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The Dynamic Nature of the Herbaceous Layer
Synthesis and Future Directions for Research

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Like many other plant ecologists of the past several generations, we have long been impressed and influenced by the work and writings of Henry Chandler Cowles, particularly his turn-of-the-twentieth-century work on the vegetation of the Indiana dunes. With his well-known, succinct description of succession as "a variable approaching a variable, not a constant" (Cowles 1901, p. 81), he articulated perhaps more clearly than did any other ecologist the dynamic nature of plant communities in general. We have adopted such a view in this book, attempting to highlight the spatially and temporally dynamic nature of the herbaceous layer of forests.

One of the reasons for conveying the story of the term *step-overs* as a collective synonym for *herbaceous layer* (chapter 1, this volume) was to emphasize the low regard forest managers commonly and traditionally have had for the lower vascular strata of forests. In this final chapter, we would like to bring back into focus several of the various conclusions brought out in previous chapters to demonstrate the misguided nature of such a view.

Certainly, one of the consequences of ignoring the ecological significance of herb layer species is their demise, particularly as a result of land-use practices. Although it is clear that, relative to shrub, hardwood, and conifer species, herbaceous species have the highest rates of natural extinction (Levin and Levin 2001; chapter 1, this volume), it is less clear what the specific effects of land-use practice are on herb layer biodiversity. The debate concerning the effects of forest harvesting practices on species diversity continues (Noble and Dirzo 1997; Reich et al. 2001) and has been presented in several forms throughout this book (chapters 5, 6, 10, 13, this volume). This is an area worthy of much more intensive research. In this concluding chapter we

emphasize this need, along with other areas as future directions for herb layer research.

In addition to attempting to convey new knowledge regarding the ecology of the herbaceous layer of eastern North American forests, a major impetus behind this book was to bring together in a single volume, to the extent possible, what is known of herb layer ecology. Thus, we begin this chapter with a brief synthesis of the major points brought out in each chapter. Rather than simply providing summaries on a chapter-by-chapter basis, we use the parts of the book, namely, "The Environment of the Herbaceous Layer" (part I), "Population Dynamics of the Herbaceous Layer" (part II), "Community Dynamics of the Herbaceous Layer Across Spatial and Temporal Scales" (part III), and "Community Dynamics of the Herbaceous Layer and the Role of Disturbance" (part IV) as a basis for the synthesis.

Synthesis

Research on the forest herbaceous layer has increased dramatically in the past several decades. This increase has been as timely as it has been essential, given the naturally high diversity of the herb layer and the ongoing concern over loss of biodiversity. Indeed, this work has done much to increase our understanding of functional roles of herb species in forest ecosystems.

Plant ecologists with an interest in the ecology of the herb layer should expect to find a wide variety of synonyms for this vegetation stratum in the literature. Vegetation scientists of North America tend to use *herbaceous/herb layer* more than other terms, whereas those of Europe tend to use *ground vegetation* more often. Rather than calling for strict uniformity in use of terminology, we use this opportunity to advise researchers what to expect among published studies, particularly when carrying out literature searches.

Similarly, the literature contains numerous definitions of the herb layer, reflecting the considerable variation in vegetation structure and composition among forest types. Most definitions of the herbaceous layer focus on its physical aspects, especially height, rather than on growth form. Although we offered a commonly used definition of the herb layer as the forest stratum composed of all vascular species that are ≤ 1 m in height, the maximum height limit and exclusion/inclusion of nonvascular plant species varies substantially in the literature, with most height limits generally falling between 0.5 and 1.5 m.

Once again, we do not call for a uniform definition of the herb layer. Vegetation scientists should have the freedom of adapting their definitions in ways that are appropriate for the particular forest type being studied. Because the literature contains several studies that do not provide a clear definition of the herb layer, we ask that researchers state explicitly their working definition of the herb layer and base their definition on the biological and physical structure of the forest system.

We presented a simple conceptual framework for the forest herbaceous layer, comprising two functional groups: resident species and transient species. *Resident species* are those with life-history characteristics that confine them to maximum above-ground heights of no more than about 1.5 m. *Transient species* are those with the potential to develop and emerge into higher strata, and thus their existence in the herb layer is temporary, or transient. Juveniles of overstory species compete as transient species with resident species and either pass through this layer or die.

