

The roles of plant pathogens in old-growth forests

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Abstract. Old-growth forests are considered a benchmark for naturalness and models to which one compares managed forests. The comparison led to debates around biodiversity and its conservation, structure and dynamics, polarizing conservationists and forest practitioners. Plant pathogens are frequently disregarded as components of forests biodiversity, the common perception referring to this category of organisms as important biotic stressors. However, pathogens are building several functional groups such as necrotrophic and biotrophic pathogens, endophytic pathogens, sapro-parasitic species, in highly natural forests including old-growth forests. They are establishing interaction networks with several other functional groups of organisms such as hyperparasites, consumers, disease facilitators, indirect opportunistic species (such as tree hollow dwellers), saprotrophs or mutualists. Being connected to old trees (rare or missing components of managed forests) or to endangered forest plants, pathogens become indicators of naturalness and biodiversity. The gradient going from saprotrophs, to sapro-pathogens and generalist/specialist pathogens characterizing forest ecosystems is linked at great extent to wood and bark, being connected to nutrient cycling as ecosystem level process. As long as disease is maintained within the baseline mortality of the trees, pathogens play the important role of control factors and contribute directly and indirectly to forest biodiversity. The current disease ecology progresses, the biodiversity integrative studies, and the new holistic approaches shaping modern ecology bring in the focus rare, endemic pathogens. These play several roles: as important control factors for plant populations, as components of the plants' phenotypic niche and of the global biodiversity, as potential providers of services (sources of medicines) and as components of the intricate ecological webs. However, the comparisons between old-growth and managed forests biodiversity should be focused on species evenness (high evenness in old-growth forests versus low evenness in managed forests) and not particularly on species richness. Still, there are pathogens responsible for major biotic disturbances in forests worldwide, the invasive, alien or emerging pathogens threatening both old-growth forests and managed forests.

Keywords: old-growth forests, plant pathogens, biodiversity, biotic disturbances, disease ecology, species interaction networks.

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Introduction

If someone is strolling across an ideally managed forest according to best commercial practices, the striking characteristic is the presence of the perfectly manicured trees, without cavities and almost without disease symptoms. The same activity in a natural, maybe old-growth forest (OGF hereafter) will reveal a different image: of veteran trees harboring tree holes, dead branches, a considerable amount of dead wood littering the soil and almost all trees with hardly visible disease lesions or on the contrary, conspicuous disease symptoms.

The most widespread approach to tree pathogens stems from general principles of classical plant pathology. There is growing evidence that things are not linear and simple and pathogens are important contributors to overall biodiversity. Since 1996, when Gilbert and Hubbell stated that the scientific community was reluctant in admitting that plant diseases were important in forest conservation, little has changed. They stressed that epidemic diseases may provoke dramatic changes in forest ecosystems but endemic diseases contribute to forest community dynamics and composition stability (Gilbert and Hubbell 1996). If endemic pathogens are common components of forest ecosystems, epidemic diseases are caused by introduced pathogens or triggered by previous climatic vagaries and human induced disturbances (logging included). How managed and unmanaged, particularly OGF cope with plant pathogens (most important, tree pathogens) represent a focal problem at the interface between plant pathology, biodiversity conservation, forest management, management of protected forested areas. It became a key argument in the long-standing debate on the intrinsic versus instrumental value of the forests (Proctor 1997). The context can be placed even in a larger frame, of the reconciliation with nature (Rozenzweig 2003) compromised not only by overexploitation, but by environmental crises including pests and pathogens and by war destruction lately. One must

1. The magnitude of pathogen-hosts interactions differs in managed forests and plantations compared to old-growth forests.
2. There are pathogens that function as indicator species of naturalness, habitat integrity and biodiversity.
3. The gradient encompassing saprotrophic life style, sapro-pathogens and generalist/specialist pathogens is linked mostly to wood and bark and is connected to nutrient cycling as ecosystem level process.
4. The interactions of tree pathogens are complex and include also other species than their hosts, establishing complex ecological networks.

Box 1 The general frame of the present essay

stress from the very beginning the idea that the war became the greatest threat to managed and unmanaged forests. Information gathered by the European Wilderness Society have shown that Biosphere reserves and protected areas during the Ukrainian war suffered massively from shelling, bombing and chemical or radiological pollution. Under threat are at the moment protected forested areas in Eastern Carpathians such Zacharovanyi Krai National Park which includes beech OGF (Vacuna 2022), if war zones will extend.

To move on to the initial academic purpose of the present essay, this work is centered on two main aspects: i) pathogens as components of forest biodiversity; ii) pathogens as threatening factors in OGF. As plant populations in forests pertain to different life-forms, one must take into consideration the contribution to overall biodiversity of the pathogens linked not only to trees. The categories of plant pathogens are important for the conservation of OGF but from different perspectives.

However, the focus was historically almost exclusive on tree pathogens, therefore centered the present synthesis on this category, with several references to plant pathogens targeting the herbaceous layer in forests.

The health of forests

To start with, classical concept of plant dis-

ease and plant pathogens dates back to Robert Hartig's time: Disease represents an unhealthy condition of the forest. The present-day paradigm has a holistic frame based on pathosystems and microbiome interactions, reshaping our understanding of what means healthy tree and healthy ecosystem.

