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Arthropods and Nematodes: Functional Biodiversity in Forest Ecosystems

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1. Introduction

Despite the great diversity of habitats grouped under a single name, forests are ecosystems characterized by the dominance of trees, which condition not only the epigeal environment but also life in the soil. Unlike other ecosystems such as grasslands or annual agricultural crops, forests are well characterized by precise spatial structures. In fact, we can identify three main layers in all forests: a canopy layer of tree crowns, including not only green photosynthesizing organs but also branches of various sizes; a layer formed by the tree trunks; a layer including bushes and grasses, which can sometimes be missing when not enough light filters through the canopy. To these layers must be added the litter and soil, which houses the root systems. Other characteristic features of forests, in addition to their structural complexity, are the longevity of the plants, the peculiar microclimates and the presence of particular habitats not found outside of these biocoenoses, such as fallen trunks and tree hollows. Even in the case of woods managed with relatively rapid cycles to produce firewood, forests are particularly good examples of ecosystems organized into superimposed layers that allow the maximum use of the solar energy.

The biomass of forests is largely stored in the trees, with the following general distribution: ca. 2% in the leaves and almost 98% in trunks, branches and roots. In conditions of equilibrium between the arboreal vegetation and animal populations, saprophages, which use parts of plants and remains of organisms ending up in the litter, play a very important role. Indeed, the consumption of living tissues by other organisms included in the second trophic level is minimal, ranging between 0.1% and 2.5% of the net primary production. Any interruption of the mechanisms of demolition and degradation of organic substances would quickly lead to an accumulation of organic matter harmful to the operation of the forest system. For example, in Italian Apennine beech woods, the mean production of leaves reaching the litter is ca. 2.7 t/ha (Gregori & Miclaus, 1985), while for beech woods in southern Sweden it has been estimated at 5.7 t/ha. This mass of organic material reaching the ground would submerge the beech woods within several decades. In truth, however, the functioning of these woods would decline much earlier due to the lack of recycling of immobilized elements. If we turn our attention from temperate woods to tropical forests, we can see that the process would soon lead to the rapid collapse of the system. In fact, rapid decay of material reaching the ground (an estimated mean value of 20 t/ha is considered reliable) (Rodin & Bazilevich, 1967) is a *conditio sine qua non* for a system with great luxuriance of vegetation but rather poor and fragile soils.

The oldest inhabitants of this planet are for the most part trees. Yet, even without discussing the great patriarchs of the Earth, we must consider that growth cycles of over a century are the norm for many European forests. These rhythms were used for the oak forests that furnished the wood for the ships of the Most Serene Republic of Venice and even earlier for the Roman galleys. Vikings ships were constructed in Scandinavia with wood obtained from large old growth trees, especially oaks. The earliest forests can be identified on the basis of fossilized trees and forest soils from the mid-Devonian, between 400 and 350 million years ago. Starting from this period, we see an increasing number of remains of trees as well as a parallel exponential increase of the biodiversity of terrestrial zoocoenoses, with particular reference to the increased numbers of arthropod species (Retallack, 1997).

Forests are relatively stable ecosystems in which the tree component mediates the flows of organic matter by means of its long-term cycles. They support complex plant and microbial communities and represent, even in temperate climates, the largest storehouses of animal biodiversity, largely belonging to the Phyla Arthropoda and Nematoda. In table 1 are reported the values estimated in abundance of arthropod fauna living in a tropical forest (Seram rain forest).

Biotopes	N (millions/ha)
soil	23.7
leaf litter	6.0
ground vegetation	0.1
tree trunks	0.5
canopy	12.0
Total	42.3

Table 1. Abundance of arthropod fauna estimated in a tropical forest (Stork,1988).

Present-day forests host a diversified and largely specific fauna able to use not only the trees but also bushes and grasses. Trees are also more or less covered by microalgae, epiphytic lichens and mosses which can serve as food for phytophages, estimated to make up 20% of the total number of species in Danish beech woods (Nielsen, 1975). The primary production of epiphytes in many temperate forests is comparable to the production of the herbaceous layer, and some groups of arthropods specifically associated with these food substrates, such as Psocidae, can reach a density of 4,000 individuals per square metre of bark (Turner, 1975).

Moreover, the levels of biodiversity can vary enormously among different types of woods and within the same forest according to the age of the tree populations or the spatial heterogeneity characterizing woods of different ages. There are also trees with an extremely reduced arthropod fauna due to the production of phytoecdysones similar to moulting hormones, which act as repellents. In contrast, other trees host a much higher number of primary consumers due to the presence in their tissues of salicylic acid derivates, which act as attractants.

It is important to underline that when we speak of biodiversity we are often referring to three principal components:

- genetic diversity;
- diversity of species;
- diversity of habitats or ecosystems.

However, a fourth component was recently proposed, namely “FUNCTIONAL DIVERSITY”, based on the trophic role of the species and the interactions among organisms and between them and their environment.

In forest ecosystems, the animal component is distributed differently in the various layers, playing a fundamental role in terms of the following functional groups:

- primary consumers or herbivores;
- demolishers;
- degraders (often associated with symbiotic micro-organisms).

Arthropods in the different functional groups can be further divided into ecological-nutritional subgroups or categories based on their feeding behaviour:

- leaf suckers - species that puncture plant organs or tissues and suck the cell contents or substances circulating in the trees;
- defoliators - species that feed on green parts of the trees (leaves, buds and unlignified bark) throughout the life cycle or only in some stages;
- xylophagous - species able to feed throughout their life cycle or for part of it on lignified tree structures Xylophagous are further subdivided into:
    - corticolous,
    - corticolous-lignicolous,
    - lignicolous.

2. Tree crown

Arthropods that live in tree crowns present a great variety of biological aspects. They are represented mainly by insects, spiders and mites, and to a lesser extent by representatives of other groups such as Apterygota, Chilopoda and Diplopoda. Not all of these animals live stably in the canopy, with various species using the crown only for part of their biological cycle (various lepidopterans feed on leaves but when their larval development is completed they move into the soil to undergo metamorphosis, e.g. *Lycia hirtaria* (Clerck) in European temperate forest and *Erannis tiliaria* (Harris) in Canadian mixedwood boreal forest. In contrast, other arthropods, such as coleopterans of the genus *Polydrusus,* only feed on leaves and needles as adults after living in the soil as larvae and feeding on roots.