Thus, as a stratum of forest vegetation, the herb layer is the intimate spatial and temporal coincidence of resident and transient species—two otherwise disparate plant groups. In addition to the more obvious differences between them in growth habit and form, they differ in the factors that determine their distribution, patterns of reproduction, and respective mechanisms of seed dispersal. Whereas wind and vertebrate herbivores are predominant mechanisms for transient species, invertebrates are predominant dispersal vectors for resident species (especially myrmecochory, seed dispersal by ants). Such differences between resident and transient species in the herbaceous layer of forest ecosystems create a forest stratum with impressive spatial and temporal variability.

The Environment of the Herbaceous Layer

The microenvironment of the forest floor, the one that most closely influences plants of the herbaceous layer, provides stark contrast to that of an open field or that above the forest canopy. Forest overstory species alter the quality and/or quantity of virtually all aspects of the environment that are essential to the survivorship and growth of herb layer species. Here we focus primarily on nutrient and light availability.

Foliar concentrations of essential nutrients are generally much higher in herbaceous species than in woody overstory species, with spring ephemeral herbs having particularly high foliar concentrations of nitrogen, emphasizing yet another important contrast between resident and transient species of the herb layer (chapter 2, this volume). Surprisingly, foliar nutrient concentrations exhibit little variation within herb species occupying contrasting forested sites, possibly the result of shifting carbon sinks (i.e., whereas enhanced foliar growth would occur on nutrient-rich sites, increased mycorrhizal support would occur on nutrient-poor sites). There is evidence that herbaceous species are capable of rapid uptake and temporary storage of nutrients during periods of high nutrient availability; this is followed by retranslocation of these nutrients to support growth during periods of active biomass accumulation. Therefore, although herbaceous species do not exhibit luxury uptake of nutrients in the more traditional sense (i.e., as evidenced in intersite variation), they do exhibit seasonal patterns of luxury uptake supporting subsequent growth during periods of limited nutrient availability (chapter 2, this volume).

Clearly, the most spatially and temporally variable component of the environment of the forest floor is light availability. The light environment to which herb layer species are exposed varies at many levels of scale over space and through time. Accordingly, we refer to this environment as a *dynamic mosaic*, for light penetrates the forest canopy to reach the forest floor in a mosaic of discrete patches of varying size (i.e., sunflecks), the size and distribution of which vary at time scales from the diurnal to the seasonal. Time-lapse photography would reveal the constant dance of these sunflecks across the forest floor.

The presence of herbs in the understory of temperate deciduous forests depends greatly on their ability to grow in this dynamic mosaic light environment. In turn, variations in irradiance can influence other microclimatic factors, including temperature, relative humidity, and water availability. Adaptations to the dynamic nature of this environment are expressed physiologically and morphologically at multiple scales—from subcellular to leaf to whole plant (chapter 3, this volume).

There is a selective advantage for herb species that are physiologically active during the warmer portions of the year when temperatures are more favorable for photosynthesis and nutrient uptake. Other selective advantages among forest herbs include adaptations to increase light absorption in the forest understory, such as a well-developed spongy mesophyll to scatter light, reflective lower leaf surface to direct light back into the leaf, and adaxial surface cells that are concavely shaped to direct light toward cells containing chloroplasts (chapter 3, this volume).

Despite the fact that the importance of nutrients in influencing plant growth and survivorship often is considered independent of that of light, the two factors exert their influences simultaneously and synergistically. Thus, although the nutrient environment of the herbaceous layer of deciduous forests may be relatively rich, the light environment may affect herbaceous species' ability to exploit available nutrients (chapter 4, this volume). Severe light limitation may decrease demand for nutrients because nutrient uptake may be limited by accumulation of biomass by individual plants and their specific nutrient saturation points. Efficiency of nutrient resorption may also decrease in herb layer plants in an environment of nutrient availability that is high relative to demand.

