bolstad in prep), which varied among topographic positions.

Leaf respiration was measured for 18 canopy and sub-canopy tree taxa, including all dominants and important understory species (measurement at the species level result in a direct linkage with the demographics work described in section V.A.2). Respiration measurements identified significant differences in leaf respiration/temperature response functions among species (Mitchell et al. 1998; Bolstad et al. 1998 a) ([Figure 12a](#)). More important, response functions differed by light levels, both among and within species; thus, canopy respiration will depend on species composition, leaf biomass, and the vertical distribution of leaf light environment. Annual estimates of canopy-integrated leaf respiration indicated that species do matter, with differences in species causing up to 30% variation in canopy respiration ([Figure 13](#)).

Species-level stem respiration measurements also identified significant differences among species ([Figure 12b](#)). Stem temperature had the largest effect on stem respiration, and stem temperature varied with topographic position, aspect, and tree size (Kloeppel et al. in preparation). Though tree stem temperature explains the largest portion of the variation in woody respiration (approximately 55% depending upon species), species-level variation in sapwood volume also explained a significant portion of the remaining variation (approximately 25%, depending upon species). In order to scale these measurements from the chamber to the tree- and plot level, we have developed sapwood-diameter allometric relationships for the ten dominant species in the southern Appalachians ($R^2 = 0.89$) (Martin et al. 1998). These data, when combined with regional sampling and temperature

measurements, appear to be the most promising method for scaling respiration estimates from the plot- to the landscape-scales.

V.B. New Research

V.B.1. Impacts of anthropogenic disturbance on vascular plants and small animals. Research will continue on the interactions of patch size, historical land uses, and life history traits on vascular plant species. In particular, we will continue manipulative transplant experiments wherein we determine the tolerance of selected species to factors associated with anthropogenic disturbance. Manipulated factors will include grazing, light, soil compaction, and loss of soil organic matter. These experiments will allow us to unambiguously identify the disturbance-related factors responsible for the declines and losses of specific vascular plant species.

We will also continue to monitor the disturbance-influenced population dynamics of both vascular plants and small vertebrates to determine if rates of survivorship and recruitment differ by environmental gradients and site conditions (e.g., cove vs. ridge, low vs. high elevation). These experiments will allow us to relate plant diversity to the legacy of past land uses ([Appendix B](#)). When integrated into the simulation models and 1950's, 70's, and 90's landcover data (II.A), these studies will allow us to estimate the effects of historical landscape changes on biodiversity. We will use these data to predict future conditions, in that the field surveys and transplanting experiments will help define suitable habitat for vascular plant and small vertebrate species. We will combine this information with landcover from the socioeconomic models to predict the future distribution of suitable habitat for selected species. We recognize that these predictions will be complicated by future climatic changes that may alter habitat suitability. In particular, we anticipate that soil moisture, fertility, and temperature will be especially important determinants of habitat suitability. By monitoring those variables where plant populations are introduced, we will determine how these variables influence the viability of certain species. Ultimately, we will link our landscape models to regional climate and land use change models in order to predict future community and species distributions.

V.B.2. Regional Canopy Demographics and Recruitment in the Aggrading Appalachian Forests. In the next four years we will complete the parameterization of the forest stand recruitment and dynamics model, conduct analysis of recruitment responses to environmental gradients and forest fragmentation, and complete the fire/vegetation/climate change analyses. Parameterization of the stand model includes the completion of seed bank, seedling, and tree studies, with special emphasis on canopy analysis from low-altitude photos. Two classes of hypotheses will be addressed with the stand model. First, given that each species is limited in different life history stages at different locations along the elevation gradient, we can postulate a range of possible responses to climate change that affect these elevation relationships in the future. Simulations and analytical models will be used to address these hypotheses. Second, we plan a series of experiments based on inverse modeling of dispersal ([Appendix B](#)). These experiments will assess the relative importance of patch edges vs. long-distance dispersal in the reforestation of fragmented landscapes and

migration into new areas. These analyses will involve both Coweeta and other North American sites.

