The Whole Story of the Herbaceous Understory

The herbaceous understory is the lowest, ground-level layer of plants and fungi in the forest. What is its role and importance in the main ecological processes occurring in forest ecosystems?

Herbaceous understory in an oak-hornbeam forest in early spring, Babki Forest District

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Although trees are important in terms of shaping the physiognomy of forest ecosystems, they are not the only layer of the forest that is significant to its functioning. Far below the canopy, shorter plants create their own layer in the forest, known as the herbaceous understory. It may be variously defined by its height and by the dominant plants, but it is usually conceived of as a layer made up of all plants that are under 1 meter in height (including fungi and lichens). This definition includes species that are always present in herbaceous understory, as well as juvenile trees, which in later stages of life can move up to higher layers of the forest. Various other notions of herbaceous understory differ in terms of the height limit adopted, as well as whether mosses and woody plants are included.

The importance of herbaceous understory in forest ecosystems is significant, although often underestimated and overlooked. This is a habitat not only for plants, mushrooms or lichens, but also for animals. Ecological studies usually concern four aspects of its impact on the forest ecosystem, i.e. the contribution of herbaceous understory plants to the species richness in the forest, the impact of herbaceous understory on the composition of species in the forest stand and vice versa, the contribution of herbaceous understory in matter circulation and energy flow, and the ability of herbaceous understory plants to respond to natural and anthropogenic disturbances, including climate change.

Species richness in forests

In the professional literature, it is often stated that it is herbaceous understory plants that crucially determine the species richness and diversity in forests. However, this is rarely supported with specific figures. For example, F.S. Gilliam in the article "The ecological significance of the herbaceous layer in temperate forest ecosystems" (*BioScience* 2007, 57: 845–858) – summarizing studies on the species richness of forest stands and herbaceous understory plants in the same area, and on this basis calculating the share of the herbaceous understory in forest biodiversity (the ratio of the number of herbaceous understory plant species to the number of tree species found in a specific area) – reported that the figure averaged 5.7. It fluctuated between 2 and 10, which means that forevery tree species found in the forest there are about six herbaceous understory species. In other words, herbaceous understory constitutes more than 80% of the species richness of forest vegetation. The richness of plant species in various forest plant communities is strongly diversified, as evidenced by the data collected during phytosociological studies (those that describe and classify plant communities). For example, in Poland (in average areas of vegetation) we can find about 20 species of vascular plants, mosses and ground lichens at the forest floor in pine forest communities, about 30–50 species in oak-hornbeam and riparian forests (i.e. fertile deciduous forests), and about 50–60 species or more in thermophilous oak woods and alders. Contemporary extinction of forest species is affecting herbaceous understory plants to a large extent, while the protection of forest ecosystems also protects herbaceous understory plants and vice versa. In addition, herbaceous understory plant species, having specific, often narrow ecological requirements, are used as indicators (indicator species) signaling certain

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habitat characteristics (defined as general climatic and soil conditions in the specific conditions of the geographical and topographic location), or the presence of specific disturbance factors.

Competing with trees

Herbaceous plants respond very dynamically to both small and larger disturbances (e.g. fires, windbreaks, mass insect invasions) in forest ecosystems. Juvenile trees, seedlings and thickets, must compete with them for above-ground and underground resources (space, water, light, macro- and microelements). Only winning this battle gives them a chance to grow and make it up to the canopy layer. There are various ways in which herbaceous understory species can stunt the growth of young (juvenile) trees. For example, studies of the competition between ferns and American bird cherry seedlings show that the former inhibit the growth of bird cherry mainly by restricting access to light. Winning this competition is crucial for survival and further development. Herbaceous plants take away nutrients from young trees, including nitrogen, phosphorus, and potassium. Herbaceous understory plants can also favor selected tree species, hindering the growth of other species. In summary, herbaceous understory affects all early life stages of the dominant trees in the stand, so the herbaceous understory has the potential to determine or at least affect the stand's species composition.

The species composition of the herbaceous understory can affect that of the stand and vice versa, which means there is a relationship between these forest layers, with changes in the spatial distribution of the species composition in one layer entailing changes in the other. To determine these relationships between forest layers we must conduct simultaneous studies of the species composition of all layers in the same area. This phenomenon has been described in detail for several types of forests. Interestingly, it was found that it occurs in mature forests, rather than young ones. This is most likely due to the varied responses of individual forest layers to the environmental factors in young stands. This response becomes increasingly more similar as the stand ages. Thus, in young stands, herbaceous understory plants are particularly "sensitive" to changes in the concentration of calcium, magnesium, and potassium ions in the soil solution, while the tree canopy layer is more "sensitive" to changes in phosphorus content. To exclude environmental factors from the above theory, we conducted common-garden studies in various single-species stands growing on a similar soil substrate in the area of the external spoil heap of the Bełchatów coal mine. Published studies clearly indicate the association of herbaceous species with the dominant species in the stand. Moreover, herbaceous understory species are more closely linked to the tree species than to abiotic conditions (inanimate elements of the environment). In addition, the dominant tree species in the stand not only influence the absence or occurrence of a given herbaceous plant species in the understory, but also the amount of biomass it produces.

