Section 4.3:
The Ecological Importance of Understory Herbaceous Plants

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Introduction

The Biodiversity Debate

Maintenance of species diversity is of major interest to both land managers and the scientific community. For nearly half a century, ecologists have debated the attributes of species diversity. Ecologists in the early 1960s proposed several hypotheses regarding the importance of species diversity in maintaining ecosystem integrity[22], but very little research has been conducted to evaluate the functional importance of a diverse ecosystem. Despite the lack of consensus by the scientific community on this issue, the commonly held belief among non-scientists seems to be that high species diversity directly corresponds with efficient ecosystem processes and high ecosystem stability. There may be some truth in this statement, but species poor ecosystems are not always inefficient and unstable. Some of the world's most extensive and ancient ecosystems, such as boreal forests, bogs, and heathlands, all typically have relatively low species richness.[6] Therefore, such generalizations about the functional role of biodiversity remain flawed and are in need of further examination. Thus, concrete knowledge of the functional role of diversity is a crucial area of study and is important for understanding the importance of biodiversity and evaluating how changes in vegetation impact ecosystem processes (e.g. net primary productivity).

The Function and Origin of Biodiversity

Grime, in a recent issue of *Science*, stated: "there is no convincing evidence that ecosystem processes are crucially dependent on higher levels of biodiversity."[6] This sentiment resonates with several hypotheses of the origin of biodiversity.

Holdgate describes one theory regarding the origin of biodiversity.[8] As ecosystems develop, initially productivity, diversity, and biomass increase together. However, as systems become even more diverse and complex, the rates of production are likely to level off as available nutrients are shared between a larger number of competitors and consumers, even though diversity may continue to increase with time[8]. The classical ecological explanation is that ecosystems develop in such a way that the available energy is parceled out between greater

numbers of species, each specialized to fill a particular ecological niche. If so, diversification is a process of elaboration within the system, and is not essential for ecological integrity.

Another theory on the origin of biodiversity states that diversity depends not only on the rate of species input (by immigration and speciation) and species output (by emigration and extinction), but also on the ecological history of the region. Therefore, much observed diversity is merely a reflection of the movement of species across a world with great variety in geography and climate and, in functional and ecological terms, involves considerable duplication.[8] Yet again, in this case, diversity is not critically essential for the integrity of the functional unit.

The most commonly held belief by the non-scientific community seems to be that all biodiversity is desirable and that it directly confers efficient ecosystem processes and high ecosystem stability. Tilman concluded from a grassland-savanna experiment that species diversity does have significant effects on plant productivity, and both functional diversity and functional composition had significant impacts on four of the six ecosystem processes tested (productivity, plant % nitrogen, plant total nitrogen, and light penetration).[20] Another study conducted by Hooper and Vitousek concluded that changes in net primary productivity did not correlate with increasing functional group richness, and that increasing productivity was attributed to increases in species diversity.[9] These studies support the hypothesis that species diversity stabilizes community and ecosystem processes. Except for one important process, net primary productivity, the weight of evidence seems to show that above a threshold number of species, increases in species diversity do not improve function.[3, 8, 12]

The role of species diversity in ecosystem functioning and stability remains a mainstay of ecological debate and has spawned an intriguing alternative theory.[2, 6, 8, 9, 10, 20, 21, 23, 24, 25]

The Functional Group Concept and the Redundancy Theory

The redundancy theory hinges on a functional group concept, in which ecosystem processes are determined primarily by the functional characteristics of component organisms (e.g. species composition) rather than species diversity.[1, 8, 9, 12, 23, 24, 25] If there are numerous species, many occupying closely linked ecological niches, and conditions alter to disrupt the ecosystem and eliminate key components, it is more likely that there will be replacements at hand than if the system were simple. Thus, the principal ecological importance of biological diversity may well be its storage of a great quantity of genetic information out of which healthy ecosystems can be reconstituted under an enormous range of conditions and circumstances.[8, 9, 24]

In any ecosystem, it is virtually certain that there will be a range of species existing in sub-optimal conditions, among but subordinate to, those best suited by current conditions. Some of these are of great potential importance as the founder stocks for new ecosystems if conditions change.