Nutrient availability may mediate interactions between herbaceous species and organisms outside the plant kingdom. Mycorrhizal associations are more common when nutrients are limited and may indirectly mediate water stress for some species, although such associations have a high carbon cost to the host plant. Nutrients may also increase susceptibility of herbaceous species to invertebrate or vertebrate herbivores. Finally, natural or anthropogenically altered nutrient environments may shift physiological responses and community patterns in such a way that nutrients reside in the herbaceous layer for shorter periods of time and possibly become more susceptible to being leached from forest ecosystems (chapter 4, this volume).

Population Dynamics of the Herbaceous Layer

An appreciation of the highly variable nature of the environment in which species of the herbaceous layer have evolved is essential to understand the complexity of life-history strategies that governs population dynamics of herb layer species. This is particularly pronounced for forest herbs and their light environment. The distinct seasonality of the light environment has resulted in the evolution of diverse phenological patterns among herb species—spring ephemerals, summer greens, wintergreens, evergreens, heteroptics, and parasitic and saprophytic plants. In addition to their obvious contrasts in temporal variation in growth characteristics, these phenological groups exhibit contrasting reproductive modes.

Because many forest herbs are cryptophytes, vegetative reproduction is commonly considered the predominant reproduction mode for forest herbs. Sexual reproduction, however, plays a major role in the persistence of these species, many, if not most, of which are relatively long lived (e.g., 15–25 years). Still, it is difficult to generalize about breeding biology and mating systems of forest herbs because current estimates of breeding systems are often inaccurate. Pollination is often insect mediated. Population spread can be limited by seed dispersal, with rates of spread often < 1 m per year and rarely > 10 m per year. Vegetative spread may equal or exceed spread by seed dispersal. The role of the seed bank for most taxa is unknown. Most species exhibit some type of seed dormancy (largely physiological or morphological) at dispersal, which can reduce the risk of extinction (chapter 5, this volume).

Numerous vascular taxa of the forests of eastern North America have been identified as endangered and threatened. Demographic studies have been conducted on only a limited number of species. In spite of the usefulness of matrix projection models, few have been used for herbs of forested eastern North America, especially rare taxa. Newer methods, including elasticity and sensitivity analysis and variance decomposition, are potentially useful for predicting population changes through time. The metapopulation approach that uses measures of site occupancy, recruitment, and extinction is potentially useful for community-wide surveys of species in declining habitats, but unfortunately it has seldom been used. Furthermore, adequate demographic data for transition matrices or metapopulation analyses are not widely available for many species.

Despite their importance, quantitative modeling of population sizes using metapopulation dynamics and population viability analysis (PVA) has been underutilized for forest herbs of eastern North America. Indeed, only nine herbaceous species that occur in forests of eastern North America have been used in notable PVA studies (chapter 5, this volume).

After 20 years, the questions originally posed in the seminal paper by Bierzychudek (1982a) are still relevant today and warrant further attention in the future (see section on "Future Research," this chapter): what factors

regulate population sizes of forest herbs? How stable are population sizes of forest herbs? How much site-to-site variation occurs in population behavior?

Community Dynamics of the Herbaceous Layer Across Spatial and Temporal Scales

Land-use practices and natural disturbances have created a complex patchwork within the landscape of eastern North America. Beginning at the time of the first European settlers, agriculture and logging throughout this region, once essentially covered with pristine forests, eliminated much of the primeval forest, resulting in limited coverage of what is often called *old-growth forest*. Although this term has been the subject of much debate, consensus is growing as to how to define old-growth forest. Unfortunately, the herbaceous layer is generally not included in these definitions, a serious omission considering the high species diversity of this stratum. Preservation or conservation efforts using functional groups, rather than individual species, within the herb layer should allow better standards to emerge for assessing old-growth status, ultimately assisting with land management decisions (chapter 6, this volume).

Likely because of the logistical demands of field sampling, studies based on one-time samples of the herb layer are prevalent in the literature. Unfortunately, this approach does not lead to an appreciation of the great temporal variability of forest understory communities. A large emphasis on the spring vernal herbs often occurs at the expense of studies of the flora throughout the rest of the growing season. Certainly, we must expand our observations beyond the level of the stand and single-year study to fully understand spatial and temporal patterns in the understory.