The New Paradigm states that (Manion 1991, 2003) in order to evolve, forests need a certain amount of disease because: 1. Pathogens are disease agents acting as regulators, terminators or resource recovery factors (are density dependent factors of tree populations) and 2. Their effect is quantified by the baseline mortality of tree populations, that is (Manion 2003): the amount of mortality required to indefinitely maintain the current forest structure. In OGF, pathogens eliminate trees within the limit of baseline mortality corresponding to a low disturbance effect. Pathogens reduce the density of plant population leading to greater vigor and reproductive output of the survivors (Alexander and Mihail 2000).

In the same context is placed the debate concerning the definition of disease and by default, of the healthy individual and by extension, of the ecosystem (Costanza et al. 1992) which deserves a special comment. Traditionally, disease at tree level is defined (among many existing definitions) as deviation from the normal functioning of a plant caused by some type of persistent agent (Manion 1991). One must admit however, that the healthy adult tree rarely occurs in natural settings, consequently leading to an idealized situation. The definition derived from human medicine is partly inapplicable to a modular individual, and trees, (as any other plant) are modular organisms (Harper 1980, Schmid 1990). It implies the partial autonomy of their modules and, at any moment during the life cycle, some of the modules may carry pathogens without inflicting disease or inflicting mild, even asymptomatic disease. It is therefore, correct to hypothesize that a healthy tree presents few disease signs, mostly attacking few modules (with the exception of systemic diseases which propagate within whole

individual at a certain moment), not reducing significantly physiological functions. The theory of holobiome brings more clarity in the general picture of multiple interactions maintaining the state of equilibrium of the healthy individual.

In what concerns forests and ecosystem health, the definitions range from utilitarian to ecological perspectives, sometimes mutually exclusive. Also, the goals and the appropriate measurements of forest health are different when considering commercial forests and OGF and other types of natural forests (Kolb et al. 1995). For managed forests, the consistency with management goals is one of the conditions included in the definition of forest health. To begin with, when the focus is on forest ecosystem, one must consider the fact that forest health cannot be reduced to the health of single trees and cannot be only a metaphor featuring the traditional definition of health employed in human medicine. A valuable starting point in defining such a complex state is the distress syndrome described as the state of reduced primary productivity, loss of integrity, resilience and stability due to nutrient and biodiversity loss, increased fluctuations of key populations (such as trees). It is characterized by successional retrogression by which opportunistic species replace more specialized ones and by the spread of pathogens and insect pests (Haskell et al. 1992, Rapport 1992). Other ecological principles are included to complete the picture such as homeostasis, complexity or emergent properties which are sometimes debatable or non-operational. From utilitarian perspective, main aspects are linked to the loss of some important goods and ecological services (Rapport et al. 1998, Cherubini et al. 2021) when forests are perceived through their instrumental value. Despite the definition dilemma, forest health monitoring had become an important integrative set of measurements and indices meant to give a quantifiable interpretation to the health status of the forests. In the context of ecosystem health perspective, healthy state is circumscribed by vigor, organi-

zation and resilience (Rapport et al. 1998). The pathogens play a major role in as disturbance factors compromising forest health.

Many critics of the concept make reference to the health metaphor as equivalent to ecosystem resilience and sustainability devoid of operational value (Lackey 2001), ill-defined normative concept (Callicott et al. 1999) or politically motivated (Jamieson 1995). However, many critics are philosophers and scientists preoccupied by the social-environmental synthesis. Those are focused on values and societal needs, seeking conceptual frameworks for sound and beneficial nature conservation, mostly for human benefit.

Currently, forest health is an operational concept benefitting from well-defined indices and indicators. It must be stressed that indices and indicators largely employed in monitoring programs (Bussotti et al. 2018), give an average image of the forest health based on individual trees health assessment. For instance, in Romania, among indicators used to assess forest health during the National Forest Inventory, were considered crown condition and the level of defoliation (Popa et al. 2017) among other types of assessments (soil condition, tree growth, phenology, etc.). More elaborate monitoring schemes employed elsewhere include: tree mortality and standing dead trees, lichen communities (biotic proxies for air pollution), vegetation profile, fragmentation, regeneration and recruitment (Morin 2020). In Europe, the framework for sustainable forest management focused mainly on commercial forests, includes among other criteria the criterion 2 concerning the maintenance of forest ecosystem health and vitality (compromised by both biotic and abiotic stressors) and criterion 4 concerning the maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems, both important goals for all member states of EU. However, the framework works mostly for the commercial aims and ecosystem services (Linser and Wolfslehner 2022). One of the main conclusions in 2020 referred to the state

of (managed) forests which was deteriorating in Europe where insect pests, weather conditions and fungal diseases were reported as major causes of defoliation (Raši 2020). These conclusions refer to the modest proportion of primaeval and natural forests, 3.3% of the total forested area in 2020, consisting of small scale and fragmented forests (Barredo et al. 2021). Fragmentation and the diminished areas of protected OGF play an important role in amplifying the threats represented by native and exotic pathogens. However, OGF as other types of unmanaged forests, such as primary forests are considered reference ecosystems for managed forests (Kuuluvainen and Aakala 2011) They are considered models for forest structural features, dynamics, continuity and resilience after biotic or/and abiotic disturbances. This statement implies that highly natural forests are more resilient and recover after biotic disturbances.