V.B.3. Impacts of Land use Change on Carbon Pools and Fluxes. Landcover analyses indicate large-scale reversion of agricultural land back to forest over the last 50 years. More than one-half the area of many large watersheds was cleared for agriculture by the late 1940s: most of these watersheds have seen partial to full reversion to forests. However the ten to 40 years in agriculture has lasting effects, particularly on soil properties. While forests may return rather rapidly, changes in soil chemical and physical properties may persist for decades or centuries. Sampling in the current grant has identified lower soil C and higher soil bulk densities in aggraded forest plots, even 40 years after forest regrowth. Our detailed landcover maps ([Figure 2](#)) will allow us to establish a fine sampling template, in which we can identify agricultural disturbance intensity and age since abandonment. We will establish a set of plots in which we will measure long-term changes in forest soil conditions and C stores and fluxes. Theoretical and chrono-sequence studies have established slow rates of C accretion in aggrading soils, requiring a long study time (we propose sampling over a chronosequence of >80 years). Resource limitations and the desire to minimize site impacts preclude yearly measurements, and inherent variation in soil variables requires large subsampling for aerial representation, so we propose sampling every 5 years at approximately 40 sites, 5 replicates of each of two landscape positions (coves and broad terraces/valleys) at four disturbance intensities/ages. We will sample soil C and N, bulk density, fine and coarse-root biomass, overstory and understory composition and structure, soil carbon flux (three times yearly, diurnal patterns with concomitant temperature, moisture, and C and N measurements).

V.B.4. Scaling Carbon Flux. Our data sets and analyses are designed for point to region process based scaling. We have measured flux rates for the major components (leaves, stem, litter, and soil/roots) across the range of biotic and environmental variation found in the Southern Appalachians. When model development is complete, we will combine these models with spatially organized driving variables (regional temperature, forest composition and biomass, leaf mass and nitrogen, precipitation, terrain, elevation, and others) to scale carbon flux. We will shortly complete development of the spatial stack of data required to predict carbon flux based on our process-based models. When our models are complete (early in the next year), we will have a tool for predicting current carbon flux for daily, seasonal, annual, or longer time periods. Our studies will be unique in that we will have extensive, direct local measurements of all important flux pools, processes, and driving variables. This allows variance estimates for input parameters, and hence quantitative assessments in error propagation through the models. A combined error approach will allow us to identify the sensitivity of predicted outcomes to uncertainties in the data. For example, Davidson (1995) and Lathrop and Peterson (1992) have identified soil variation due to a cartographic generalization and interval representation as a significant factor in estimating regional flux estimates. However they were unable to partition uncertainty, or provide improved resolution beyond

already available data (e.g., SURGO).

This work will entail a set of sub-tasks for model validation. For example, independent quantitative assessments of component flux will require additional field sampling, including stem, leaf, and soil respiration, and photosynthesis. Driving variables and flux rates will be measured at a set of sites, e.g., stem temperature, sapwood area, and respiration measured locally (Macon County, in which the Coweeta Lab is located) and regionally (sites across the study region). Daily (or weekly) integrated carbon flux model estimates will be compared to field measurements, and the source of bias and imprecision (input parameter estimation or model lack-of-fit) identified. These errors may then be carried through the point to region scaling, inflated or smoothed, depending on component and aggregate response surfaces (Pierce and Running 1996).

The assembled paleo record, historical landcover data, and current landcover/land use data will be combined with developed landscape carbon pool and process-based flux models to estimate regional changes in pools and fluxes associated with human activities (II.A, III.A.1). The combined data sets will provide a unique, quantitative, spatially explicit record of the major variables governing landscape carbon flux. Point process models will all be based on local to regional measurements, and will provide component and integrated carbon flux estimates. This record will provide estimates of carbon release due to land conversion, and of the magnitude and rate of carbon accretion in the aggrading forests. When combined with past and future predictions based on socioeconomic models, we will also extend estimates into the future.