Crown arthropods can be grouped as follows:

- phyllophages, which feed on leaves or needles, eroding them from the outside (mainly lepidopterans plus some hymenopterans and coleopterans);
- leaf and bud miners (above all lepidopterans plus some coleopterans);
- floricolous arthropods:
    - anthophages,
    - pollenophages;

- arthropods that develop by eating fruits (carpophages) and seeds (spermophages);
- arthropods that induce the formation of galls, with shapes that vary according to the species involved (cinipid hymenopterans, dipterans and mites);
- suckers of cell contents and sap (mainly but not exclusively elaborated sap – above all Rhyncota insects of the suborder Homoptera);
- herbivores that feed on algae (algophages), fungi (mycetophages) and lichens (lichenophages) (mainly psocopterans);
- detritivores (including dermapterans, psocopterans,…);
- predators (many coleopterans but also some arboricolous orthopterans, Heteroptera Miridae, etc.);
- parasitoids (primarily hymenopterans but also many dipterans).

Primary consumers prevail in the canopy layer, especially phytophages in the ecological-nutritional categories of defoliators (with a masticatory buccal apparatus for feeding on leaves and green buds) and leaf suckers (provided with a puncturing-sucking buccal apparatus). A study conducted on oaks, black locusts and birches in England and South Africa showed substantial similarity of the crown arthropod communities between the two areas, with phytophages representing ca. one quarter of all species, half of the biomass and two thirds of all individuals (Moran & Southwood, 1982).

Defoliator insects are common in all coniferous and broadleaf forest ecosystems. They are an integral part of the forests and they can be useful to the ecosystem or harmful to the conservation and productivity of these habitats according to the quantity of photosynthesizing material removed and the possible repetition of severe attacks. In many forest formations, a primary role is played by various families of defoliator lepidopterans. Formations purely or prevalently of oaks provide a particularly important example. In Italy, there is a wide variety of biogeographical contexts within a relatively small surface area, and this is reflected in the number of *Quercus* species. The middle European oaks, often distributed in a fragmentary manner on plain and hilly terrains now largely dominated by agriculture, are joined by the larger contingent of Mediterranean species, the most important being the cork oak and holm oak. These oaks are very important in helping to form some of the most complex forest ecosystems in Italy, with an extremely various phytophagous arthropod fauna able to utilize the different ecological niches available in relation to seasonal conditions, composition, age and silviculture treatments. This heterogeneous complex of wooded formations, where human activities have profoundly modified the phytocoenoses, supports a rich and diversified lepidopteran fauna. Over 200 lepidopteran species belonging to 32 families feed on the green parts of the crowns of these Fagaceae, eroding buds, leaves and shoots from the outside or mining into them (Luciano and Roversi, 2001; Cao and Luciano, 2007). They constitute the most numerous group of phytophagous insects. The pre-eminence of this group is related to bio-ethological characteristics common to most of the species:

- the more or less strong polyphagy, which allows them to best utilize the occasionally available food;
- the possibility of laying eggs on different substrates without being bound to the trees that will serve as food for the larvae;
- the great variability of biological cycles, with species that pass the winter in different developmental stages;
- the absence of diapause (with rare exceptions), allowing the species to express the maximum potential for numerical increase in each generation;

- amphigonic reproduction, which provides the species with greater adaptability;
- the ability to carry out migrations or at least medium- and long-term movements, favouring rapid diffusion into suitable territories;
- possibilities for passive diffusion by some species, particularly in the first larval stages.

Lepidoptera are also cited as major defoliators of tropical forest trees and there are actually an increasing number of publications dedicated to the attack in neotropical forest environments (Nair, 2007; Haugaasen, 2009).

Thanks to these characteristics, a small group of oak-defoliating lepidopterans can give rise to spectacular numerical explosions or "outbreaks" with the sudden defoliation of whole stands, as in the case of mass *Lymantria dispar* (L.) infestations (Fig. 1). From an ecological point of view, outbreaks present characteristic phases of population abundance.

Fig. 1. *Lymantria dispar* larvae on *Quercus pubescens*.

After remaining at low numerical levels for years, becoming almost impossible to observe (latency phase), the phytophage populations show rapid density increases (progradation phase) which in several years lead to true numerical explosions or mass infestations (peak phase), followed by a more or less rapid decline (retrogradation phase) toward a new latency phase. In some defoliator lepidopterans, these mass changes are fairly common and are regulated by various biotic and abiotic factors that strongly affect the vitality and survival of the individuals. The main factors include climate (able to influence populations directly, e.g. allowing a higher or lower number of individuals to survive winter, and indirectly, by modifying the phenology of the host trees and thus the quantity and quality of food available for species that feed on the trees at the beginning of spring) and the set of natural antagonists (predators, parasitoids, pathogens) (Fig.2).

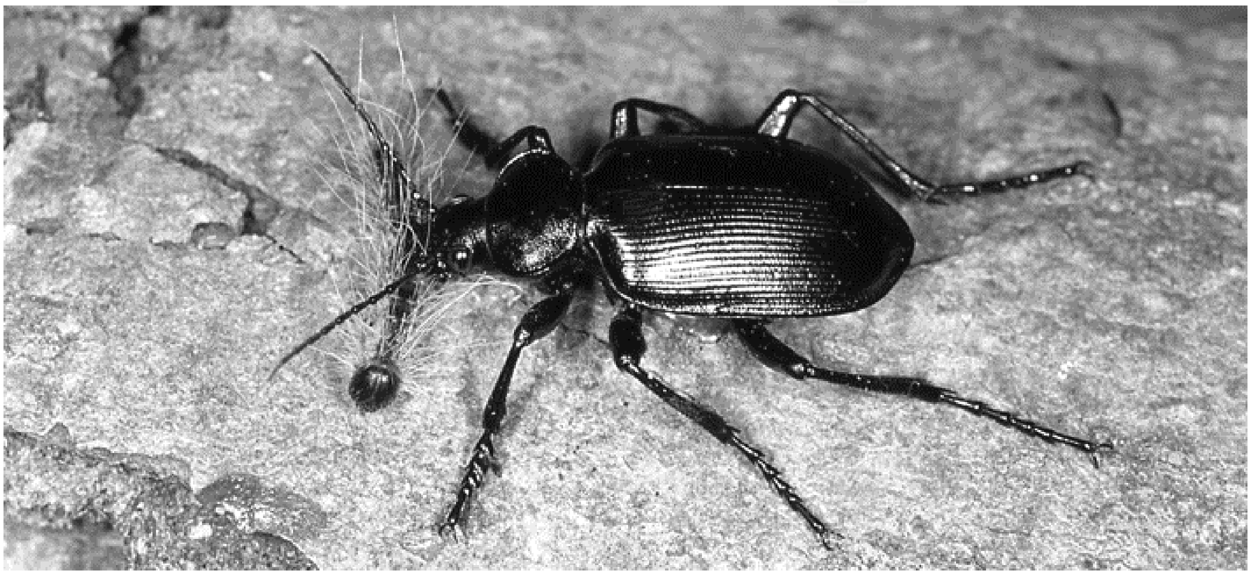

Fig. 2. *Calosoma sycophanta* a voracious Carabid consumer of caterpillars.