Another important, although purely theoretical perspective is the fact that OGF provide evidence for evolutionary issues related to pathogen-tree host interactions due mainly to the fact that there are frequent examples of trees living their full life-cycle in natural setting, not encountered in managed forests. Moreover, the introduction of the holobiont concept about the co-evolution of pathogenic guilds linked to the host (Janzen 1980, Margulis and Fester 1991, Medina et al. 2021) brings an important argument in considering endemic pathogens from a conservation perspective. Holobionts are in fact communities/networks of diffusely or intimately interacting partners (Bascompte 2019). This New Paradigm (microbiome+trees=holobiont) is characterized by high degree of integration, from molecular to community level, if systemic approach is incorporated. The paradigm still fails to incorporate health as normal state since metaphorically, the holobiont can be assimilated to an ecosystem (Inkpen 2019). Pathogens are engaged in symbiotic interactions with hosts. The main relationship with trees being trophic, from molecular level to population level, this interaction exerts a pow-

erful control on host populations. Also, the interaction with hosts generates a mutual phenotypic adjustment which generates the phenotypic niche (Hunter 2009, Preston 2017), one of the dimensions of the plant pathogens' niche with important consequences for the evolution.

However, the roles they play in ecosystems go beyond the trophic interactions with their hosts, as we will see.

Bottomline, pathogens are forest community members and are significant for biodiversity, nutrient cycling, forest dynamics and successional processes.

Old-growth forests

Why the discussion focuses on old growth forests? Because of their stability and multiple patterns and pathways that establish the complexity of these unique forest ecosystems. The studies centered on high-naturalness forests were oriented traditionally on structure (Westphal et al. 2006, Burrascano et al. 2008, Fantini et al. 2020), successional pattern, dynamics (Piovesan et al. 2005, Diaci et al. 2010, Lábusová et al. 2019, Bottero et al. 2011), biodiversity (Welsh 1990, Spake et al. 2016), dead-wood (Lombardi et al. 2012) or conservation issues, tree pathogens being addresses seldomly (Vujanovic and Brisson 2002) and mostly from the perspective of biotic threats.

OGF remains currently a loose and debatable concept (Spies 2004). However, these forests together with primary forests represent a benchmark for naturalness and a model to which one compares managed forests, establish conservation goals and mitigate climate change (Kameniar et al. 2022).

A broad definition takes into consideration the prioritization of the conservation value. Alternative terms which are not entirely synonyms include: Primary Forest, Virgin Forest, Primeval, Ancient, Climax, Late-successional, Overmature Forests. Sadly, one of the practical consequences of the vagueness in defining these

forests is logging leading to worldwide shrinkage of areas covered by highly natural forests.

According to the hierarchical classification of forests using the naturalness criterion (Bauhus et al. 2009), OGF display several particular traits functioning already at the smaller scale of the forest stand but going beyond this spatial limit. We will mention only those relevant for the current context (Box 2).

Apart from the mentioned categories, there is a growing interest toward secondary OGF characterized by the existence of the non-aggressive management at some point during their history (Vandekerckhove et al. 2011), a concept which relaxes the conservation criteria, worth to take into consideration.

In this context, one has to mention the concept of forest hospitality toward other forest organisms (habitats, nurture the saplings, etc.) (Gilhen-Baker et al. 2022) stressing the importance of the holistic approach to forests and giving a new dimension with new opportunities for the conservation of high naturalness forests.

To summarize:

- i) OGF are cultural landmarks and the origin of many myths, of art and religious beliefs.
- ii) Are responsible for carbon sequestration

- No direct human impact is detectable or documented,
- Multilayered canopies, large variation of tree sizes,
- Tree size and age distribution includes old trees = habitat trees. Managed forests are quite young since old and habitat trees are considered a nuisance,
- Composed of indigenous species,
- The dominant successional stage – climax. Due to disturbances, there are also areas pertaining to earlier successional stages and seres,
- Large quantities of dead wood are accumulated as results of baseline mortality,
- Are governed by natural processes, not managed for human interests,
- Natural disturbances represent the main drivers of change,
- High biodiversity/species richness,
- High conservation value.

Box 2 Characteristics of OGF

in wood but in soil (greater than young-plantation forests) (Dean et al. 2020, Yang et al. 2021). OGF account for 10% of temperate and boreal forests in terms of C sequestration (Luyssarert et al. 2008).

iii) N-fixing organisms such as lichens, mosses, liverworts are more abundant in OGF (Lesica et al. 1991).

iv) They create stable macroclimates that function as refuges for many species, of which some being endangered and mitigating indirectly in this way the climate change (Frey et al. 2016).

v) Habitat trees are local hotspots of biodiversity.

vi) OGF contain valuable genetic pools.

vii) The preserved OGF like other highly natural forests are important for mitigating new pandemics in human population through their high diversity and containment of potential animal vectors within their natural and endemic range (Vora et al. 2022).

viii) They harbor endangered or vulnerable habitats such as, for instance Western Carpathian subalpine spruce forests or Banat pine forests (Rizman 2014).

OGF, virgin and near-virgin forests in Romania represent at most 1% of the forested area and the occupied area is exposed to shrinkage due to abiotic and biotic factors (Biriş 2017, Luick et al. 2021a) no matter how much effort was engaged in the identification and protection of these forests in the frame of the grand project The Catalog of Romanian Virgin and Near-Virgin Forests (2012-2021). Before this, several other joint projects involving Romanian, European scientists and volunteers focused on identifying and formulating proposals for the conservation of valuable OGF in Romania: PINMATRA project 2001-2005 (Biriş and Veen 2005), OldGroFor (Virgin & Old Growth Forests in Romania - Safeguarding European Biodiversity Heritage) (2018-2020), mapping of OGF performed by WWF Romania and Greenpeace Romania, PRIMOFARO project (Potential Primary and Old-Growth Forest Areas in Romania)

(Schickhofer and Schwarz 2019), REMOTE project (REsearch on MOUNTain TEMperate Primary Forests) (2011-ongoing). Probably it is worth to mention in this context that OGF as well as primary forests show greater resilience in the face of growing frequency and severity of disturbances, the major disturbance agents in Europe at the current moment being windstorms, bark beetles, and fires (Seidl et al. 2014).