Current emphases on sustainable use for forest ecosystems have focused on management questions. In spite of this, old-growth forests will remain an important component in our understanding of the structure and function of forest ecosystems. These will serve as benchmark ecosystems in the heavily disturbed landscape of forests of eastern North America (chapter 6, this volume).

One characteristic of older forest stands, whether true old growth or mature secondary growth, is the high degree of spatial heterogeneity in microtopography (also called *microrelief*) that naturally results when overmature trees die and tip over, creating paired, contrasting conditions of mounds (the vertically displaced root system and associated soil) and pits (the space formerly occupied by the root system). This spatial heterogeneity in microrelief provides a means by which many species are maintained in the community (chapter 7, this volume). Those species with spatial distributions across multiple microsites have the advantage of being buffered against moderate to severe environmental fluctuations. Those species restricted to one microsite, however, suffer a greater variability in population size with environmental fluctuation and have a higher risk of local extinction. For these species, microtopographic heterogeneity may limit available space, placing such species at a disadvantage.

Given the role of spatial heterogeneity and long-term, on-going changes in land use in forest communities of eastern North America, the interaction of these environmental factors should be taken into account in any study of herb layer communities. It has been proposed that an intermediate level of heterogeneity will promote greater species richness in a community (chapter 7, this volume). Extreme microsites may shift the balance to restrict species composition, whereas lack of microsites may increase overall competition with greater species overlap, eliminating safe sites necessary for some species. It has also been suggested that the current level of heterogeneity in a given forest community is likely the result of past events that either minimize or maximize microsites (chapter 7, this volume). For example, plowing and intense compaction from overgrazing eliminate mounds and pits, and the resulting second-growth stand will have a much lower spatial heterogeneity for the understory. In contrast, mature second-growth stands on unplowed land retain microtopography from the original stand and experience new treefall mounds and pits formation with age, maintaining higher spatial heterogeneity. Because these confounding factors can influence community richness, stand age alone is likely a poor predictor of patterns of species richness through succession.

Mound and pit microtopography represents only one of several ways in which the forest overstory can directly and indirectly influence the herbaceous layer. Through competitive interactions, however, the herb layer can, in turn, influence the composition of the overstory. In addition, species of both strata respond to spatial and temporal shifts in a suite of environmental factors. These reciprocating effects and responses to environmental gradients can lead to a measurable spatial correlation of the occurrence of plant species between the overstory and the herb layer. When this condition develops, the strata are said to be *linked*. It has been suggested that such linkage arises from similarities among forest strata in the responses of their respective species to environmental gradients (chapter 8, this volume). These responses may change through secondary forest succession and thus may be a function of stand age.

Although the concept of linkage among vegetation strata of forest communities has been the subject of considerable debate among vegetation scientists in the past, it is gaining wider acceptance and exhibits great potential as a concept with a high degree of ecological importance and practical application. That is, it furthers our understanding of and appreciation for the complexities underlying the structure and function of forest ecosystems, e.g., responses to disturbance and mechanisms of secondary succession. In addition, it may be applied toward landscape-level investigations of forest cover types and remote sensing.

A particularly intense disturbance that severely disrupts overstory–herbaceous layer interactions is that involving clearing of forests for agricultural practices, the agricultural practices themselves, and abandonment of agricultural fields. The response of vegetation following this abandonment is called *old-field succession*. In the Piedmont of North Carolina, where old-field

succession has been studied in greatest detail, the sequence begins with a complex assemblage of herbaceous species and ends with pine and, finally, hardwood dominance. Patterns associated with this response are best understood as a consequence of individualistic responses of species related to their ability and opportunities to disperse to and compete at particular sites (chapter 9, this volume). Although a few of the individuals of woody plant species that will dominate late in succession may arrive early and simply outlive pioneers, virtually none of the herb species common in pine and hardwood stands is found in old fields initially after abandonment.