This concept raises some difficult questions about the importance of biotic diversity because it implies that species within a functional group are equivalent or 'redundant' in their impact on ecosystem processes and that ecosystems could function equally well with fewer species.[23, 24] There are two extreme viewpoints on redundancy. The first holds that each species in an ecosystem plays a functional role, such that the removal of each species incrementally weakens the integrity of the system.[24] The second holds that a community is composed of a few functional groups, each with several ecologically equivalent species, such that species can be lost from the community with little effect on ecosystem processes, as long as each functional group is represented.[3, 12, 23, 24] In essence, the role of redundancy is to provide insurance. Because each species can tolerate only a limited range of climatic and biotic conditions, a change in environment beyond these conditions leads to a weakening of the species, or possible extinction, and a resultant negative effect on ecosystem processes.[3, 12, 23, 24] If there are several species in a functional group, some species in each group are likely to survive an extreme event and replace the gap in ecosystem process function left by the weakened or extinct species within the same functional group.

There may be some flaws in the redundancy or functional group theory. Solbrig states "The higher the diversity of an ecosystem, the more dependent the species are on the existence of diversity. In other words the higher the diversity, the narrower the ecological niche of each species".[16] If this is so, diversity is a consequence of habitat complexity, biological complexity, energy and nutrient availability, and time. It does not follow that diversity is essential for resilience, and high diversity may imply high risk because of extreme specialization. Of course, the truth in this particular debate most probably lies somewhere between these two extreme views.

Though the theory of functional groups remains a potentially valid concept, there have been few research projects that have successfully defined the functional groups for a given ecosystem. Plant species differ in the rates and pathways by which they process resources, in their effect on the physical environment, and in their interactions with other species.[2]

Nevertheless, ecologists have long been dissatisfied with the phylogenetic classification of plants by taxonomists because these classifications do not reflect the ecological functions of plants.[16] In theory, functional group definitions should be based on physiological, morphological, and/or phenological attributes of potential significance to a particular process. Nevertheless, ecologists remain a long way from being able to predict how many and which species might be expendable for any function of a given ecosystem.[1]

Understory Removal

The primary focuses of this project were to add to the body of knowledge regarding the debate on the functional role of biodiversity by examining the effects of understory removal on ecosystem processes and to make relevant recommendations on development in the Highlands Plateau. Current trends in development on the Highlands Plateau often lead to the removal of significant portions of the understory. Thus, recent trends in development, coupled with the fact that there is not a single reference in any relevant land use planning document pertaining to the conservation of understory herbaceous plants, necessitated study of the functional role of the understory in ecosystem processes. If the mass ratio theory, which states that the extent to which a plant species affects ecosystem function can be predicted from its contribution to total plant biomass, proves to be true, then the relatively meager biomass contribution of the understory, compared to the standing woody biomass in a typical Southern Appalachian oak-hickory hardwood forest, would suggest that understory plays little, if any role in the function of ecosystem processes.[7, 8, 10] On the other hand, if understory herbaceous plants prove to be a significant part of the functional biodiversity, then ecosystem processes will be affected by their removal.

Experimental Design

Three 40-m x 20-m plot-pairs located at two elevations (six replicates of treatment and six paired controls, each a 15-m x 15-m nested measurement plot) in the Coweeta Basin were used as the test sites. In summer 1998, plots were permanently marked and vegetation was measured in each 15-m x 15-m plot. Percent cover of herbaceous species was estimated using the line-intercept method along four 15-m transects for each plot. Initial biomass was estimated by clipping all herbaceous and deciduous shrubs in six 1.0-m^2 quadrats in each plot. In mid-summer 1998 (after plot establishment and vegetation measurements), all herbaceous and deciduous shrub species were manually removed from the six treatment plots. Thereafter,

treatment plots were weeded twice during the growing season (in May and July) to maintain treatment integrity.

In December 1999, dendrometer bands were placed at diameter at breast height (dbh; 1.37-m from ground level) on all woody stems ≥ 10 cm dbh in each plot pair. Woody stems with a dbh of < 10 cm were measured to the nearest 0.1 cm at dbh using a standard diameter-calibrated tape measure. In cases when the tree diameter was in the general vicinity of 10 cm at dbh, a dendrometer band was used to measure the diameter, as well as a diameter-calibrated tape measure. Woody stems with a dbh of < 1.0 cm were measured at 3 cm from the ground.