The different combinations of these factors produce more or less intense demographic variations, which allow species with a high biotic potential to reach high enough densities to cause the complete removal of the leaf mass of entire forests, even extending over hundreds of thousands of hectares. These mass appearances can occur at regular intervals or give rise to attacks irregularly distributed in space and time.

Very dramatic outbreaks often occur in degraded forest ecosystems or in marginal zones of the distribution area of the tree species where the appearances of defoliators are more frequent. This aggravates existing ecological imbalances, leading to very severe situations of widespread tree weakening, predisposing them to subsequent attacks by aggressors able to cause an irreversible decline. During such outbreaks, a large part of the organic matter produced by the trees can be diverted from the normal circuit. A good example is the activity of *Operophthera brumata* (L.), a geometrid able to defoliate entire stands in Swedish forests, whereas in the latency period the larvae remove no more than 0.004÷0.006 of the net primary production (Axelsson et al., 1975).

Leaf sucking insects have a puncturing-sucking buccal apparatus in which the mandibles and maxillae are profoundly modified to form an efficient tool similar to a hypodermic needle. They use it to suck sap and cell contents from the trees, becoming the first factor of deviation of part of the organic matter otherwise destined for the production of photosynthesizing and reproductive organs, the constitution of reserves and the accumulation of wood mass.

Three large groups of leaf sucking insects can be identified: species that feed by directly puncturing cells or groups of cells in superficial tissues (as in the case of thysanopterans) or deep tissues (as for some Homoptera Rhyncota); species that feed on elaborated sap, which stick their buccal stylets directly into the phloem conducting system (including Homoptera Rhyncota, mainly Aphidoidea, Coccoidea, Psylloidea and Aleyrodoidea); species that reach the xylem transport pathways, feeding on crude sap (including a small group of homopterans such as some Cercopidae). In these last species, also known as "spit bugs", the larval stages are found inside large foamy masses formed by the insects to eliminate the excess of water they are forced to ingest: indeed, the low concentration of nitrogen compounds in crude sap compels the Cercopidae to ingest large quantities of food in order to extract the necessary amounts of nutrients (Thompson, 1994). Adults of Cercopidae, including species that complete their larval development in the soil, also withdraw food and liquids by tapping into the xylem circuit of the leaves of host plants by means of refined behavioural adaptations: for instance, adults of *Haematoloma dorsatum* (Ahrens) puncture the needles of pines and other conifers by introducing their buccal stylets through the stomata to reach the feeding sites without an excessive energy expenditure (Roversi et al., 1990).

Leaf suckers that feed on elaborated sap consume large quantities of sugars which are not completely used and thus are expelled as drops of honeydew, highly attractive to ants, bees, wasps and adults of predators and parasitoids of aphids. Hence, these animals consume a part of the products of photosynthesis by trees that are otherwise unavailable to them. Therefore, in conditions of general equilibrium of forests, leaf suckers (particularly those that produce honeydew) are integral parts of the system, allowing an intensification of the network of interrelationships within the ecosystem and between it and other biocoenoses.

With the changing of the seasons, trees are subjected to strong variability in the transfer of nutrients and mineral salts. This is extremely important for leaf suckers, which gain their nutriment from the host tree's vascular system. In Italian environments, there can be strong differences between deciduous and evergreen trees, since the former are subjected not only to a marked translocation of crude and elaborated materials during growth resumption in spring but also to an autumn re-allocation of nitrogen substances and others when the leaves fall.

Tree crowns also host arthropods with such close associations with trees that they modify the host's local physiological processes and morphology, forcing them to create particular structures, called galls, in which the arthropods develop and shelter. There is a great morphological variety of galls, with forms and colours characteristic of each insect species. This is particularly true for structures formed by Hymenoptera Cynipidae and Diptera Cecidomyiidae, which have long attracted the attention of students of nature, starting with Francesco Redi who in the 17th century dedicated three manuscripts to them, including tempera drawings of the insects and their larvae (Bernardi et al., 1997). In some habitats such as beech woods, the unmistakable reddish leaf galls of the cecidomyiid *Mikiola fagi*, with their larval contents, are a food supplement for micromammals in an ecosystem in which food reserves for these vertebrates are particularly scarce.

On the crowns of both coniferous (various *Pinus* spp.) and broadleaf trees (oaks), we find insects that carry out most of their life cycle elsewhere, usually in subcortical and woody tissues, but which require a relatively brief period of feeding on vigorous shoots for maturation of their reproductive apparatus. They include Coleoptera Scolytidae of the genera *Tomicus* and *Scolytus*, which burrow galleries in the shoots, and Cerambycidae of the genus *Monochamus*, which erode young bark, all widely distributed in temperate forests. The alternation of feeding sites between woody tissues of trees often weakened by pathogenic infections and peripheral parts of the crown introduces another peculiar aspect into the relationships among very different groups of animals. Scolytidae and Cerambycidae with this behaviour can act as vectors, not only carrying fungal spores directly into contact with living tissues of new host trees but also becoming efficient vehicles of inoculation of healthy plants with phytopathogenic nematodes, which benefit from the damage caused by the xylophages to reach the conductor system of the host trees. Among the various relationships between nematodes and arthropods, especially insects, the associations established by the phoretic entomophilous nematodes of the genus *Bursaphelenchus* can have very severe consequences. In favourable conditions, they can allow the nematodes, transported by beetles under their elytra or in the trachea, to multiply with extreme rapidity in the conducting tissues of the trees (Covassi & Palmisano, 1997).