VI. CONCLUSIONS

Coweeta's more than six decades of forest ecosystem research has provided significant insight into the role of environmental gradients and small-scale disturbances on ecosystem function and it provides a solid foundation of understanding "baseline" conditions of southern Appalachian ecosystems. Research conducted under the Augmentation Award has expanded Coweeta's focus to include humans as key components of ecosystems, and has greatly increased our knowledge and understanding of the cascading effects of human land use decisions on local to regional ecological processes and ecosystem functions. Land use change analysis has quantified the pervasive impacts of agricultural and urban disturbance in the southern Appalachians in the recent historical past. Companion research has focused on the root social causes of land use decisions, establishing a link between regional and national social and economic conditions and land use change, and developed quantitative economic assessments and predictive models of future land use patterns and the factors influencing land use transitions.

Concomitant field sampling and analyses have identified the importance of natural and anthropogenic disturbances on both terrestrial and aquatic ecosystems. In terrestrial systems we have established how fecundity, dispersal, and early survivorship vary in natural forests and gaps, and how these factors influence recruitment among the dominant overstory and the most diverse understory plants. These results have both local and global

significance as they facilitate analysis of gap dynamics, edge and compositional effects on old-field recolonization, and rapid long-distance post-glacial dispersal. We have identified changes in canopy N content, productivity, C stores and C cycling rates which relate to environmental gradients, have determined how these change with human and natural disturbance, and have established the importance of species-level parameters in local and regional C cycling, and shown that C stores in the soil influence terrestrial biodiversity. Finally, our work provides important data and new insights in the function and responses of aquatic ecosystems to anthropogenic disturbance. We have identified large changes in fish and aquatic invertebrate composition in response to land use change, up to seven decades after forest cutting and four decades after land use reversion from agriculture to forest. Invertebrate biodiversity is higher in forested streams, particularly where trout are absent. Forested streams support either native fishes or introduced trout, but not both, and this loss of native fishes disrupts the trophic dynamics and reduces native stream biodiversity. Invertebrate diversity is higher in forested than in agricultural streams and in old growth and mature than in early successional forests. Reduced biodiversity is chiefly due to sedimentation, which changes habitats from swift, shallow, clear bottoms to finer bottomed, deeper pools, favoring pool-dwelling exotics and changing trophic dynamics. These substrate effects persist well after reforestation of agricultural streams. The theme of legacies of past land use is at the center of both the aquatic and terrestrial research in this project.

This work is unique in the tight linkage and interaction between the socioeconomic and physical/biotic studies, interactions which will intensify in our future work. The predictive models allow us to in effect sample ahead of land use change, to get pre- and post-disturbance response in a manner which would otherwise be much less probable. We feel we have laid a solid foundation in performing relevant, important science directly in line with the mission of the Long-Term Ecological Research Program.

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VIII.A. Publications

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Kloeppel, B.D., D.C. Feldkirchner, S.E. Crowley, J.M. Vose, P.V. Bolstad, W.H. Burch. 199_. Chronosequence dynamics of stem wood respiration across topographic gradients. *Functional Ecology* 00: 000-000. (In preparation)

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Mitchell, K.A., P.V. Bolstad, and J.M. Vose. 1998. Interspecific and environmental variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiology* 00: 000-000. (Submitted)

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Pearson, S.M., A.B. Smith, and M.G. Turner. 1998. Forest fragmentation, land use, and cove-forest herbs in the French Broad River Basin. *Castanea* 00: 000-000. (Submitted)

Pearson, S.M., M.G. Turner, and K.R. Cox. 1998. Population persistence on

fragmented landscapes: interactions between life history strategy and landscape pattern. *Conservation Biology* 00: 000-000. (Submitted)

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Pitelka, L.F., J. Ash, S. Berry, R.H.W. Bradshaw, L. Brubaker, J.S. Clark, M.B. Davis, J.M. Dyer, R.H. Gardner, H. Gitay, G. Hope, R. Hengeveld, B. Huntley, G.A. King, S. Lavorel, R.N. Mack, G.P. Malanson, M. McGlone, I.R. Noble, I.C. Prentice, M. Rejmanek, A. Saunders, A.M. Solomon, S. Sugita, and M.T. Sykes. 1997. Plant migration and climate change. *American Scientist* 85: 464-473.