Plant pathogens and complex species interactions

We chose to use network approach for the analysis of the interactions among plant pathogens and other forest organisms to demonstrate the complexity of these interactions in a holistic setting. Network science provides tools for the analysis of complex networks, ecological networks included (Strogatz 2001). Originating in the graph theory, network science explores the properties of real-world networks (technological, social, ecological, biochemical, etc.) using a set of metrics and rules. The general properties make comparable networks of different nature and demonstrate in this way their universality (Barabási 2016). The basic structure of a network consists of nodes (which stand for any type of real entity) and links between nodes that indicate the functional relationships between nodes.

Plant pathogens, particularly tree pathogens establish complex direct and indirect interactions, not restricted to their hosts but with endophytic and mycorrhizal mutualists, opportunists such as saproxylic organisms or hollow dwellers and various groups of consumers. Biodiversity is organized in species interaction networks (Hagen et al. 2012). Therefore, exploring the interactions of plant pathogens is shedding light on their real position within the forest ecosystem and their participation share to biodiversity. Using the network representation (mainly as a heuristic tool under the present essay) lends to species interactions a prominence previously neglected in the area of

disease ecology.

Many examples are connected to insect-plant pathogen interactions; in some cases, pathogen attack (especially foliar pathogens) is facilitated and magnified as a consequence of the previous consumption of the foliar mass by insects, in other cases the interaction is mutualistic and insects function as vectors of tree disease. It is important to stress the functional perspective on the pathogen perceived as one functional unit sharing several species of hosts (except for specialist/monophagous species). In this context, the three-way species interactions among trees, pathogens and insects are considered to shape forest communities (Tack and Dicke 2013, Gross 2016).

Pathogens establish functional groups within the tree microbiome and interact with other species/functional units apart from the host. Most of the empirical ecological networks are resolved at the species level. There is a possibility to employ another approach; instead of building the network using a list of species and one type of interaction (trophic, linked to dispersion, competition, etc.), one can aggregate species according to some functional criterion in coherent interacting groups and explore the resulted architecture and the topological prop-

erties of the network. The links depict different types of interactions, trophic (such as mycophagy) and non-trophic (such as facilitation).

According to the life strategies and pathogenic properties, within the plant-pathogen functional group there are several nested subgroups incorporating biotrophic, necrotrophic pathogens and sapro-pathogens. Empirical data conveying information on interactions between plant-pathogens and other groups of organisms (apart from host) are scattered in a number of publications. We aggregated the information on species interactions by differentiating the groups according to the type of interaction involved: hyperparasitism, facilitation, mutualism, opportunism, consumption, saprophytism. Below are provided few examples to validate the links connecting the nodes/functional groups. The resulted network is synthetic but based on empirical data.

Interspecific interactions of tree pathogens are complex and insufficiently studied. Figure 1 illustrates how these functional groups interact with trees and among them. For instance: pathogen facilitators are creating infection sites or debilitate the trees. An example is the extended infection with *Erysiphe alphitoides* (Erysiphales: Ascomycota) of the second fo-

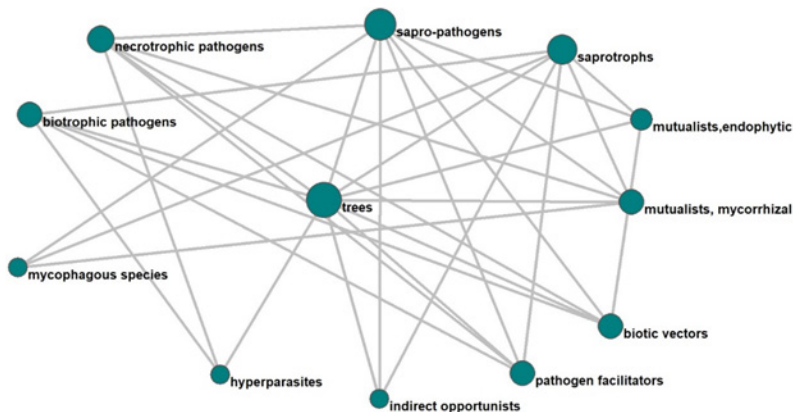


Figure 1 Conceptual framework of interspecific interactions between trees - pathogens and pathogen-associated organisms. Interaction network: *host trees*, *pathogen functional groups*, *hyperparasites*, *biotic vectors* (such as bark beetles), *mutualists associated to trees*, *facilitators* (such as defoliators facilitating infections with powdery mildews), *indirect opportunists* (such as hollow dwellers following wood rot fungi), *mycophagous species* (developing in wood-rot and mycorrhizal fungi). The size of circles is proportional to the number of interacting partners corresponding to each node's degree (number of direct links).

liar flush in *Quercus* spp. after massive defoliation due to insects, such as *Lymantria dispar* (Lepidoptera: Erebidæ) or *Melolontha melolontha* (Coleoptera: Scarabeidæ).

