

PART FIVE

SYNTHESIS

22 The Dynamic Nature of the Herbaceous Layer

A Brief Synthesis

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It is likely that the lion's share of plant ecologists over the past ~ 100 years have been inspired by the work and writings of Henry Chandler Cowles, particularly his extensive fin-de-siècle opus on the vegetation of the Indiana Dunes. His succinct and often-quoted description of succession as “a variable approaching a variable, not a constant” (Cowles 1901, 81) defined the dynamic nature of plant communities more clearly than any other ecologist before him or since. Indeed, his view has been adopted for this book to highlight the spatially and temporally dynamic nature of the herbaceous layer of forests.

One of the reasons I related my experience as a young graduate student at Duke University with the term “step-overs” as a collective synonym for the herbaceous layer (chapter 1, this volume) was to emphasize the low regard that those in the forestry profession have commonly and traditionally had for the lower vascular strata of forests. In this final chapter, I would like to bring back into focus several of the various conclusions brought out in previous chapters to demonstrate how unfortunate such a view is.

As is becoming increasingly apparent, the herb layer is an integral component in maintaining the structure and function of forest ecosystems (Gilliam 2007). Just as apparent, however, is that one of the consequences of ignoring the ecological significance of herb layer species is their demise, particularly as a result of land-use practices that fail to take into account the essential role these species play in forests. 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 7, 8, 13, and 18, this volume). This is

an area worthy of much more intensive research, and it is particularly encouraging to note that research focusing on disturbance ecology of the herb layer has been increasing in recent decades (fig. 13.1, chapter 13, this volume).

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, I conclude this book with a brief synthesis of the major points brought out in the preceding chapters. As with the first edition (Gilliam and Roberts 2003), this will be done using the sections of the book, rather than simply providing summaries chapter by chapter, as a basis for the synthesis: “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).

SYNTHESIS

Research on the forest herbaceous layer has increased dramatically in the past several decades (fig. 1.2, chapter 1, and fig. 13.1, chapter 13, this volume). 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 being a call for strict uniformity in use of terminology, this is an 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 a commonly used definition of the herb layer is 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 vary substantially in the literature, with most height limits generally falling between 0.5 and 1.5 m.

Once again, this is not a call for a uniform definition of the herb layer. Vegetation scientists should have the freedom to adapt 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, researchers should explicitly state their working definition of the herb layer and base such definition on the biological and physical structure of the forest system.

I 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 aboveground 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 in 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. The focus here is 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 over time. Accordingly, this environment can be envisioned 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 of 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). Among the many challenges in understanding the complex ecophysiology of forest herb species are the various changes that are occurring, and will continue to occur, in the context of global change (chapter 3, this volume).

Despite the fact that the importance of nutrients in influencing plant growth and survivorship is often considered independent of the importance 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.

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 govern 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, winter-greens, 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 its 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 6, this volume).

After 30 years, the questions originally posed in the seminal paper by Bierzychudek (1982a) are still relevant today and warrant further attention in the future: 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 7, 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, observations should be expanded 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 7, 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 8, 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 8, 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 8, this volume). Because these confounding factors can influence community richness, stand age alone is likely a poor predictor of patterns of species richness through succession.

Pit and mound 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 9, 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.

The herbaceous layer of southeastern forests and woodlands not only often displays impressive species richness, but also does so in ways that vary greatly with the scale of observation (chapter 10, this volume). Among the dominant processes driving patterns of species diversity in this region are cation availability, natural and anthropogenic disturbance, mass effects, and the relative size of the species pool. The various processes that govern community assembly function at different spatial scales, with biotic interactions and local environmental filtering operating at finer spatial scales,

and dispersal and species pool size becoming more important at broader spatial scales (chapter 10, this volume).

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 11, 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, account 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 11, this volume).

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, high correlations between compositional variations and patterns of environmental variation should be expected. 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 11, 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 12, this volume).

Whereas high fire frequencies favor the presence of ericaceous species and terricolous lichens, lower frequencies are associated with higher richness of herb and shrub 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 12, 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 12, this volume).

Community Dynamics of the Herbaceous Layer and the Role of Disturbance

Although disturbances are often regarded only in terms of their initial effects, 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 from both natural and anthropogenic sources and to apply this knowledge to the wise conservation and management of the forests of eastern North America (chapter 13, this volume). Disturbance-mediated changes in environmental conditions often make forests more habitable for invasive species, which 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 the categorization of disturbance severity as the degree of disruption of the overstory and understory/forest floor (chapter 13, this volume), greater invasions should occur in environments where both understory and overstory disturbance is severe.

The life history characteristics of species interact with disturbance characteristics 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 (chapter 14, this volume). In addition to the direct effects of disturbance on the herbaceous layer, there are also indirect effects, like herbivory on trees and shrubs, that influence the micro-environment 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 the 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 15, this volume). The presence of novel species in eastern forests is increasingly being noted, and it is apparent 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 categorized 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.

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. The influence of novel species may result in a very different post-disturbance 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 (chapter 15, this volume).