A significant proportion of the variability in herbaceous species composition of old fields is correlated with soil variables, regardless of successional stage. At the landscape scale, soil moisture conditions, a function of topography and proximity to streams, accounts for much of the variation. Soil chemistry is also highly correlated with herb species distributions and overall species richness. The correlation between soil site variables and species composition diminishes sharply among late-stage pine stands, a decline that has been suggested to be a consequence of changes in stand structure (e.g., creation of canopy gaps from increased pine mortality) that increase variability of the light environment (chapter 9, this volume).

Temporal change in species richness during old-field succession is dependent on spatial scale. At the spatial scale of a 0.1-ha sample, mean herbaceous species richness is remarkably similar (i.e., 50 species) among successional ages. However, when comparing among ages the total list of species encountered across the full range of environments, species richness appears to increase over time. The key difference among these ages is in the numbers of species occurring in only a few stands at relatively low abundance, coinciding with the prediction that low-abundance, stress-tolerant species should become more abundant in later stages of succession.

Although it is clear that changes in the relative availability of resources are important in explaining successional patterns, much effort to explain variability in the distribution of herbs on successional landscapes has focused on the importance of competitive interactions in the context of changes in resource availability. If such interactions were the only factors shaping temporal and spatial variability of herb species, we should expect high correlations between compositional variations and patterns of environmental variation. Although such correlations do explain significant amounts of variation in composition, often the majority of such variation remains unexplained. Other mechanisms are likely equally important, precluding the creation of a unified theory of change (chapter 9, this volume).

The combination of forest clearing and agricultural practices that ultimately leads to old-field succession represents an extremely intense form of disturbance. Forests of the boreal region (often called taiga) also experience intense, often frequent, disturbances of a very different nature—fire and forest management practices. It is not surprising that variability in disturbance regime influences the distribution of herbaceous layer species of boreal forests (chapter 10, this volume).

Whereas high fire frequencies favor the presence of ericaceous species and terricolous lichens, lower frequencies are associated with higher richness of herbs and shrubs species. Because boreal species have evolved to persist in a context of fire, their spatial distribution is closely linked to fire frequency. Thus, the apparent co-occurrence of overstory cover types and herb layer species may only reflect similar responses to a particular disturbance regime. Although the canopy cover can modify the abiotic conditions of a stand, thus affecting the composition of the understory, many understory species are not restricted to a specific canopy, but rather to specific abiotic conditions (chapter 10, this volume). Herbaceous layer diversity at the boreal landscape level is generally highest with intermediate frequency of fire, independent of cover and site type, supporting the intermediate disturbance hypothesis.

It is clear that herb layer species of boreal forests have developed different reproductive strategies to persist under particular fire regimes. It is not surprising, then, that patterns of herb layer richness and abundance will be directly affected by disturbance characteristics. Accordingly, when the predominant disturbance regime shifts from fire to forest harvesting, herb species are exposed to a very different disturbance regime for which they lack particular adaptive traits. Clearcutting does not necessarily have a direct negative impact on the diversity of vascular herb species; however, it does change the relationships among species in boreal communities and contributes to change in community composition. Clearcutting has been observed to greatly alter the successional processes under certain abiotic conditions. Herbaceous layer communities are not only part of the rich biodiversity of boreal forests, they can also play important roles in boreal forest dynamics (chapter 10, this volume).

Community Dynamics of the Herbaceous Layer and the Role of Disturbance

Although the study of community dynamics and response of the herbaceous layer to disturbance have long been popular and important avenues of inquiry, the appreciation of the importance of *novel species* (nonindigenous species) in the forests of eastern North America is more recent (chapter 12, this volume). The presence of novel species in eastern forests is increasingly being noted, and we have come to realize that temperate forests may be more susceptible to invasions of novel species than other types of communities. Indeed, different regions of eastern forests support different novel species, with species often emerging as invasive only in subsections of their range.

The impacts of novel species can be better understood when we categorize them by their degree of invasiveness rather than painting them all with a broad brush as invaders (e.g., capable of high impacts). Novel species may not be fundamentally different from indigenous species in terms of their ability to colonize. Although invaders of forest communities share traits of colonizers of successional communities, they must also be adapted to low light. In addition, some are either less susceptible or more resilient to herbivory, or

both, compared to native species. The ability to invade may be linked more closely with phenotypic plasticity than with a single trait.