Vectors establish interactions with tree pathogens as mutualists (strong interactions in the case of bark and wood beetles) or accidental phoresy (weak interactions, in the case plasmodia of myxomycota transporting fungal propagules). They transport and facilitate infections with biotrophic, necrotrophic and sapro-pathogenic species. There are mentions on mycorrhizal inocula transportation by insects, mainly by mycophagous species feeding on the basidiophores of mycorrhizal fungi (Hosaka and Uno 2012). Also, wood-inhabiting Coleoptera are vectors for wood pathogenic and sapro-pathogenic fungi such as *Fomitopsis pinicola*, *Fomes fomentarius*, *Trametes versicolor* (Polyporales: Basidiomycota) (Jacobsen et al. 2017).

Mycophagous (fungivorous) species are placed among insects, nematodes, gastropodes and vertebrates – feed on mycorrhizal and wood-inhabiting fungi (pathogens, sapro-pathogens and saprotrophs). The link between saproxylic fungi (found on living trees) and fungivorous insects extends beyond the trophic relationship, the basidiocarps of fungi being used as habitats, an example being the association between *Fomes fomentarius* (L.) Kickx and the monophagous beetle *Bolitophagus reticulatus* (L.) (Coleoptera: Tenebrionidæ) (Midtgaard et al. 1998), considered a common association due to the commonness of the tinder mushroom. However, these associations are threatened by habitat fragmentation and loss correlated with managed and OGF as well, due to the fact that insects are important dispersers for fungal spores (Jonsson and Nordlander 2006).

Indirect opportunists are species such as birds or small mammals employing the tree hollows for nesting but can be represented by entire micro-ecosystems occupying specific micro-habitats in the case of flooded basal hollows harboring short-lived dendrothelmata. Tree hollows are the direct consequence of the

activity of wood parasitic fungi and function as characteristic tree micro-habitats (Asbeck et al. 2021). The diversity of tree-microhabitats, especially those determined by the activity of parasitic fungi increases with tree age, therefore the presence of veteran trees, mostly in unmanaged forests is closely linked to biodiversity and highly structured stands (Michel and Winter 2009).

Pathogens interfere with mutualist species of the trees, an example being the case of direct competition for the colonization of metabolically active roots by soil borne pathogens and mycorrhizal species (Fitter and Garbaye 1994).

Hyperparasitic species, long time neglected in plant disease studies and ecology, play the important role of control of the pathogen/parasite populations, mostly within the plant host, making this tripartite interaction important directly for the pathogens and indirectly for plant hosts (Kiss 2001, Parratt and Laine 2016, Sadhu et al. 2021) as well as for the food webs. Superficially resembling predators by exerting a top-down control on pathogen populations, hyperparasites contribute to stability of plant-host populations (Gleason et al. 2014) but remain a less approached topic in forest plant pathology. The hyperparasites follow two life strategies: they are either necrotrophic or biotrophic pathogens of their fungal hosts (Huth et al. 2021, Sun et al. 2019). The best-known example remains to the days *Cryphonectria hypovirus-1* (CHV1) which targets the tree pathogen *Cryphonectria parasitica*, the causal agent of chestnut blight, the hyperparasitic virus being responsible for the reduction of growth rate and virulence of the fungal host (Milgroom and Cortesi 2004). Trees infected by powdery mildews (Erysiphales: Ascomycota), at a closer and more attentive look display hyperparasite species of the genus *Ampelomyces*, considered to have evolved from pathogenic fungi. Hosts for these hyperparasitic fungi are *Erysiphe alphitoides*, *E. hypophylla*, (on *Quercus* spp.) or *Sawadea tulasnei* (on *Acer* spp.) (Sucharzewska et al. 2012) pointing to

The presented interaction network is unipartite and undirected comprising some of the most important functional pathogenic and pathogen-linked groups centered on trees. It is a synthetic network following the principle of co-occurrence networks (Freilich et al. 2018, Goberna and Verdu 2022) with nodes representing functional groups and links, trophic and non-trophic interactions.

The most simple network metrics are presented here in order to give to the reader a basic grasp of the complexity of such networks. In a more analytic oriented setting such networks are resolved at species level.

The above depicted network contains 12 nodes representing functional groups attached to the focal node – the trees and 32 edges/links. The average degree of a node is 5.3 and the connectivity is 0.48, these being the simplest descriptors of the network topology. For the given network, the connectivity is high.

We considered that the metric betweenness centrality employed in this context illustrates the best the degree of interaction among the considered functional groups.

Betweenness centrality (BC) is defined (Freeman 1979) as a metric that quantifies the proportion of shortest path q between any two nodes i and j that pass the the focal node v .

$$BC_v = \frac{\sum_{i \neq v \neq j} g_{ij}^{(v)}}{g_{ij}} \quad (1)$$

The nodes with highest values of BC are by default, the tree (0.204) followed by sapro-pathogenic species (0.136), saprotrophic species (0.116) and necrotrophic pathogens (0.051). The position of a node in BC hierarchy shows how important is the node for the given network taking into consideration the constraints and opportunities in occupying such a position (Borgatti et al. 2009). Most of sapro-pathogenic species in forests are connected to wood and, by consequence are important for nutrient cycling.

The analysis and graphical representation were performed using the software Pajek ver. 5.14 (Batagelj and Mrvar 2010–2021). Pajek is a program package for the analysis and visualization of large networks, providing basic information on network metrics (such as node degrees, number of links, connectivity) and complex analyses such as community detection, clustering, centrality measures, etc. Visualization is achieved using different methods of generating the network layout. The Figure 1 was obtained using the Kamada-Kawai optimization method based on minimization of the total energy of the system (which is a graph theoretic distance approach). The size of vertices is proportional to the node degrees.

the fact that hyperparasitism is more frequent in the case of specialized fungal pathogens (Bermúdez-Cova et al. 2022). As we will see, specialized pathogens having a long history of co-evolution with their host plants are biodiversity markers for highly natural forests and their hyperparasites become important for forest biodiversity too.