Rutledge, D.T. and M.G. Turner. 1998. Predicting forest community distributions across a southern Appalachian watershed. *Ecological Applications* 00: 000-000. (Submitted)

Turner, M.G., S.R. Carpenter, E.J. Gustafson, R.J. Naiman, and S.M. Pearson. 1998. Land use. Pp. 000-000 in M.J. Mac, P.A. Opler, C.E. Puckett Haecker, and P.D. Doran, eds. *Status and trends of the nation's biological resources*. U.S. Department of Interior, U.S. Geological Survey, Washington, DC. (In press)

Turner, M.G., R.H. Gardner, and R.V. O'Neill. 1995. Ecological dynamics at broad scales. *BioScience*: S29-S35.

Turner, M.G., D.N. Wear, and R.O. Flamm. 1996. Land ownership and land-cover change in the southern Appalachian Highlands and the Olympic Peninsula. *Ecological Applications* 6: 11501172.

Vose, J.M. and P.V. Bolstad. 199_. Factors determining variation in soil CO₂ evolution across the landscape. *Ecology* 00: 000-000 (In preparation)

Wear, D.N., R. Naiman, and M.G. Turner. 1998. Land use along an urban-rural gradient: implications for water quality. *Ecological Applications* 00: 000-000. (Submitted)

Wear, D.N. and P. Bolstad. 1998. Land use change in southern Appalachian landscapes: spatial analysis and forecast evaluation. *Ecological Applications* 00: 000-000 (Submitted)

Wear, D.N., R. Chowdhury, G. Arthaud, and D. Newman. 1998. Land use regimes in the southern Appalachians. *Natural Resource Modeling* 00: 000-000. (Submitted)

Wear, D.N., M.G. Turner, and R.O. Flamm. 1996. Ecosystem management with Multiple owners: landscape dynamics in a southern Appalachian watershed. *Ecological Applications* 6: 1173-1188.

Wear, D.N., M.G. Turner, and R.J. Naiman. 1998. Institutional imprints on a developing forested landscape: implications for water quality. *Ecological Applications* 00: 000-000. (Submitted)

Winter, K.A. and T.L. Gragson. 1998. Appalachian contrast: the paradox of folk heritage and modern economy in the Southern Blue Ridge Mountains. *Journal of Appalachian Studies* 00: 000-000. (Submitted)

VIII.B. Graduate Students (Dissertations and Theses)

Bennett, Barbara. In progress. Comparison of invertebrate diversity in pasture streams with forested versus cleared headwaters. M.S., Virginia Polytechnic Institute and State University, Blacksburg. VA.

Chowdhury, Rinku Roy. 1996. Socioeconomic and locational factors influencing land use change in Macon County, North Carolina. M.S. Thesis, University of Georgia, Athens. GA.

Collins, Fred. 1995. Spatially explicit temperature prediction models, Ph.D. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg. VA, 218p.

Cooley, D. Robert. In progress. Social and management issues associated with recreational fishing in the southeastern United States. Ph.D., University of Georgia, Athens, GA.

Gardiner, Edward P. In progress. Landscape filters and stream functions: spatial-analytical techniques for regional syntheses. Ph.D., University of Georgia, Athens, GA.

Harrison, Barbara Ann. 1997. The Georgia public and its forests: attitudes and knowledge regarding forest resource use. M.S. Thesis, University of Georgia, Athens, GA.

Lynch, Jason A.. In progress. The role of fire, cultural influence, and climate change in southern Appalachian forests. M.S.. Duke University, Durham, NC.

McTammany, Matthew. In progress. Comparison of stream invertebrates along an urbanization gradient. M.S., Virginia Polytechnic Institute and State

University, Blacksburg, VA.

Mitchell, Katherine. In progress. Measuring and modeling canopy respiration at a range of spatial scales. Ph.D., University of Minnesota, St. Paul, MN.

Morgan, Jennifer. In progress. Land ownership fragmentation and land use change in three North Georgia counties. M. Forest Resources, University of Georgia, Athens, GA.

Pape, Hunter. In progress. Multi-scale analyses of terrain shape indices. M.S., University of Minnesota, St. Paul, MN.

Rosi, Emma. In progress. Changes in food quality of fine particulate organic matter in streams along longitudinal and anthropogenic disturbance gradients. Ph.D., University of Georgia, Athens. GA.