The intended duration of this project is 15 years, with this interim summary representing a third-year evaluation. Throughout the project duration, aboveground net primary productivity (ANPP) was calculated annually to estimate the rate of conversion of resources to biomass per unit area per unit time, along with carbon nitrogen ratios derived from litter samples. Net primary productivity is a complex measure of the net effects of both abiotic and biotic processes within an ecosystem and serves as a convenient, single index for comparing behaviors of different ecosystems.[14] ANPP has essentially two components: woody biomass and foliage biomass. Woody biomass was estimated annually using a set of species-specific diameter-based allometric equations derived for Southern Appalachian pine-hardwood forests.[5, 13] The diameters of each tree within the measurement plots were taken each December using either dendrometer bands (for woody stems ≥ 10 cm at dbh) or diameter tapes (for woody stems < 10 cm at dbh). In the case of having two different diameters (one derived from the dendrometer band and one from the tape measure), the data taken from the tape measure readings was used to calculate the woody biomass over the entire measurement plot due to the increased accuracy of these measurements compared to those of the dendrometer bands, which take two or three years to settle around the tree and provide accurate measurements. Foliage biomass was estimated using two methods: (1) species-specific, diameter-based allometric equations and (2) a system of litter collections using baskets of a set area evenly spread out within the measurement plot. The woody biomass and the foliage biomass component were then combined to produce annual total biomass values. The difference in the total biomass values each year represented the ANPP.

The other component of this project dealt with estimating the carbon and nitrogen content if the litter samples. First, litter samples from each collection basket were sorted into four categories (deciduous leaves, Hemlock or *Tsuga canadensis* leaves, *Rhododendron maximum*

leaves, and other – which included seeds, twigs and branches, flowers, and any other biotic material that does not fall into the three previous categories). After biomass measurements were made, each sample from each collection basket was processed to give the percent carbon and nitrogen in each sample. From these data, carbon and nitrogen content was calculated, along with carbon to nitrogen ratios, and tabulated and summarized by measurement plot.

Study Area

The study area is a rich, cove forest located within the Coweeta Basin, western North Carolina (35°02'N latitude, 83°27'W longitude). Schafale and Weakley described this rich, cove community as a mesic site, at moderate elevation (1,065 m to 1,220 m), with rich and generally deep soils, and primarily broad coves and lower slopes (low terrain shape index; 4,500-5,000).[15] Soils are described as Cullasaja-Tuckasegee complex, loamy-skeletal or coarse-loamy, mixed, mesic Typic Haplumbrepts.[17] Mean annual precipitation is 190 cm with most months receiving at least 10 cm.[17] Mean annual temperature is 13°C, and average temperatures are 6.7°C in the dormant season, and 18.5°C in the growing season.[17]

The forest has a dense canopy of mesophytic trees, including *Liriodendron tulipifera*, *Tilia americana*, *Acer saccharum*, *Aesculus octandra*, *Betula lenta*, *Magnolia acuminata*, *Prunus serotina*, *Tsuga canadensis*, *Fraxinus americana*, and *Fagus grandifolia*. The herb layer is lush and diverse. The cove has a minimal evergreen shrub (*Rhododendron maximum* and *Kalmia latifolia*) component and absence of known 'keystone' species (e.g. nitrogen fixers, calcium accumulators) in the herbaceous layer.

Results

Analysis of the effects of understory removal was divided into essentially two components: aboveground net primary productivity (ANPP) and carbon to nitrogen ratios.

Aboveground net primary productivity (g/m^2) was calculated using an allometric estimate for standing woody biomass (Table 4.3.1) and three different foliage estimates (biomass from allometry, total litter, and total minus other litter) (Table 4.3.2). For 1999, the ANPP calculations for the control plots were 759 ± 76, 696 ± 60, and 637 ± 63 g/m^2 respectively, while the ANPP values for the treatment plots were 811 ± 41, 679 ± 28, and 618 ± 27 g/m^2 respectively (Table 4.3.3). For 2000, the ANPP calculations for the control plots were 875 ± 45, 830 ± 31,

and 784 ± 28 g/m^2 respectively, while the ANPP calculations for treatment plots were 1041 ± 73, 923 ± 53, and 853 ± 57 g/m^2 respectively (Table 4.3.3). While only two years of data exist at this point, an increase in aboveground net primary productivity was seen from 1999 to 2000 in both the control and the treatment plots, with average difference in the control and treatment plots being 132 ± 9 g/m^2 and 236 ± 4 g/m^2, respectively. Most of this observed difference could be attributed to an increase in woody biomass, while foliage production in 2000 remained close to that in 1999. However, there is a difference in the allometric foliage estimates as compared to the physical litter collections. This difference can be attributed to the fact that not all of the branches of trees in the test site shed leaves within the measurement plots, making the litter collection foliage estimates less than the allometric foliage estimates. In 1999, treatment plots were on average 5 g/m^2 greater than the control plots, but in 2000 this figure rose to 51 g/m^2.