Acari living in the forest canopy (on leaves and small and main branches) are represented by various groups with different densities. Phytophagous mites belonging to the Tetranychidae, Tenuipalpidae and Eriophyidae, feed on the tree sap or cell contents. Their behaviour and densities are influenced by the environmental conditions and by the cohort of their predators, mainly Acari Mesostigmata and Prostigmata (Figs. 3 and 4) of the families Phytoseiidae, Stigmaeidae, Cheyletidae, Anystidae, Cunaxidae, Bdellidae and Trombidiidae. Their behaviour is also influenced by the type of plant, i.e. broadleaf or evergreen. Phytophagous species living on deciduous trees in unfavourable periods tend to move onto the branches and trunk to find micro-environments suitable for overwintering. On coniferous and evergreen trees, which keep their leaves even in winter, phytophagous mites tend to shelter at the base of the leaf nervation or in cracks in small branches.

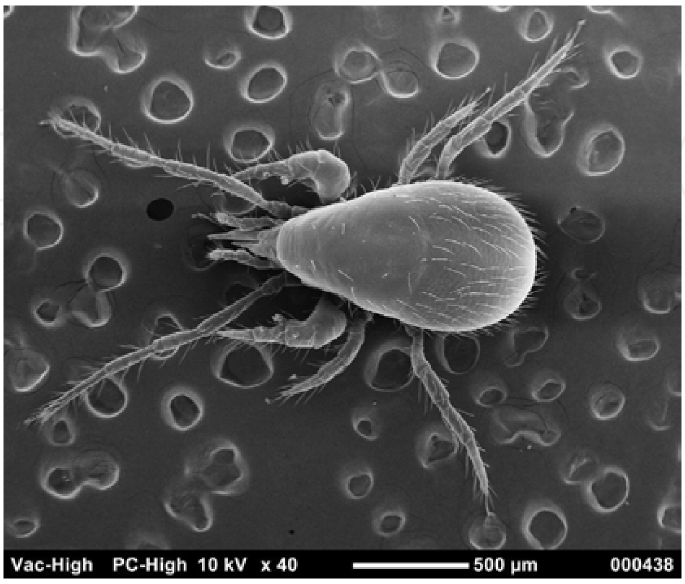

Fig. 3. A predatory mesostigmatid mite living in the forest canopy (SEM x 40).

Fig. 4. A predatory prostigmatid mite living on bark of tree trunks.

Tree crowns host a wide variety of Acari: fungivores, algophages or those associated with mosses and lichens. These Acari belong to different groups, including Oribatida or Cryptostigmata, Astigmata and Prostigmata Tydeidae and Tarsonemidae, in fine equilibrium with their predators, generally Acari Mesostigmata and other Prostigmata, which habitually frequent leaves and small branches.

3. Tree trunks

The bark of tree trunks is an important element of forest ecosystems. It creates particular microclimates and provides micro-habitats that differ greatly according to the rugosity and irregularity of the surface, particularly in terms of the presence of deep fissures. In this spatial sector, which hosts phytophages as well as various predators and detritivores, the dominant groups are spiders, mites and insects, mainly springtails, psocids and some coleopterans and dipterans (Funke & Summer, 1980).

The trunk can contain mites associated with mosses and lichens but also strictly corticolous species, which find food and protection there. Galleries burrowed under the bark by scolytid, cerambycid and buprestid beetles host Acari belonging to Astigmata, Mesostigmata and particularly Prostigmata Tarsonemidae, which feed on the fungi typical of this environment. Other mites live in rifts in the bark caused by cortical cancers, feeding on fungal mycelia and fruiting bodies or on the associated microflora.

Also active on trunks are leaf suckers able to reach the tree’s lymphatic system with long buccal stylets, e.g. the highly mimetic Heteroptera Rhyncota of the genus *Aradus* and cochineals of the genus *Matsucoccus*. Trunk-living insects with a puncturing-sucking buccal apparatus also include predators with a high degree of adaptation; this is observed especially in species of the genus *Elatophilus*, whose body is very flattened and admirably adapted to working its way between bark scales (Covassi & Poggesi, 1986).

Bark and especially wood constitute the main reserves of organic matter and mineral elements, with values that can vary enormously according to the vegetational composition, age of the woods and their conservation state. A beech wood of the Fontainbleau Forest in France had an estimated total tree biomass of over 280 t/ha, of which 195 represented by trunks, 48 by branches, 41 by roots, 3.2 by leaves and sprigs, and 0.9 by reproductive organs (Dajoz, 2000). In the so-called "Old Forests" of the western United States, consisting of coniferous associations with a mean age of 450 years, the epigeal biomass varied from 492 to 976 t/ha, with woody residues varying between 143 and 215 t/ha (Spies et al., 1988).

However, bark and wood tissues are degraded much more slowly than leaves. Arthropods, and xylophages in particular, play a primary role in accelerating the processes of decomposition and mineralization, often acting simultaneously with various fungi. In a transverse section of a trunk with, from external to internal, bark or rhytidome, phloem, cambium and xylem or real wood (separated into sapwood and heartwood), we can see a progressive change in the composition in terms of cellulose, hemicellulose, lignin, pectin, suberin, starch, nitrogen compounds, lipids and minerals, with a clear prevalence of the first three compounds. Cellulose, a polymer formed by the association of a high number of carbohydrate molecules in both the amorphous form and crystalline form, constitutes from 40 to over 60% of the dry weight of wood and can be hydrolyzed only by fungi, bacteria and some isopods, diplopods and insects provided with cellulase.

Only a few insect species can completely degrade cellulose since many xylophages that feed on bark, subcortical tissues or wood have only one of the three enzymes necessary for the final conversion into glucose. Among the few arthropods able to totally degrade cellulose are Thysanura (Lasker & Giese, 1956), Dermaptera (Cleveland, 1934), Isoptera, Hymenoptera Siricidae, Coleoptera Anobiidae, Buprestidae, Cerambycidae and Scarabeidae. However, occasionally in the wild, some xylophagous species can ingest bacteria, fungi and protozoa, using them as a source of enzymes to increase their ability to digest cellulose, hemicellulose and lignin. In the case of Hymenoptera Siricidae that develop in the wood of coniferous trees, their ability to utilize this food depends on the fact that the larvae ingest wood invaded by fungi of the genus *Amylostereum* and establish a mutualistic symbiosis with them, which provides the digestive enzymes necessary to use the pabulum on which the larvae develop (Kukor & Martin, 1983).

Lignin forms 18-38% of the durable tissues of trees. However, this term groups very different complex substances into a single category and these substances make the degradation of wood even more difficult since no animals, including insects, produce enzymes able to degrade them. Micro-organisms that can decompose lignin include fungi, bacteria and protozoa, many of which live in the digestive apparatus of arthropods, establishing mutualistic symbioses that allow the hosts to degrade lignin.