Invaders are most likely to appear in forest habitats that have higher light availability, such as light gaps or along forest edges, and that are proximate to a seed source. Invasion susceptibility should increase in areas with higher degrees of anthropogenic disturbance, especially those close to populated areas. Using our categorization of disturbance severity as the degree of disruption of the overstory and understory/forest floor (chapter 13, this volume), we would anticipate greater invasions in environments where both understory and overstory disturbance is severe.

Novel species may be competitively superior to indigenous species and better able to respond to disturbance. In the long term, novel species can change the composition of the bank of potential colonizers, thereby reducing the ability of indigenous species to respond. The implication for management is that removal of novel species may lead to further invasions. Thus, novel species add another dimension to the process of community recovery following disturbance, as depicted in figure 13.1. The influence of novel species may result in a very different postdisturbance composition of the herbaceous layer. As a result, invasion by novel species may be not only an immediate response to disturbance, but also a chronic disturbance itself.

Past management of novel species has been based on the assumptions that novel species are undesirable and that novel species must have negative impacts on preserved forests. In reality, gains and losses of species over time in preserves is common. Management actions may be justified only where management goals are explicit, impacts of novel species clearly compromise management goals, and the impacts of management activities are known.

Identifying the nature of understory—overstory interactions is one of the keys to understanding herbaceous layer dynamics; indeed, it has been one of the main themes of this book. Again, using the terminology set forth in the opening chapter and summarized at the beginning of this chapter, transient species influence the microclimate and competitive relationships in the understory and control the composition and spatial distribution of understory plants. There may also be an element of passive linkage among understory and overstory canopy strata which results from similar responses of different strata to the physical environment (Chapter 8, this volume). Another important form of interaction is that resident species can exert control over the germination, survival, and growth of transient species. Indeed, the influence of herbaceous plants on tree seedlings can be highly selective (i.e., species-specific), with long-term consequences for the composition of tree species (chapter 11, this volume).

The microenvironment under the herbaceous layer is characterized by lower light, more litter (under some ferns and shrub species), and in some cases increased seed predation. These conditions decrease seed germination for some tree species, as well as decreasing seedling survival and reducing overall seedling density. Shifts in tree species composition occur under some herbaceous layer species, such as ferns and shrubs. Species-selective reduc-

tions in seedling growth changes the competitive relationships among the trees.

Different understory species alter the microenvironment below their canopies to varying degrees, depending on leaf morphology and area, clonal density, phenology, stature (height), litter quantity and quality, and belowground resource capture. The clonal growth habit of many understory species and the segregation of understory species in different microsites leads to spatial heterogeneity in the intensity of the selective filtering influence on tree seedlings. The understory mosaic, then, can result in the aggregation of seedlings of different tree species into patches. Once these distinct patches of transient species emerge from the herbaceous layer and become the overtopping canopy, they can be expected to have their own reciprocating influence on the herbaceous layer through their effects on forest structure and the forest floor microenvironment (fig. 13.1). Thus, extending the concept of the selective filter (chapter 11, this volume) to multiple canopy layers, we would expect the resident species of the herbaceous layer and the transient species to exert selective filtering effects on each other in turn as dominance shifts from one group of species to the other.

After canopy disturbance, understory plants may increase in cover, compensating at least partially for canopy opening below them. Other patterns of change in understory canopy density are also possible, including no change or a decrease in density, depending on the nature of the disturbance and other factors. For example, the major changes after gap formation are often in species abundance rather than species presence. Disturbance to the litter layer, however, can promote the establishment of new species. In the final analysis, the extent of the change in the filtering activity of the understory layer depends on the degree to which understory plants preempt, neutralize, and/or modify available resources.

Herbaceous layer dynamics in response to disturbance has been another main theme of this book. Novel species and the influence of the understory layer on tree seedlings are intimately tied to the process of disturbance dynamics. Disturbance severity, in terms of the degree of destruction of both the overstory and understory layers (including the litter and surface soil layers) exerts control over the response of the herbaceous layer, including the invasion of novel species and the selective filtering effect of the understory layer on tree seedlings (chapters 11 and 12, this volume). We have emphasized the importance of evaluating disturbance in terms of these two axes of severity in addition to disturbance frequency, size, and shape.