Carbon to nitrogen ratios in 1999 for control and treatment plots were 59 and 61 respectively, while in 2000 both control and treatment plot C:N ratios increased to 64 and 67 respectively (Table 4.3.4).

Conclusions

Given the fact that only three years of data have been collected on this 15-year research endeavor, well-supported conclusions cannot be drawn at this time. Nevertheless, it seems likely that understory herbaceous plants may fall in some important functional group within this oak-hickory hardwood forest ecosystem. It is important to recognize that the species in a functional group are not the same in all respects. If an ecosystem is stable (if its dynamics are such that all of its species are likely to persist), it is reasonable to expect that those functional groups that ensure its stability are likely to include a number of species.[2, 3, 23, 24] Within such plant functional groups, because of the continuum of vegetation organization, there will be differentiation in species responses to environmental gradients. The overlapping responses allow the plant community as a whole to respond to changes in environmental factors. The compensatory behavior in the set of functionally equivalent species maintains the function performed by the group. The species are therefore the same with respect to the process that ensures stability, but different in terms of their individual responses to the environment. It seems inevitable that, throughout the wide spectrum of understory herbaceous plants, many would fall into some

crucial functional group, and thus have effects on the productivity of the trees and the long-term stability of the ecosystem.

If this prediction proves to be true, the ramifications for development are immense. Many current development and landscaping practices in the Highlands Plateau often lead to the destruction of the understory herbaceous layer and, therefore, a potential weakening of local ecosystem stability and a decrease in the function of ecosystem processes. Furthermore, the landscaping replacements for the removed understory often include a variety of exotic plants that are typically not effective substitutes for native plants with regard to ecosystem process function. Future development practices must consider implementing strategies that either minimize the amount of the understory removed in the initial development and landscaping processes, or that seek to adequately replace the damaged or removed understory with a variety of native plants. While these recommendations may provide adequate means of conserving the understory herbaceous layer for the time being, it is still important to further the general understanding of the functional role of the understory in the various ecosystems within the Highlands Plateau.

The first step in gaining a further understanding of the precise functional role of biodiversity in these ecosystems is to establish the important functional types of organisms.[12, 23, 24] In other words, it is necessary to determine which biological and functional variables are pertinent to ecosystem persistence, in effect reducing the complexity of the system by describing the essential structure (form) of the ecosystem and then the critical processes (functions) that shape and maintain it.[23, 24] In the case of this experiment, plants are categorized in essentially two groups: tress and herbaceous understory plants. These classifications do not represent functional groups in themselves. However, the data collected from the above recommendations, in conjunction with the finalized results of this experiment, could serve to holistically describe the role of the understory in ecosystem processes, function, and stability.

Recommendations

With regards to this particular project, it is imperative that the data collection process be continued for the remainder of the 15-year duration. Furthermore, the process of data collection needs to be refined and improved upon. It is crucial that accurate and consistent measurements be taken for the diameter at breast height. In many cases, due to irregularities in the data collection, diameters decreased by up to 0.5 cm each year. While these errors may seem small,

when extrapolated into woody biomass data, they have the potential to significantly affect both the wood and the total aboveground net primary production values. Some of these errors can be attributed to dendrometer bands settling into the wood over the first two or three years and variations in the bark layer due to exfoliation or damage. However, in the case many of the flawed diameter-calibrated tape measure readings, it is simply inconsistency in the data collection process that has led to these errors. Over time, the trends in aboveground net primary productivity will be more apparent, and appropriate recommendations for development and zoning policy will follow. It is crucial, however, to keep the Highlands Biological Station and the Highlands capstone internships in connection with this project, because they will serve as the liaison between the Coweeta Hydrologic Lab and the relevant policy-making bodies of the town of Highlands and Macon County.

In the meantime, given our inadequate understanding and knowledge of how many and which kinds of species occur in an ecosystem, the best way to approach the problem of conserving them all is to ensure that the system continues to have the same overall structure (in the case of terrestrial ecosystems, the vegetation and three-dimensional spatial distribution of biomass, both live and dead) and function (the level of primary productivity; rates and pathways of nutrient cycling, and the sizes of available and unavailable nutrient pools; the trophic pattern and dynamics, including kinds and levels of herbivory and predation; the pathways and efficiency of water use).[23, 24] Underpinning this view is a central tenet of biology and ecology: the relationship between form and function. A change in one leads inexorably to adjustments and changes in the other. This philosophical approach to conservation endorses none of the current theories on functional biodiversity, but rather approaches the management of land in a practical manner that will likely protect the fundamental nature of the landscape.