Plant pathogens and forest biodiversity

As OGF are extended at landscape and regional scales, plants and pathogens co-exist as a collection of populations that vary in their isolation and persistence (Burdon et al. 2006).

It is easier to locate diseased individuals in man-managed woodlands than in OGF hence, many pathogens and their prevalence remain undetected. The detection is dependent on the pathogen's developmental stage (as being quiescent endophyte in some host tissue, for instance). At present, the advances in DNA sequencing and community metabarcoding provide an enhanced framework for biodiversity studies in various ecosystems, forests included (Alem et al. 2022, Jimu et al. 2018). The tool was employed at a lesser extent to investigate tree pathogens in OGF hence, the important research niche that should be filled.

Endophytic species (spreading along the entire gradient from mutualists to pathogens) should be considered from conservational perspective especially when their hosts are rare or endangered (Blackwell and Vega 2018).

In few cases plant pathogens such as foliar species were considered as part of biodiversity on the premise of the niche diversity and availability represented by trees in OGF (Vuajnovic and Brisson 2002).

The special case of the wood inhabiting fungi (the gradient spanning from pathogens, mutualists as mycorrhizal taxa to saprotrophic species) exposed to modifications of their guild/

Box 3 Important topological properties of the network depicted in figure 1

community composition in managed forests became the flagship of naturalness indicator species. In a more restricted sense, the fungi grouped under the classical order Polyporales, mostly wood degrading fungi (including wood parasitic fungi) represent a heterogenous morpho-group as molecular data show, but nevertheless one well defined functional group (Runnel et al. 2019a, Floudas et al. 2012). Regardless of the fact that heart-rot and butt-rot fungi create problems in managed forests, their important ecological role in creating new microhabitats such as tree cavities for the various forest fauna (Remm and Lõhmus 2011) is to be considered when conservation issues are envisaged. The authors show that the density of tree cavities is higher in natural forests compared to managed forests, a characteristic linked to higher diversity of wood inhabiting fungi.

The analysis of endangered wood inhabiting species revealed that 115 species of wood polypores are threatened in Finland (Rassi et al. 2000) whose remnants of OGF cover only 0.5% of the forested area (Hanski 2000). In this context we refer to another important concept connected to OGF conservation, the extinction debt: the number of species which are expected to eventually go extinct due to the past adverse environmental change (Tilman et al. 1994, Hanski 1999). It is expected that the growing

extinction debt will affect not only pathogenic to saproxylic polypores but saproxylic insect communities which harbor a significant number of endangered species, indicators of naturalness. The phenomenon is linked to the shrinkage of the area occupied by OGF. In Estonia, where an extended and thorough survey took place on polypores from unmanaged and managed forests, data showed that highest diversity of wood inhabiting fungi was linked to late-successional and mid-successional forests where was found the highest number of endangered species (Runnel et al. 2021).

Among other provided ecological services, wood sapro-pathogenic fungi represent potential sources of new pharmaceuticals (if only taking into consideration ecological services provided by OGF), an example being the boreal species *Fomitopsis officinalis* (Stamets 2005). In a larger context, the main concerns about biodiversity loss take into consideration the common threats affecting plants and fungi. The proportions differ but the threats act in a similar way, leading to populations' shrinkage or even extinction. For instance, climatic change affects the diversity in 4.1% of plants and in 9.4% of the fungal diversity. The use of biological resources affects 21.1% of plant diversity and 13.1% of fungal diversity, the extension of transportation networks and of the access corri-

Table 1 Tree pathogens' biodiversity -comparison between managed forests and old-growth forests

Old-growth forests	Managed forests
Native pathogens which have co-evolved with their tree hosts dominate.	Exposed to invasive species which can build epidemic populations
Declining tree populations after high perturbations (epidemics, pests, fire) give place to secondary natural successions	Declining tree populations appear frequently after anthropogenic perturbations – stands with new tree composition artificially established.
The abundance of pathogen species within functional groups is relatively stable and highly even.	The abundance within functional groups varies depending on management intensity and there are many episodes of building epidemic populations.
Wood and bark depending pathogens, sapro-pathogens are diverse and some species indicate naturalness.	The number of species of bark and wood pathogens and sapro-pathogens is determined on whether old trees are removed or not.
Keystone element: habitat trees harboring rare heart rot fungi.	Habitat trees/old trees seldomly occur in managed forests

Table 2 Examples from a near-virgin forest in Poiana Ruscă Mountains, Romania (Species linked to old, dying or dead trees encountered mainly in old growth forests.)

Species	Characteristics
<i>Hericium erinaceus</i> (Bull.) Pers.	Rare, white rot fungi, red-listed in 13 European countries due to shrinkage of natural forests' areas pertaining to <i>Luzulo-Fagetum</i> forests (9130) Although edible, the picking of this species is restricted in Great Britain (Antonelli et al. 2020)
<i>Sparassis crispa</i> (Wulfen) Fr.	Root pathogen on conifers, under threat, indicate naturalness.
<i>Meripilus giganteus</i> (Pers.) P. Karst	White rot fungi on oaks and beech, rare, endangered, indicating naturalness.

dors affect 2.5 % of plant diversity and 4.4% of fungal diversity (Antonelly et al. 2020).