The bark of tree trunks also constitute "highways" for the daily (ants of the genus *Rufa*) or seasonal movements of species that migrate from the soil or litter to the tree crown during their cycles. Many species use the bark of the trunk as mating, egg-laying or wintering sites. In some cases, the bark becomes a summer refuge for species that live on the crown but abandon it when the temperatures reach their summer peak, as in the case of the woolly oak aphid (Binazzi & Roversi, 1990).

The subcortical layers are the site of development of various species, mainly insects and especially scolytid and cerambycid beetles. The Scolytidae are one of the most important groups of phytophagous insects, linked mainly to forest habitats and particularly coniferous woods (Figs. 5 and 6). There they express their maximal diversity of cycles and modes of development, behaviours and abilities to settle on trees in different vegetative conditions, often becoming dominant elements in the mechanism regulating ecological successions (Chararas, 1962; Pennacchio et al., 2006). In Europe, 39 species have been recorded on *Pinus* alone. The family Scolytidae numbers over 6,000 species of small insects, usually of more or less cylindrical shape and less than 2 mm long, with mandibles that move horizontally and the initial part of the intestine provided with sclerified denticles that act as a filter preventing the ingestion of excessively large wood fragments. The family includes polygamous species, such as those in the genera *Ips*, *Orthotomicus*, *Pityophthorus*, *Pityogenes* and *Pityokteines,* or monogamous ones such as those in the genera *Tomicus* and *Cryphalus*, which burrow characteristic systems of breeding galleries where they lay their eggs. The galleries of adults and those dug by the larvae to complete their development are well determined for each species; indeed, it is possible to make an *a posteriori* identification of scolytid species that have developed on a given tree merely by examination of the damage.

Very many other insects, mites and non-hexapod invertebrates with diversified alimentary regimes are found in the subcortical galleries burrowed by Scolytidae. They contribute substantially to the maintenance of high levels of biodiversity of the animal communities living under tree bark.

Fig. 5. Galleries on Pine produced by *Tomicus minor*.

Fig. 6. Galleries in Spruce produced by *Ips typographus*.

Most scolytids attack trees with integral phloem and cambium tissues. However, these trees are often weakened for various reasons, including drought and attacks by other phytophages, primarily defoliators but also a small number of species that colonize trees in more or less advanced stages of decay with active fermentation processes in the subcortical tissues and with low levels of starch and protein contents, e.g. species in the genera *Dryocoetes* and *Hylurgops*.

It is important to underline that, even in scolytid species that attack only a single host, not all the trees are equally attractive. These small hexapods are refined aggressors able to perceive with their sensory organs changes in the spectrum of substances emitted by each individual tree as a result of biotic and abiotic stresses. The manner in which thousands of individuals of a given scolytid species swarm onto single trees among thousands of other unaffected trees illustrates the precision of these beetles' stimulus perception mechanism.

The relationships among trees, semiochemicals and xylophagous insects constitute one of the most interesting research fields in forest entomology, not only for an understanding of the subtle mechanisms that allow their correct functioning but also for their practical implications. The use of semiochemicals for the monitoring and mass capture of these phytophages is a current strategy for the management of biotic adversities in many forest areas because of the possibility of limiting beetle population increases via agents with low environmental impact and without the use of synthetic biocides.

Examples of species well known for their ability to modify the structure and species composition of wooded formations are various *Dendroctonus* in North America and *Ips typographus* in Europe. The latter species caused the loss of over 5 million cubic metres of timber in Norway in the period 1970-1982 alone. In the Palaearctic Region, *Scolytus* species on elms have been responsible, in association with the fungal agent of Dutch elm disease *Ophiostoma novo-ulmi* Brasier, for the devastation of elm trees, while *Tomicus* species have been a constant threat to pine woods along coastlines and on hills and mountains.

The Cerambycidae are medium to large-sized beetles with a lengthened body and generally long antennae, very common in forests since the larvae of most species develop under bark or in wood. They are important both for conservation and for maintenance of the functionality of the woods; although some species cause damage, others actively contribute to the degradation of dead wood, intervening effectively in the first phase of demolition of durable tree structures. Species of the genus *Monochamus*, particularly *Monochamus galloprovincialis galloprovincialis* (Olivier) in Mediterranean pine woods, are able to rapidly kill trees that are only momentarily weakened (Francardi & Pennacchio, 1996). The harmfulness of these and other beetles of the family is also due to their role as vectors of phytopathogenic nematodes of the genus *Bursaphelenchus* (Fig.7).

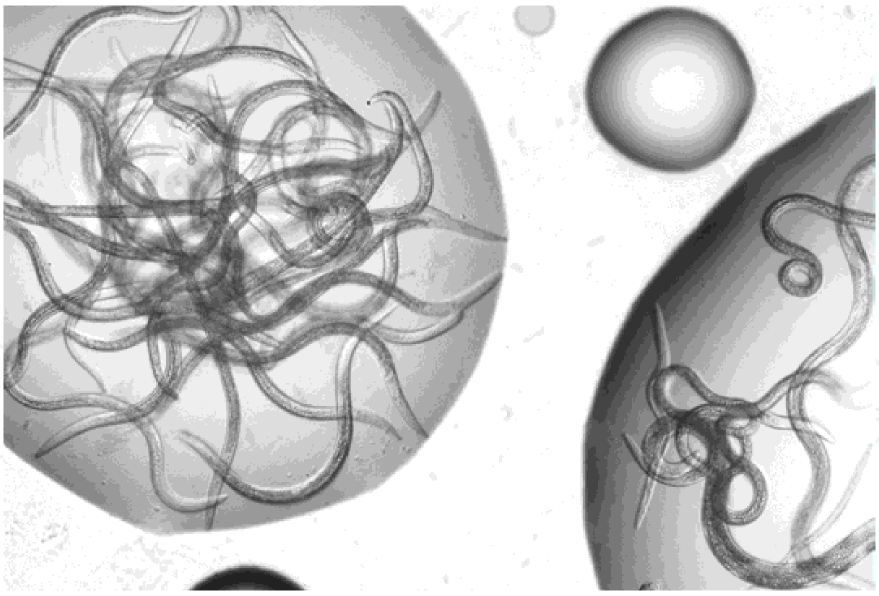

Fig. 7. *Bursaphelenchus eremus*: a phytoparasitic nematode living on *Quercus* spp.