Schofield, Kate. In progress. Effects of human activities on crayfish populations of the southern Appalachians. Ph.D., University of Georgia, Athens, GA.

Scott, Mark. In progress. Impacts of land use change on fish assemblages of the southern Appalachians. Ph.D., University of Georgia, Athens, GA.

Sutherland, Andrew. In progress. Effects of sediments on juvenile fishes in the southern Appalachians. M.S., University of Georgia, Athens, GA.

Wagner, Paul. In progress. Comparison of aquatic insect biodiversity in streams draining old growth versus second growth forests. Ph.D., Virginia Polytechnic Institute and State University, Blacksburg, VA.

Winter, Kimberly A. 1997. Cultural and natural resource management in the buffer zone of the Cotacachi Cayapas Ecological Reserve, Ecuador. M.A. Thesis, University of Georgia. Athens, GA.

VIII.C. Undergraduates

Total undergraduates supported and/or student volunteers: 89

Undergraduates supported by Research Experience for Undergraduates (REU) funding: 5

VIII.D. Presentations

Arthaud, G. and Chowdhury, R.R. December 1996. Factors affecting forest land use change in Macon County, North Carolina. Southern Forestry

Geographic Information Systems Conference, Athens, GA.

Beckage, B. and J.S. Clark. August 1997. Canopy gaps, *Rhododendron maximum*, and tree recruitment in the southern Appalachians. Ecological Society of America Annual Meeting, Albuquerque, NM.

Benfield, E.F. and J.S. Harding. August 1997. Variations in temporal land use disturbance and functional responses of stream assemblages. Ecological Society of America Annual Meeting, Albuquerque, NM.

Bennett, B.L. and E.F. Benfield. August 1997. Does headwater landuse affect downstream invertebrate assemblages in agricultural streams? North American Benthological Society, Annual Meeting, San Marcos, TX

Bolstad, P.V. August 1997. Causes and consequences of landcover change in the Southern Appalachians. Invited presentation, LTER Special Symposia, Ecological Society of America Annual Meeting, Albuquerque, NM.

Bolstad, P.V., J.M. Vose, and E.H. Pape. August 1997. Landscape carbon pools and fluxes on a range of spatial and temporal scales in the southern Appalachians. Ecological Society of America Annual Meeting, Albuquerque, NM

Clark, J.S. February 1996, Recruitment limitation in forest trees. Department of Botany Seminar, University of Vermont, Burlington, VT.

Clark, J.S. June 1996. The role of dispersal in the Holocene expansion of forest trees. National Center for Ecological Analysis and Synthesis Workshop, Santa Barbara, CA.

Clark, J.S. October 1996. Plant dispersal and migration in response to climate change. Workshop, Bateman's Bay, Australia.

Clark, J.S. February 1997. Quantifying seed dispersal and implications for tree migration. Bodega Marine Laboratory, University of California-Davis, Davis, CA.

Clark, J.S. August 1997. Rapid tree migration: confronting theory with dispersal biology and the paleo record. Ecological Society of America Annual Meeting, Albuquerque, NM.

Clark, J.S. September 1997. Long term environmental dynamics. Symposium, Wengen, Switzerland.

Clark, J.S. October 1997. Global change and terrestrial ecosystems: landscape scale processes. IGBP Workshop, San Diego, CA.

Clark, J.S. January 1998. Dispersal and tree population dynamics: from communities to continents. Ecology Seminar, University of Minnesota.

Clark, J.S. February 1998. Dispersal and tree population dynamics: from communities to continents. Ecology Seminar, State University of New York at Stony Brook, Stony Brook. NY.

Gragson, T.L. August 1997. Characterization of human disturbance regimes in southern Appalachia. Ecological Society of America Annual Meeting, Albuquerque, NM.

Gragson, T.L. May 1998. Human disturbance regimes in the southern Appalachian Blue Ridge. 7th International Symposium on Society and Resource Management, Columbus, MO.

Harding, J.S. and E.F. Benfield. June 1996. Temporal landuse changes and their influence on benthic diversity in southern Appalachian streams. Annual Meeting of the North American Benthological Society, Kalispell, MT.