The loss of species and ecosystems is proceeding faster than research aimed at identifying priorities. The response to this by most conservationists is to fight for as much land for conservation as possible and to worry about management later. This confrontationist approach, aimed at securing fragmented conservation reserves, is less likely in the long term to achieve the overarching conservation goal of maintaining species diversity than one involving a range of resource-use strategies covering whole regions. It is simply not possible to conserve all species in a region by means of reserves. Conservation has to be achieved outside of reserves,

with a range of uses from reserves, through various forms of multiple-use with conservation easements, to full-scale use such as industry, agriculture, and mining.[6, 7, 8, 24]

Conservation efforts in the Highlands Plateau have made great strides in the last decade in acquiring ecologically delicate or critical tracts of land. For instance, organizations like the Highlands Land Trust seek to acquire ecologically important tracts of land and to procure conservation easements on private land. Nevertheless, it is the duty of both the town of Highlands and the Macon County board of commissioners to seek to direct development in residential, commercial, and industrial areas in a way such that the water and land resources of the Highlands Plateau are protected and conserved for years to come. As mentioned before, it is not only the pristine tracts of land that are important to protect, it is also the wildlife migration corridors, riparian areas, and ecosystems in various succesional stages that occur in less pristine areas that have already been developed. Potential means of fostering change include, but are not limited to, amendments to the Zoning Ordinance of 1977, the Land Use Plan of 1989, and the recently discussed Sedimentation Ordinance, reemphasizing the protection of ecologically critical areas such as those mentioned above through well-defined and rigorously enforced regulations. Public education regarding the economic and environmental benefits of land conservation easements could also aid in furthering the conservation of a wide range of ecosystems in various development regions. Fortunately, development on the Highlands Plateau remains relatively sparse compared to many towns, and there is time to develop a system in which the natural land and water resources can be conserved for generations to come.

Table 4.3.1: Allometric equations to estimate annual wood and foliage biomass (g m^{-2})

Common Tree Species	Wood Biomass	Foliage Biomass
Acer rubrum	(Log^{-1}(Log(D)*2.591-1.096)*1.003	(Log^{-1}(Log(D)*1.778 - 1.620)*1.052
Acer pensylvanicum	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Aesculus octandra	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Betula allegheniensis	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Betula lenta	(Log^{-1}(Log(D)*2.728-1.254)*1.016	(Log^{-1}(Log(D)*2.628 – 3.086)*1.041
Castanea dentata	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Carya species	(Log^{-1}(Log(D)*2.773-1.349)*1.005	(Log^{-1}(Log(D)*2.356 – 2.595)*1.217
Cornus florida	(Log^{-1}(Log(D)*2.760-1.384)*1.008	(Log^{-1}(Log(D)*2.048 – 2.160)*1.157
Fraxinus americana	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Hamamelis virginica	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Liriodendron tulipifera	(Log^{-1}(Log(D)*2.646-1.258)*1.008	(Log^{-1}(Log(D)*1.981 – 2.192)*1.080
Magnolia acuminata	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Miscellaneous hardwoods	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Nyssa sylvatica	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Quercus prinus	(Log^{-1}(Log(D)*2.926-1.619)*1.013	(Log^{-1}(Log(D)*2.214 – 2.323)*1.142
Quercus rubra	(Log^{-1}(Log(D)*2.651-1.279)*1.011	(Log^{-1}(Log(D)*2.326 – 2.514)*1.097
Rhododendron maximum	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Robinia pseudoacacia	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Tilia americana	(Log^{-1}(Log(D)*2.681-1.281)*1.021	(Log^{-1}(Log(D)*2.022 – 2.122)*1.158
Tsuga canadensis	(Log^{-1}(Log(D)*2.3421-1.0891) + (Log^{-1}(Log(D)*2.0805-1.0440)	(Log^{-1}(Log(D)*1.3954 – 0.9472)

D = diameter in cm at breast height

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The Effects of Land-Use Change on the Biodiversity of the Highlands Plateau:

A Carolina Environmental Program Report

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