Some lepidopterans develop by feeding on durable tree tissues, such as species of the genus *Dioryctria*. They are known as “pine resin moths”, even though they can also live on cedars and red firs. Their larvae dig subcortical galleries exclusively on conifers thanks to their ability to isolate themselves from the abundant resin emitted by the trees in an attempt to defend themselves. To do so, they create tunnels lined with sericeous tissue.

Isopterans, various coleopteran families (including Scolytidae, Cerambycidae and Buprestidae), Lepidoptera Cossidae and Sesiidae, Hymenoptera Siricidae and some dipterans contain xylophagous species able to develop for part of their life or for the entire larval period by feeding on living wood or wood at various stages of decay. In the first case, we are referring to species included in the corticolous-lignicolous group whose larvae feed first on the phloem and later on the xylem, moving deep inside trunks and branches to complete their development and undergo metamorphosis. The second case involves xylophagous species *sensu stretto* or lignicolous ones that feed exclusively on woody tissues. They are fundamental in accelerating the decay of tree branches and trunks, and the group includes some of the largest of all arthropods. For instance, among Cerambycidae, the larvae of *Ergates faber* found on pines, oaks, chestnuts, elms, cherries and other hosts in Italy reach 8 cm in length, while the larvae of *Acrocinus longimanus,* distributed from Mexico to South America, are up to 13 cm long. The larval activity of these true burrowers can demolish age-old trees, even reaching the most resistant portions of the heartwood. Some xylophages *s.s.* are found on only one host species, although many develop by feeding on different trees; some species, mainly linked to decayed wood already invaded by fungi, are able to accept hundreds of coniferous and broadleaf species. On account of the poor pabulum, many species in this group, particularly those in relatively dry habitats, require several years to complete their larval development, even up to six years. Examples are the cerambycid *Hylotrupes bajulus* L. and a scarabaeid that lives in dead wood and is one of the best known and most characteristic of insects, the stag beetle (*Lucanus cervus* L.), whose adult males are provided with unmistakable long but absolutely harmless mandibles. Some xylophages found in dead wood in humid tree hollows are among the rarest of protected insects worldwide, e.g. the Scarabaeidae Dynastinae *Osmoderma eremita*. Various other coleopteran families include important xylophagous species, e.g. Buprestidae, Melandryidae (*Serropalpus barbatus*), Anthribidae and Tenebrionidae. The Diptera families Tipulidae, Cecidomyiidae and Asilidae contain species often found in dead wood.

Therefore, many xylophagous insects are important components of forest ecosystems, and, in conditions of equilibrium with the host trees, help maintain the vigour of the system, assuring the dynamism of the biocoenosis. In fact, forest insects and pathogens:

1. colonize trees suitable for their development, modifying the structure and composition of the woods and modelling the tree population to the conditions offered by the site.
2. participate in tree turnover via elimination of the less fit trees, accelerating the availability of elements and other substances to the healthier trees. Indeed, the action of corticolous, corticolous-lignicolous and lignicolous insects contributes to the decay of the durable tree parts, thus favouring the action of nitrogen-fixing bacteria and saprophytic micro-organisms which mineralize and liberate elements for roots and mycorrhizae.
3. create peculiar habitats, via deformations of the crown, the death of some trees and the opening of clearings, and make available nutrients for other species that play a critical role in the maintenance of forest stability and productivity. A good example is the formation of suitable habitats and refuges for insectivorous birds.

Hence, the action of xylophagous insects and associated pathogenic agents plays a primary role in the maintenance of productivity and biodiversity levels in forest environments.

Fig. 8. Adult of *Ergates faber*.

4. Litter and soil

Although leaf-sucking and defoliator arthropods prevail in the crown layer, demolishers are of great importance in the lower layers and especially the litter, which receives not only leaves but also large amounts of organic matter in the form of fallen trunks and branches. Indeed, their role becomes essential in the phase of breakdown and decay of organic substances (Fig.9). To underline the complexity of the trophic networks, we should also mention that nematodes form an important part of all the functional groups in the soil, from phytoparasites active on root organs to bacteriophages with densities that can reach 30 million individuals/m^2 in forests.

The forest litter and soil are the environment with the greatest animal biodiversity and the site of recycling of materials and nutrients. The dominant groups of soil organisms, in terms of number and biomass, are micro-organisms such as bacteria, fungi and yeasts, representing ca. 85% of the biomass. However, other extremely important and complex components are represented by animals with sometimes very diverse dietary regimes, such as protozoa (amoebas, flagellates, ciliates), nematodes (bacteriophages, fungivores, omnivores, predators), Enchytraeidae, Lumbricidae and micro-arthropods, mainly mites (bacteriophages, fungivores, predators), springtails (fungivores and predators), and dipteran and coleopteran larvae, which make up the remaining 15% of the biomass. Nevertheless, the systematic spectrum of large taxonomic groups is limited with respect to the specific variety found within the same groups (Fig.10).

Table 2 summarize the soil fauna living in a temperate forest.

Fig. 9. *Abies alba* windfall in the Vallombrosa Forest (Central Italy).

Zoological groups	**Number of individuals/m^2**	**Weight in g**
Protozoa	100 to 1000 x 10^6	2 to 20
Nematoda	1 to 30 x 10^6	1 to 30
Lumbricidae	50 to 400	20 to 250
Enchytraeidae	10 to 50 x 10^3	1 to 6
Acari	20 to 500 x 10^3	0.2 to 5
Pseudoscorpionida+ Araneidae+Opilionidae	60	0.06
Collembola	20 to 500 x 10^3	0.5 to 5
Protura	200	insignificant
Diplura	150	insignificant
Thysanura	few individuals	insignificant
Formicidae	variable according to site	-
Coleoptera larvae	100	1
Diptera larvae	400	3.5
Symphyla	1000	0.1
Chilopoda	50	1
Diplopoda	1 - 200	8
Isopoda	100	4

Table 2. Division of the forest soil fauna in temperate regions (values estimated from data of different authors). (From Bachelier, 1971).