It is important to consider the reciprocal effects of the overstory and understory layers on each other, as noted above, in assessing herbaceous layer dynamics after disturbance. The predisturbance canopy structure and presence of a subcanopy of shade-tolerant tree or shrub species have important effects on herbaceous-layer response. At the same time, the selective filtering effect of the understory on tree seedlings leaves its mark over time on the composition and structure of the canopy above the herbaceous layer.

The life-history characteristics of species interact with disturbance char-

acteristics to determine herbaceous layer response. For example, whether the disturbance primarily affects the overstory canopy or the understory, along with the severity of those effects in each canopy layer, will control in situ survival, vegetative regeneration, regeneration from the seed bank, or regeneration from dispersed propagules. In addition to the direct effects of disturbance on the herbaceous layer, there are also indirect effects, such as herbivory on trees and shrubs, that influence the microenvironment for the understory. Most forms of agriculture constitute the extreme in disturbance severity for the herbaceous layer because of the outright destruction of preexisting plants and the removal of propagules of forest species. Forestry practices typically engender less dramatic changes in the herbaceous layer than do agricultural practices, although treatments that severely disturb both the canopy and understory (e.g., whole-tree harvesting with heavy mechanical site preparation) can greatly modify the herbaceous layer. Our knowledge of the long-term effects of forestry practices on the herbaceous layer is limited by the lack of long-term studies addressing forestry practices in isolation from other anthropogenic disturbances such as agriculture.

Although we tend to think of disturbances in terms of their initial effects only, it is important to consider the long-term effects of the disturbance on herbaceous-layer recovery. Our ultimate goal is to predict herbaceous-layer response over the long term to disturbances of both natural and anthropogenic sources and to apply this knowledge to the wise conservation and management of the forests of eastern North America.

Future Research

Before putting together this final synthesis, we asked chapter authors the following question: what do you see as important areas of future research for better understanding of the ecology of the herbaceous layer? As with the synthesis, we have organized these responses by the major sections of the book instead of organizing them by individual chapters. In contrast to the synthesis, however, we are presenting these areas for future research without additional narrative. Rather, we present them as separate, individual topics within the general sections of the book.

The Environment of the Herbaceous Layer

- Role of high potassium concentrations in physiology of herbaceous leaves, especially water relations.
- Phenological (seasonal) patterns of nutrient uptake in relation to external availability and internal demand.
- Role of herbaceous layer in altering throughfall chemistry via either additions of leached nutrients or removal of absorbed nutrients.
- Detailed analysis of the phenological patterns of nutrient absorption and

release by vernal herbs in comparison to the same patterns in the soil microbial community.
- Potential role of spring ephemerals in promoting nutrient loss by stimulating decomposition processes.
- Morphological, biochemical, and physiological processes involved in the response of herbs to the dynamic light environment of the deciduous forest understory.
- Water relations of understory herbs across the phenological strategies.
- Contribution of understory herbs to forest community-level carbon gain, production, and CO_2/H_2O exchange with the atmosphere.
- Influence of herbivory on light—nutrient interactions in herbaceous layer species.

Population Dynamics of the Herbaceous Layer

- Better understanding of the basic life-history characteristics of herbaceous layer species.
- Long-term demographic monitoring and quantifying difficult phases of the life cycle (e.g., dispersal and the seed bank) of rare taxa of concern, notably endangered and threatened species.
- Collection of data for analysis with and empirical tests of demographic models, including transition matrices and population projections, metapopulation dynamics, elasticity and loop analysis, and PVA.
- Analysis of the spatial structure of populations to allow scaling up from individual- and population-level foci to landscape-level inferences.
- Synthetic approaches to population biology that combine the development of theoretical, empirical, and experimental tests of models.
- Development of user-friendly computer software to apply such models.
- Metapopulation studies of herb layer populations of ecosystems controlled by large disturbances and submitted to fragmentation.
- Use of new genetic markers to more fully understand the genetic structure of herb layer populations.