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 that results from similar responses of different strata to the physical environment (chapter 9, this volume). Another important form of interaction occurs when resident species 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 14, 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 reductions in seedling growth alter the competitive relationships among the trees (chapter 14, this volume).

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 lead 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 micro-environment (fig. 13.1, chapter 13, this volume). Thus, extending the concept of the selective filter (chapter 14, this volume) to multiple canopy layers, it is likely that the resident species of the herbaceous layer and the transient species do exert selective filtering effects on each other in turn as dominance shifts from one group of species to the other.

Another disturbance that threatens the herbaceous layer of forests is overconsumption of foliar and woody material (overbrowsing) by vertebrate herbivores. In contrast to western North American forests, where this commonly results from introduced herbivores, in eastern North American forests, the problem is largely a function of overpopulation of native species, such as white-tailed deer, caused by the removal of top carnivores, such as wolves and mountain lions (chapter 16, this volume). Evidence clearly demonstrates that the diversity of herbaceous communities in forests throughout eastern North America has declined substantially in areas with high densities of white-tailed deer (chapters 16 and 17, this volume), with some browsing-sensitive species (e.g., *Trillium* spp.) being used as indicators of browsing intensity. In extreme cases, many of which exist in northeastern United States, overbrowsing by deer can severely retard forest regeneration following intense canopy-removing disturbances, including windthrow and timber harvesting (chapter 17, this volume).

Timber harvesting and other management practices can represent both acute and legacy forms of disturbance. Although there is evidence that harvesting of second growth can allow rapid recovery of forest herb communities (chapter 13, this volume), recent work has demonstrated that recovery to “pristine” (old-growth) pre-harvest levels requires more time than typical harvest rotations allow (chapter 18, this volume). A likely more profound legacy effect than harvesting is agriculture. Much of the currently forested landscape of eastern North America arose from conversion of primal forest to agriculture, followed by forest regrowth after abandonment of farms (chapters 11 and 19, this volume). Such historical events have created long-lived influences on the species composition and diversity of the herbaceous layer. Herb layer communities of forests that have recovered following agricultural abandonment are typically depleted in native species, compared to non-cleared forests (chapter 19, this volume).

Total atmospheric deposition of N to terrestrial ecosystems is predicted to increase greatly as a result of a variety of human activities. Recent research has shown that such increases in N loading to forests may alter forest species composition and species diversity of the herbaceous layer. Although sensitivity to N deposition varies widely among sites, declines in species richness often follow several stages: (a) initial increases in herb layer cover; (b) decreases in species richness, caused by the loss of numerous species that are efficient under low-N conditions; (c) decreases in species evenness, caused by the increasing dominance of relatively few species that require high N availability; and (d) loss of forest biodiversity as a result of these decreases in species

richness and evenness. The N homogeneity hypothesis predicts that as excess N inputs reduce the naturally high spatial heterogeneity in soil, N availability (i.e., patchiness) that helps to maintain the species diversity of the herbaceous layer of affected forests will decline (chapter 20, this volume).

Current increases in concentrations of CO₂ can have direct influences on plant ecophysiology, eliciting novel responses among herb layer species (chapter 3, this volume). Simultaneously, increasing CO₂ contributes greatly to global change in general and global warming in particular. The current distributions of herb layer species, especially those considered range-restricted endemic species, may still be profoundly affected by historical patterns of climate change. Many of such endemic species would be predicted to be at increased risk from modern climate change due to small range size, compounded by long-term, broad-scale dispersal limitation (chapter 21, this volume). Thus, current patterns of climate change are likely to significantly threaten forest herb biodiversity (chapter 21, this volume).

SUMMARY

It should be clear from this chapter that, to paraphrase a well-known line from Alfred Lord Tennyson's "Ulysses" ("Tho' much is taken, much abides"), although much has been learned about the ecological dynamics of the herbaceous layer in 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 the first edition of this book (Gilliam and Roberts 2003) was the belief that the time had come to synthesize our understanding of the basic ecology of the herb layer. A theme that seemed to emerge from that initial compilation, however, was the conservation ecology of the herb layer. In this regard, the book entered the realm of applied ecology. Certainly, given the spatial coincidence of high population densities with the distribution of eastern North American forests, both basic and applied approaches are relevant and essential to studying and understanding the spatial and temporal dynamics of the herbaceous layer. Conservation ecology is now firmly established 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. Among the many challenges facing conservation ecologists is that, as discussed in chapter 7, examples of such minimally altered states (i.e., old-growth stands) are all too infrequent in eastern North America.

Thus, it is not surprising that this second edition further delves into the disturbance ecology of the herb layer of forest ecosystems. The final observations of the first edition merit repetition here. 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; this is a call for the preservation of such areas. Second, the remaining forest stands of eastern North America represent a variety of responses to myriad types and intensities 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, researchers, particularly those working on the landscape scale, should 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. It is imperative that all embrace the concept of sustainable use of natural resources, such as forests, that will allow continued use of those resources by future generations. Forest ecosystems have indeed always been essential to the survival, success, and well-being of human civilization. At the foundation of these forests is the diminutive herbaceous layer—the forest between the trees.