Table 1 summarizes important differences in terms of biodiversity between OGF and managed forests, leaving the list opened as our knowledge progresses and the research interest rises given the societal orientation toward mitigation of global climate change.

The comparisons between biodiversity of OGF and managed forests show in many cases higher biodiversity in OGF. However, monitoring fungal biodiversity at large in OGF and managed forests remain a challenge (Runnel et al. 2021).

Same comparison revealed that natural forests harbored a greater diversity of macro-fungi, particularly, wood inhabiting species of which indicator species were more diverse than in managed forests (Dvorak et al. 2017).

There are instances when managed forests display high biodiversity at the level of indicator groups of organisms (insects, wood decomposing fungi, mycorrhizal fungi, birds, etc.). Using a management gradient of beech forests in Denmark, Atrena et al. (2020) demonstrated that wood inhabiting fungal species richness was driven by dead wood high volume and size, increased naturalness due to management abandonment or shift to natural models, and stand features as age and existence of canopy gaps.

The number of species attached to any of the important or indicator groups may not be larger in OGF for the reason of limiting factors as in the case of boreal conifer forests or peatland forests characterized by few plant species of which

a considerable proportion is represented by rare or endangered species (Luick et al. 2021b). It applies to specialized plant pathogens.

From holistic/systemic perspective, in a given ecosystem at equilibrium, there is an optimal biodiversity which can be high under optimal environmental conditions or relatively low in ecosystems exposed chronically to harsh conditions.

For instance, even common and widespread wood inhabiting fungi are numerically increasing in OGF such as *Fomes fomentarius* while other species maintain stable populations across time such as *Piptoporus betulinus* and *Ganoderma lipsiense* (Vandekerkhove et al. 2011). However, even highly fragmented areas harboring OGF are able to conserve for long periods wood inhabiting fungi such as *Phellinus nigrolimitatus* and *Phellinus ferugineofuscus* reported on spruce in Finland (Komonen et al. 2021). During our field work in Romanian OGF, we encountered rare wood inhabiting fungi (Table 2), an important finding for the high conservative value of those forest stands.

We assume that the important difference between natural and managed forest is the evenness component of the pathogens' biodiversity: under stable conditions, evenness is high in natural forests and low or at least lower in managed forests. This observation implies the fact that proportions of abundances expressing the representation of each species are different in managed and OGF forests given approximately the same composition. A hypothesis

worth to verify in future studies.

Biotrophic pathogens are of particular conservation interest since they are specifically linked to their plant host lacking the saprotrophic phase in their life cycles. The highly specialized taxonomic group of ord. Uredinales (rusts) are important drivers of community dynamics and diversification (Toome and Aime 2013) and the product of long host-pathogen coevolution (Thompson and Burdon 1992, Giraud et al. 2008). There are known rather few species attacking trees but not less important, species attacking the forest herbaceous plants, biodiversity components if only taking into consideration the indicator species. One example is the rust *Uromyces erythronii* (Pucciniales, Pucciniaceae) associated with *Erythronium dens-canis* (Liliaceae), (Nagy et al. 2019). The host is characteristic for *Quercus*, *Carpinus betulus*, *Fraxinus* woodlands, on eutrophic and mesotrophic soils in Central and Eastern Europe (G1A1 EUNIS habitat type classification). Rare rust species are linked to rare plant species and there is a conservation concern about these dual systems (Helfer 1993). Also, the presence of heteroecious rust species (alternate hosts represented by tree/other woody or non-woody species) signals the presence of rare, endangered or endemic species being the case of *Chrysomyxa rhododendri* (DC.) de Bary (Coleosporiaceae, Pucciniales) with *Picea* spp. as aecial host and species of *Rhododendron* (as well as other species of fam. Ericaceae) as uredial hosts. In Romania, the hosts are represented by *Picea abies* and *Rhododendron kotschy* Simonk, the latter being a protected species (Oltean et al. 1994) and considered vulnerable within its areal according to IUCN.

It is true that introduced rusts are able to develop epidemic populations such being the case of *Melampsoridium hiratsukanum* S. Ito ex Hirats. f (Pucciniales, Pucciniaceae) on alders and larches (EPPO 2021, Negrean and Anastasiu 2006) and *Cronartium ribicola* J.C. Fisch. (Pucciniales, Cronartiaceae) on five-needled pines and species of *Ribes*

(Newcombe and Dugan 2010, Blada 1990). *Chrysomyxa abietis* (Wallr.) Unger, monoecious species on *Picea* spp. needles (Bontea 1985, Grudnicki and Tănase 2003), although native species to Europe and Asia, became invasive in the temperate zone of other continents (Hansen 1997).

Order Taphrinales is another taxon containing biotrophic pathogens, important for global forest biodiversity and considered from conservation perspective (Balckwell and Vega 2018). *Taphrina betulina* on *Betula* spp. in Europe (Bacigálová 1997) is an example.

Examples of Red Listed species such as *Amylocystis lapponica* (Polyporales), present populations are recovering in OGF reserves (Runnel et al. 2019b). In Romania, among the Red-Listed wood-inhabiting fungi are *Lariciformes officinalis* considered endangered species, *Hericium erinaceus* as vulnerable species and *Hapalopilus croceus* listed as endangered species in Romania and vulnerable in Europe, on oak and chestnut (Tănase and Pop 2005, Dahlberg 2019). An important fact linked to this category of fungi, species with large, perennial and robust fruitbodies is that they are most exposed to forest management practices (Abrego et al. 2017). Fungi are very good dispersers (Kirk et al. 2008), long distance dispersal events (Stenlid and Gustafsson 2001) ensure stable inocula as long as their hosts and substrates exist, old trees included.