Community Dynamics of the Herbaceous Layer Across Spatial and Temporal Scales

- Assessment of patterns of herbaceous layer diversity along chronosequences that include old growth.
- Determination of sampling methods and sample sizes required to encounter a greater percentage of the complete flora of the herbaceous layer, including observations beyond the level of the stand and single-year study, as well as long-term permanent plot studies arranged in a stratified fashion throughout the landscape.
- Improving understanding of the relationships between diversity and stability of natural ecosystems in the context of their invasibility by nonindigenous plant species.

- Testing the intermediate heterogeneity hypothesis, which suggests that an intermediate level of spatial heterogeneity in microtopography will promote greater species richness in an herb layer community.
- Testing the heterogeneity cycle hypothesis, which suggests that the current level of heterogeneity in a community is likely the result of past events that either create/enhance the number of microsites or destroy/obliterate microsites.
- Testing the linkage hypothesis, which states that linkage among forest strata arises from parallel responses of strata to similar environmental gradients, using more North American forests, including varying stand types, stand ages, land-use histories, and levels of β diversity.
- Assessment of the relative importance of historical effects versus interspecific competition among mature plants in explaining secondary succession.

Community Dynamics of the Herbaceous Layer and the Role of Disturbance

- Determination of effects of the understory on future forest composition and structure in the context of both predisturbance and postdisturbance conditions.
- Determination of functional guilds in the herb layer and how are these guilds modified by landscape configuration and historical disturbances.
- Elucidation of the mechanisms by which invaders of the herb layer overcome light limitation.
- Further study of herbaceous layer response to the principal types of natural and anthropogenic disturbances in eastern forests.
- Development of new methods of characterizing disturbance that can be used across all disturbance types.
- Long-term studies that address changes in herbaceous layer composition and structure in response to anthropogenic disturbances and along gradients of natural disturbance, including disturbance type and severity.
- Development of mechanistic models of herbaceous layer response to disturbance based on interaction of disturbance type/severity and life-history characteristics of the species.

Summary

It should be clear from this chapter that, to rephrase a well-known line in Alfred Lord Tennyson's *Ulysses* ("Tho' much is taken, much abides"), although much has been learned of the ecological dynamics of the herbaceous layer of forests of eastern North America, much remains to be learned. Our awareness of what lies ahead for future research in herb layer ecology remains in spite of the increasing amount of work that is being done. Some of this awareness, however, is also because of the work being done. That is,

just like in any field of scientific endeavor, new knowledge begets new questions.

A great deal of the impetus behind assembling this book was that we believed that the time had come to synthesize our understanding of the basic ecology of the herb layer. One of the implied themes of this book, however, has been the conservation ecology of the herb layer. In this regard, the book clearly enters the realm of applied ecology. Indeed, both basic and applied approaches are relevant to studying and understanding the spatial and temporal dynamics of the herbaceous layer, particularly as they relate to forests of eastern North America.

Conservation ecology is emerging as a prominent ecological subdiscipline. Although it has been broadly defined, it generally focuses on the nature and extent of deviations of anthropogenically altered ecosystems from minimally altered states. As we learned in chapter 6, examples of such minimally altered states (i.e., old-growth stands) are all too infrequent in eastern North America. We see several lessons emerging from this observation.

First, existing old-growth stands of the region must be preserved, both as ecological legacies and as benchmarks for conservation ecologists, especially for studies of the herbaceous layer. Accordingly, we call for the preservation of such areas. Second, the remainder of forest stands of eastern North America represents a variety of responses to a variety of intensities and types of disturbances over many spatial and temporal scales. In short, if there were ever a case of a variable approaching a variable, this would be it. Thus, we remind researchers, particularly those working on the landscape scale, to bear this in mind when conducting their studies.

The highly disturbed nature of eastern North American forests will not change in the future. Rather, projected increases in human populations in the region will place an even greater demand on forested areas. The authors who have contributed to this book have provided ample evidence that responsible use of our forest resources is not necessarily inconsistent with protection of the herbaceous layer. We embrace the concept of sustainable use of natural resources, such as forests, that, by definition, allows continued use of those resources by future generations. Among those uses would be an appreciation for those forests' diminutive vegetation stratum.