Harding, J.S. and E.F. Benfield. May 1997. Biodiversity and temporal landuse disturbance: can we turn the clock back? North American Benthological Society Annual Meeting, San Marcos, TX.

Harper, J., E.B.D. Jones III, and G. Helfman. November 1996. Land use, patch size, and fish assemblages in the Little Tennessee River drainage. Southern Appalachian Man and the Biosphere Conference, Gatlinburg, TN.

Helfman, G.S. and E.B.D. Jones III. January 1995. Land use and southern Appalachian fish assemblages: a prospectus. Georgia Chapter American Fisheries Society Annual Meeting, Athens, GA.

Helfman, G.S., J.L. Meyer, J.S. Harding, E.F. Benfield, E.B.D. Jones III, M.J. Paul and H. Reed. November 1995. Landuse and aquatic biodiversity in the French Broad and Little Tennessee River basins. Southern Appalachian Man in the Biosphere Conference, Knoxville, TN.

Helfman, G.S., and E.B.D. Jones III, June 1996. Land use and fish biodiversity in southern Appalachian rivers. American Society of Ichthyologists and Herpetologists Annual Meeting. New Orleans, LA.

Helfman, G.S., E.B.D. Jones III, J.L. Meyer, and M. Paul. November 1996. Land use and fish biodiversity in southern Appalachian rivers. Southern Appalachian Man and the Biosphere Conference, Gatlinburg, TN.

Helfman, G.S., E.B.D. Jones III, J.O. Harper. June 1997. Effects of forest fragmentation on fishes and habitats in Southern Appalachian streams. American Society of Ichthyologists and Herpetologists Annual Meeting, Seattle, WA.

Helfman, G.S., E.B.D. Jones III, and J.O. Harper. August 1997. Effects of land use on the fishes and habitats of southern Appalachian streams. Ecological Society of America Annual Meeting Albuquerque, NM.

HilleRisLambers, J. and J.S. Clark. August 1997. Variability within early life

history stages of temperate forest trees. Ecological Society of America Annual Meeting, Albuquerque, NM.

Jones, E.B.D. III, J.O. Harper, M. Paul, J.L. Meyer, and G.S. Helfman. November 1996. The effects of land use on stream habitats in the Little Tennessee and French Broad River drainages. Southern Appalachian Man and the Biosphere Conference, Gatlinburg, TN.

Jones, E.B.D. III and G.S. Helfman. January 1996. The effects of land use on fish assemblages in the French Broad and Little Tennessee river basins. Annual Meeting Georgia Chapter, American Fisheries Society, Brunswick, GA.

Jones, E.B.D. III, J.O. Harper, and G.S. Helfman. April 1997. The effects of land use on fish assemblages and stream habitats in the Little Tennessee River drainage. Association of Southeastern Biologists Annual Meeting, Greenville, SC.

Kloeppe, B.D., E.F. Benfield, D.C. Coleman, and J.M. Vose. co-organizers. August 1997. Quantifying the impact of past, present, and future human and natural disturbance on changing terrestrial and aquatic ecosystems of the southern Appalachians. Contributed Paper Session. Ecological Society of America Annual Meeting, Albuquerque, NM.

Kloeppe, B.D., S.E. Crowley, W.H. Burch, J.M. Vose, and P.V. Bolstad. August 1996. Quantification of tree stem respiration dynamics between slope positions and along an eastern hardwood chronosequence in western North Carolina, USA. Ecological Society of America Annual Meeting, Providence, RI.

Kloeppe, B.D., D.C. Feldkirchner, P.V. Bolstad, and J.M. Vose. June 1997. Tree stem temperature and regional scale carbon flux dynamics in southern Appalachian forests. First Biennial North American Forest Ecology Workshop, Raleigh, NC.

Kloeppe, B.D., D.C. Feldkirchner, P.V. Bolstad, and J.M. Vose. August 1997. Tree stem temperature and respiration dynamics in southern Appalachian forests. Ecological Society of America Annual Meeting, Albuquerque, NM.

Lynch, J.A. and J.S. Clark. August 1996. How fire and anthropogenic disturbance shaped forests of the southern Appalachians Mountains USA. Ecological Society of America Annual Meeting. Providence, RI.