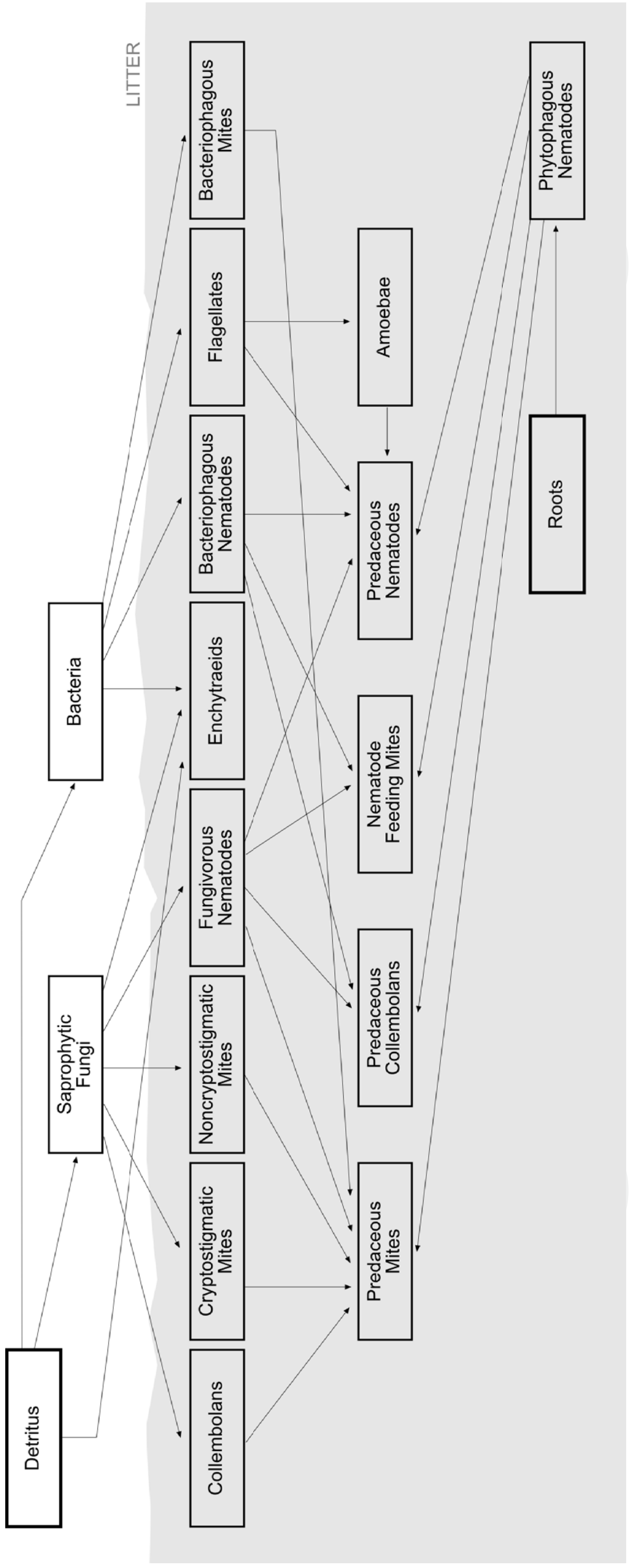

Fig. 10. Diagram of the food web in the forest floor and soil.

An important subdivision of soil-living animals is based on their size. This parameter is of primary importance in the edaphic environment since the organisms must move through the soil to search for food, breed and avoid natural antagonists and momentarily adverse conditions, as occur during periods of drought. The classification of soil animals based on size allows us to distinguish the macrofauna and microfauna from the mesofauna, which includes the major part of soil organisms and whole groups such as Diplura, Collembola and Protura as well as the majority of species of Tardigrada, Rotifera, Isopoda and especially Nematoda (Wallwork, 1976). The biological population of the soil has a dual origin: on the one hand a contingent of species living in capillary and gravitational water that fills or covers the soil cavities (protozoa, nematodes, most oligochaetes); on the other hand a different group originating from the epigeal part, which has adapted to life in the soil (almost all arthropods with the exception of small groups such as copepods). However, there is a third contingent, whose origin has been directly identified in Palaeozoic deposits, containing forms strongly adapted to hypogeal life (Insecta Symphyla, Collembola and Pauropoda, Protura and Diplura). The abundance and composition of these groups depend on the type of soil and overlying vegetation. Coniferous needles have a high C/N ratio and high polyphenol contents, which make this material more resistant to decomposition than the leaves in broadleaf litter, where the C/N is lower and decomposition is more rapid. In this type of litter, the mineral soil is much less acidic and the more active decomposer groups are favoured (lumbricids, millipedes and isopods). Soil arthropods are generally not uniformly distributed and often show aggregative behaviour, being distributed in horizontal aggregates in the same profile or in different profiles. Their densities are closely correlated to the organic matter, which is mainly concentrated in the most superficial layer of the forest soil, i.e. the litter.

The abundance of animals in the soil is negatively correlated with soil depth, since it depends on the availability of nutrient substances and oxygen. In forest soils, more than 60% of the ground fauna is typically concentrated in the first 10 cm of the superficial horizon (Peterson & Luxton, 1982). Soil arthropods make an enormous contribution to organic matter decomposition, breaking down and transforming all the material coming from the epigeal part of the forest. In fact, arthropods:

1. disintegrate the dead plant or animal tissues, transforming them into a substratum more easily attacked by micro-organisms,
2. selectively decompose and chemically modify part of the organic residues,
3. transform the plant residues into humic substances,
4. increase the surface area attacked by fungi and bacteria,
5. form complex aggregates of organic matter with mineral parts of the soil,
6. transport and mix the organic substances among the different layers,
7. disseminate propagules of fungi and stimulate their growth through symbiotic, commensal or phoretic relationships.

In temperate forests, the soil fauna remains active even in winter, under the snow cover and in the layers underlying the frozen litter. In these conditions, the breakdown and mineralization of organic matter is reduced to minimal levels.

Forest management practices can increase or reduce the ecological niches of the soil and thus influence the range of species. In environments less impacted by human activities, the diversity and stability of animal populations are correlated via interactions among the different functional groups, which tend to bring the system toward equilibrium and stability. Soil arthropods and nematodes are notoriously flexible in terms of their diet and it is not easy to assign a single trophic level to each group. According to the available resources, Acari Oribatida and Collembola can behave as detritivores but can also feed on fungi, algae and amorphous detritus. Among Acari Mesostigmata, some Uropodina species are detritivores, while others behave as specialized predators. Likewise some soil-living nematodes are phytophages, feeding on tree roots, while others are generalists and others still are preyed upon by Acari Parasitidae, Macrochelidae and fungi (Marinari Palmisano & Irdani, 1996). Acari, particularly the Oribatida (Figs. 11 and 12), are very important for the maintenance of soil productivity, actively participating in the breakdown of plant detritus, the vertical transport of organic matter and the formation of humus. Studies conducted in beech and pine woods of central Italy revealed the presence of 90 species belonging to 64 genera and 42 families (Nannelli, 1972, 1980): 72 species were recorded in a single temperate beech stand (Nannelli, 1990).