Fragmentation, the relatively small sizes of forest areas designated as protected areas are main causes for the future extinction debt both in forest plants and fungi. The areas of protected OGF in Romania are frequently too small, and surrounded by intensively managed forests. However, it is unrealistic at present moment to expect larger areas of forests to be excluded from exploitation. A compromise with societal needs in wood would be to improve the ecological quality of the managed forests by new practices of forest harvest and regeneration and to restore the forest to the late successional natural-like state (Hanski 2000).

Plant pathogens – threats to OGF in the context of global climate change

Most of pathogenic fungi of trees are opportunistic species, with some becoming endophytic without inducing disease symptoms for long time, as studies have shown in the case of several species pathogenic on oaks (Gonthier et al. 2006, Moricca et al. 2012), the disease being triggered by environmental stressors which weaken the trees (Moricca and Ragazzi 2008). However, there are considerable threats induced by pathogens due to climate change and trade globalization that will impact OGF (Pysek et al. 2011) and lately, the war affecting large areas worldwide.

How a global stressor such as the climate change will affect the balanced relationship between the tree pathogens and OGF? Generally, it is assumed that trees will suffer from higher mortality and decline (Desprez-Lousteau et al. 2007). The category of invasive alien pathogens is especially threatening considered as second most important factor after habitat fragmentation/destruction affecting forests at large (Wilcove et al. 1998, Panzavolta et al. 2021). The threat is deriving mostly from the pathogenic properties accounting for the lack of co-evolutionary history and the lack of the evolutionary history within the new environment at different spatial scales: individual tree, forest stands and forested landscapes (Parker and Gilbert 2004, Stenlid et al. 2011, Stenlid and Oliva 2016, Holdenrieder et al. 2004). By extension, one can consider the biotic environment represented by tree microbiome to which a new pathogen is not adapted, the microbiome being a part of the tree phenotype. For instance, the endophytic microbe community (part of the tree microbiome) plays the important role of helping trees to sense the shifts occurred in their environment and mediating the responses to stressors (Oliva et al. 2013). However, it should be reminded that endophytic species span the entire spectrum from mutualistic to pathogenic species and the network of interacting species is complex and in

continuous shift and adjustment.

Of particular interest is the fact that trees being long lived, they have low capacity to adapt to rapid environmental shifts and rely on their phenotypic plasticity to cope with climate change or other type of stressors. Trees may encounter difficulties in adapting fast enough by regulating morphological and life-history traits (Stenlid and Oliva 2016, Valladares et al. 2007). Various types of stressors act upon trees in managed forests cumulatively lowering their resistance to pathogens. Climate change is one of leading factors affecting forests and acting as facilitator for many tree pathogens. It was shown that resilience of the OGF is greater compared to commercial forest but main and important environmental crises such as climate change, habitat fragmentation and invasive species affect them as well. These create the context for the exposure to novel environmental conditions that may not be handled and pathogen attack can lead to decline.

Concerning OGF, the main factors involved in the introduction of invasive alien pathogens are linked to the extension of roads and other access means, tourism and the proximity of managed forests (Ascensão 2017). An example coming from our experience during the work on the OGF in the frame of the Romanian Catalog of Virgin and Near-virgin forests, stems from Poiana Ruscă Mountains harboring near-virgin beech, beech-spruce, beech-fir-spruce forests. During the field work covering two consecutive years (2018-2020) we observed how *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya (Ascomycota: Helotiaceae), responsible for the decline of alders worldwide (Gross et al. 2014, Inoue et al. 2019) was rapidly extending on riparian *Fraxinus excelsior* trees vegetating along the banks of Valea Pleșu creek (coordinates: 22°18'19" E: 45°39'28" N), sided by one of the main forest roads. Even if the road was outside of the protected area, it was close enough to the protected forest stands surrounded by commercial forests, exposed by consequence to infections.

Conclusive remarks:

Apparently, a discussion on the role of the plant pathogens in highly natural forests would bring arguments to mitigate the perils menacing the health of valuable ecosystems. A closer look and consideration of the current disease ecology progresses, of the biodiversity integrative studies, of the new holistic approaches shaping modern ecology brings in the focus rare or endemic pathogens. Those are important control factors of plant populations, are components of the plants' phenotypic niche and of the global biodiversity, are potential providers of services (sources of medicines) and components of the intricate food and other types of species interactions' webs.

The key conclusions of the present essay:

- i) Pathogens are important components of biodiversity and tree microbiome.
- ii) They are density dependent factors that control trees' populations size and factors of baseline mortality.
- iii) The interactions they build are complex, with different functional groups directly connected to trees.
- iv) Tree decline reported in OGF in many places around the globe, linked to climate change and invasive pathogens, determines new successional paths and considerable loss of the present-day biodiversity.
- v) Nevertheless, there are species of pathogens indicating the forests' state of naturalness or play the role of biodiversity indicators.
- vi) The comparisons between old-growth and managed forests biodiversity should be focused on species evenness as species richness explanatory tool.
- vii) To demonstrate the proposed hypotheses more empirical data should be gathered on pathogens dwelling in old-growth forests.

During the months of work on the present essay we witnessed scientific debates became all the sudden of minor interest: the efforts to mitigate climate change, biodiversity and habitat reduction were overshadowed by new ge-

opolitical orientations. All we can hope is the reason to prevail and valuable high naturalness forests with all associated biodiversity to remain intact.

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