McTammany, M.E., J.S. Harding, and E.F. Benfield. May 1997. Do stream invertebrate assemblages reflect variations in watershed urbanization? North American Benthological Society Annual Meeting, San Marcos, TX.

Meyer, J.L., J.B. Wallace, J.R. Webster, and S.L. Eggert. August 1997. Disconnecting a stream from its valley. Ecological Society of America Annual Meeting, Albuquerque, NM.

Mitchell, K.S., P.V. Bolstad, and J.M. Vose. August 1997. Inter-species and environmental variation in foliar maintenance respiration for eighteen deciduous tree species of eastern North America. Ecological Society of America Annual Meeting, Albuquerque, NM.

Newman, D.H., D.N. Wear, and T.L. Gragson. May 1998. Communicating the importance of scale: implementation of a socio-economic research program at the Coweeta LTER. 7th International Symposium on Society and Resource Management, Columbus, MO.

Pearson, S.M., K.R. Cox, and M.G. Turner. November 1996. Evaluating landscape pattern for species with different life histories. Southern Appalachian Man in the Biosphere Conference. Gatlinburg. TN.

Pearson, S.M., K.R. Cox, and M.G. Turner. November 1997. Evaluating landscape pattern for species with different life histories. International Association of Landscape Ecologists Conference, Durham, NC.

Pearson, S.M., A.B. Smith, and M.G. Turner. March 1996. Forest fragmentation and patterns of mesophytic plant diversity in western North Carolina. International Association of Landscape Ecologists Conference. Galveston, TX.

Pearson, S.M., A.B. Smith, and M.G. Turner. April 1997. Forest fragmentation and patterns of plant diversity in western North Carolina. Annual Meeting, Association of Southeastern Biologists. Greenville, SC.

Pearson, S.M., A.B. Smith, and M.G. Turner. November 1997. The effects of disturbances and abiotic gradients on herbaceous plant diversity in mesic forests. Southern Appalachian Man and the Biosphere Conference, Gatlinburg, TN.

Pearson, S.M., M.G. Turner, and K.R. Cox. September 1996. Forest fragmentation, land use, and coveforests of the southern Blue Ridge Mountains. Zoology Department Seminar, North Carolina State University Raleigh, NC.

Pearson, S.M., M.G. Turner, and A.B. Smith. August 1997. The effects of disturbances and abiotic gradients on cove-forest herb species. Ecological Society of America Annual Meeting, Albuquerque, NM.

Vose, J.M., P.V. Bolstad, J. Butnor, R. Webster, and W.H. Burch. August 1997. Variation in soil CO₂ evolution among land use types in the southern Appalachians. Ecological Society of America Annual Meeting, Albuquerque, NM.

Wagner, P.F. and E.F. Benfield. December 1997. Aquatic insect diversity in old growth and regrowth forests. Entomological Society of America Annual Meeting, Nashville, TN.

Wear, D.N. August 1996. Institutional imprints on a developing landscape:

Implications for water quality. Invited symposium presentation, ESA Annual Meeting, Providence, RI

Wear, D.N. October 1996. Adding humans to LTER research. LTER Network and Regionalization Workshop. Harvard Forest, Petersham, MA.

Wear, D.N. October 1996. Spatial simulations of vegetation dynamics: incorporation of disturbance and economics. The Wildlife Society Annual Meeting. Cincinnati, OH

Wear, D.N. May 1996. Land ownership and land use change at the watershed scale: explaining the past and predicting the future. The Sixth International Symposium on Society and Resource Management: Social Behavior, Natural Resources, and the Environment. The Pennsylvania State University, University Park, PA.

Wear, D.N., G. Arthaud, and D. Newman. August 1997. Evaluating land use change in the southern Appalachians. Ecological Society of America Annual Meeting, Albuquerque, NM.

Wyckoff, P.H. and J.S. Clark. August 1997. Improved mortality functions alter the predictions of a gap type forest model. Ecological Society of America Annual Meeting, Albuquerque. NM.

Wyckoff, P.H. and J.S. Clark. March 1997. Species-specific variation in the growth-mortality relationship for southern Appalachian trees: implications for forest development. US-IALE, Durham. NC.