Herbaceous understory beneath a pine stand, Niedźwiady Forest District

Ecological processes

The herbaceous plants of the understory layer are much more crucially involved in the main ecological processes occurring in forest ecosystems – that is in the production of biomass and its decomposition, or degradation – than it may seem. Herbaceous plants are of great importance in the cycles of circulation of elements in nature. This is due to their short lifespan, abundance of elements in the biomass, fast rate of decomposition, and continuously providing necromass (dead organic matter). Although the relatively small contribution of the herbaceous understory to the total plant biomass of forest ecosystems is striking (approximately 1–2% on average, up to 4%), its share in annual biomass production can reach up to 20%. In addition, despite the small contribution to overall necromass dropped on the forest floor, these plants mostly produce labile necromass, which decomposes in the first year after their death. Moreover, the inflow of litter from the herbaceous understory is continuous, and not nearly exclusively occurring in autumn, as in the case of trees. Herbaceous understory plants also differ from trees in terms of the quality of the falling litter, which is richer in some biogens

(e.g. nitrogen, phosphorus, potassium, magnesium). The plants of the herbaceous understory decompose much faster than the leaves of trees, and they usually need much less than a year to fully decompose. The exceptions are ferns and the woody plants of the understory layer. Our research on the rate of herbaceous plant biomass decomposition in a Central European oak-hornbeam forest indicates that the necromass of geophytes (herbaceous plants growing in deciduous forest herbaceous understory at the beginning of the growing season) literally "disappears" from the forest floor. The majority of their biomass consists of leaves. However, more research is required when it comes to "enormous" herbaceous plants dominating deciduous forest understory in the summer. The leaves of these plants also decompose very quickly; however, the stems, which are dominant in their biomass, are harder to decompose.

Spring geophytes are of particular ecological importance. The entire life cycle of this group of plants (growth, flowering, fruiting) occurs in early spring before the upper canopy tree leaves develop. These plants, according to the vernal dam hypothesis, create a barrier preventing nutrients from escaping into the deeper layers of soil at a time when the uptake of elements by trees is limited. Geophytes die when tree leaves develop, and then decompose within a few months. The elements collected by these plants in early spring return quickly to circulation later in the growing season when the demand for biogens (especially by trees) increases.

Response to disorder

Herbaceous plants, like forest ecosystems, are experiencing all kinds of disturbances today, both natural and anthropogenic. The former are caused by wind, fire or insects, the latter by human activity. Although not all of them do direct damage to herbaceous understory plants, they affect them by changing their living environment (e.g. lighting or temperature conditions). Disturbing factors also differ by magnitude or length of impact. All this, as well as the type of forest whose herbaceous understory we are studying, affects the response of understory plants to a specific factor and its changes. In the case of some local disturbances, such as tree felling, understory plants can return to their "normal" (pre-disturbance) state within 10 or 20 years. With large-scale and long-term disturbances, changes in the herbaceous layer can remain visible for decades, or even hundreds of years. This causes changes in the species composition (such as the number or types of species) of the forest herbaceous understory, spatial distribution of species, and may even lead to changes in the distribution of biomass of individual species for a very long time after the area ceases to be used for agricultural purposes. The worst possible outcome is the extinction of species in a given area, which may be temporary in the case of some disturbances, but irreversible in others. Further increase in atmospheric CO_2 concentration may result in changes in the growth rate of individual plant species, including herbaceous understory. In addition, there will be changes in the times of the year that are conducive to the growth of certain plant groups, such as increasing the optimal time for spring geophytes and intensifying the foraging of herbivores, which would be linked to changes in understory composition of individual forest types. Of course, it is difficult to predict the future of herbaceous understory in the face of climate change because the consequences of these changes are multifaceted. What is certain is what we can observe today, which is the transformation of forests due to the dying out of tree species that dominate the landscape, caused by global climate change and its consequences, including temperature rise and droughts.

Human activity causes disturbances in the environment with varying degrees of impact. The consequences may include drastic changes to the vegetation, including forests, and the disappearance of certain plant species, not only ones that are highly specialized. Changes in the species composition of stands observed in Europe and Poland, including the dying out of spruce or pine trees, and spontaneous appearance (or deliberate introduction) of deciduous tree species, will also go hand-in-hand with changes to the herbaceous understory. Such changes may offer a great opportunity for many understory species, while for many others they may pose a serious threat.

Herbaceous understory beneath a spruce stand in the high alpine zone, Szklarska Poręba Forest District

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