Fig. 11. A cryptostigmatic mite belonging to the genus *Carabodes.*

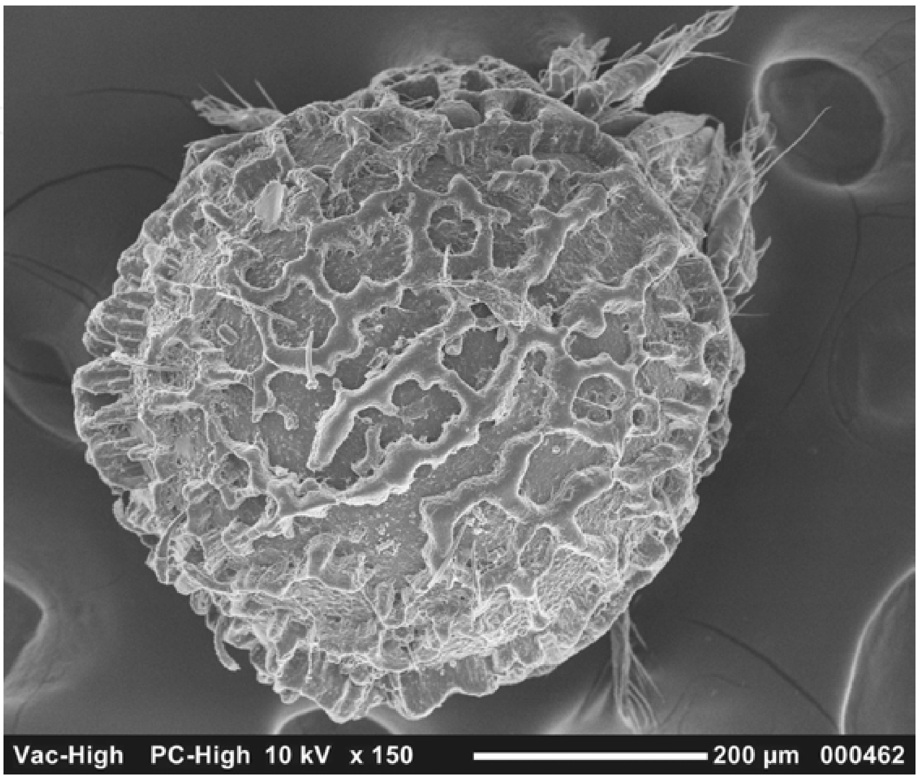

Fig. 12. A cryptostigmatic mite belonging to the genus *Pelops.*

Some soil mite groups have greater numbers of individuals in the boreal then in more southern zone. For exemple Oribatid and Prostigmatid mites are better represented in coniferous then in deciduous or tropical forest soil, and provide a significant share of total soil biomass (Petersen & Luxton, 1982).

Nematodes, perfectly adapted morphologically to interstitial habitats, are considered the most abundant animals on the Earth. The species found in soil are usually small, live in films of water lining soil and detritus particles, and feed on a wide range of substrata, including other nematodes preyed upon by many species of the same group. From the few data available, we can infer that the nematode communities of forest soils play a fundamental role in the control of microbial populations, carrying out this function even more effectively than protozoa. In some soils, microbivorous nematodes are the most numerous component of the nematode fauna (Anderson *et al*., 1978) and act not only as consumers but also as vectors of both pathogenic and useful micro-organisms, in some cases showing specific associations with particular soil bacteria.

In table 3 are reported the distributions of nematode genera, in according of your feeding behaviour, in forest soils of central Europe.

Trophic group	Genera
Nematode bacteriophages	11-18
Nematode mycophages	2-5
Nematode phytophages	7-11
Nematode predators	2-8

Table 3. Distributions of nematode genera in groups feeding on different substrata recorded in forest soils of central Europe (from Wasilewska, 1979).

Large nematode populations are found in decomposing plant detritus, inside the tissues following the action of bacteria and protozoa. By their activity, they favour the humification and structural stability of the soils.

In general, micro-arthropods that feed on micro-organisms or behave functionally as detritivores are difficult to assign to only one of either primary or secondary decomposers. Both categories include Lumbricidae, Diplopoda, Isopoda, Collembola and Acari Oribatida, whereas Enchytraeidae and Coleoptera Elateridae are assigned to the secondary decomposers.

A similar model is used for soil-living predators, with several distinct levels: indeed, we can speak of first-, second- and third-level predators. Generally Chilopoda, Araneidae, Coleoptera Staphylinidae, Acari Gamasida and Uropodina, Pseudoscorpionida and Diplura are assigned to the first two levels, while third-level predators usually include higher animals such as micromammals and birds.

5. Conclusion

Animals included among consumers, demolishers and degraders actively participate in the cycles of organic matter and mineral elements, which without the intervention of these organisms would be destined to prolonged immobilization, especially in regard to the amounts conserved in durable wood structures (Dajoz, 2000). These organisms also establish complex interactions with predators and parasitoids forming part of the next trophic levels, which in turn are often subjected to predation and parasitism. This system of relationships is fundamental for the maintenance of homeostasis of forest ecosystems since it allows the species involved in the consumption and recycling of organic matter to play their role while at the same time maintaining their population numbers within strict limits so as not to jeopardize the equilibrium of the entire system. The last aspect is particularly important because of the necessity to keep primary consumer arthropods and nematodes, which feed on green photosynthesizing organs and subcortical tissues, within the carrying capacity of the ecosystem.

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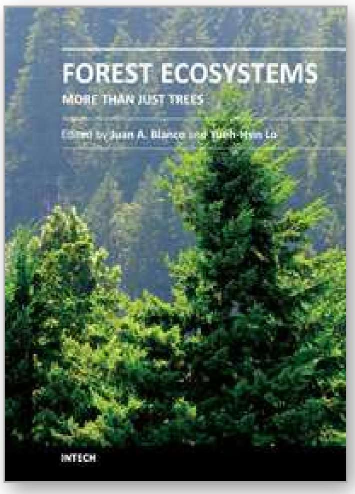

Forest Ecosystems - More than Just Trees
Edited by Dr Juan A. Blanco

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The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the �other� parts of a forest.

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