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Review

The Known, the Unknown, and the Expected: 130 Years of Research on Non-Lichenized Fungi and Fungus-Like Organisms in the Białowieża Primeval Forest, Poland

Małgorzata Ruszkiewicz-Michalska [1,2], Monika Kozłowska [3], Mateusz Wilk [4], Katarzyna Janik-Superson [5,6] and Wiesław Mułenko [3,*]

[1] Institute for Agricultural and Forest Environment, Polish Academy of Sciences, Bukowska 19, PL-60-809 Poznan, Poland; malgorzata.ruszkiewicz@isrl.poznan.pl
[2] Department of Algology and Mycology, Faculty of Biology and Environmental Protection, University of Lodz, Banacha 12/16, PL-90-237 Lodz, Poland
[3] Department of Botany, Mycology and Ecology, Institute of Biological Sciences, Maria Curie-Skłodowska University, Akademicka 19, PL-20-858 Lublin, Poland; monika@poczta.umcs.lublin.pl
[4] Department of Ecology and Environmental Conservation, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Zwirki i Wigury 101, PL-02-089 Warsaw, Poland; mwilk@uw.edu.pl
[5] Biobank Lab, Department of Molecular Biophysics, Faculty of Biology and Environmental Protection, University of Lodz, Pomorska 139, PL-90-235 Lodz, Poland; katarzyna.superson@biol.uni.lodz.pl
[6] Department of Invertebrate Zoology & Hydrobiology, Faculty of Biology and Environmental Protection, University of Lodz, Banacha 12/16, PL-90-237 Lodz, Poland
* Correspondence: wieslaw.mulenko@poczta.umcs.lublin.pl

Citation: Ruszkiewicz-Michalska, M.; Kozłowska, M.; Wilk, M.; Janik-Superson, K.; Mułenko, W. The Known, the Unknown, and the Expected: 130 Years of Research on Non-Lichenized Fungi and Fungus-Like Organisms in the Białowieża Primeval Forest, Poland. *Forests* **2021**, *12*, 518. https://doi.org/10.3390/f12050518

Academic Editors: Patrick O. Waeber and Lucienne Wilmé

Received: 27 February 2021
Accepted: 20 April 2021
Published: 22 April 2021

Abstract: The history of mycological research and current activities in the Polish part of the Białowieża Primeval Forest are presented. The review of literature-derived and unpublished data on species of non-lichenized fungi and protozoan and chromistan fungal analogues indicates a minimum of 3504 species observed in this area. The gaps in the exploration of fungi: unstudied taxa, plant communities, habitats, hosts, and substrates, as well as the limitations of former studies, are discussed. Our estimates show that a total of 8000 fungal species possibly occur in the Białowieża National Park alone, and more than 10,000 are expected to be found in the Polish part of the Białowieża Primeval Forest. Despite more than a centennial history of mycological research, the majority of data come from only a few older scientific projects and several more recent citizen-science-related activities, emphasizing the need for a modern, interdisciplinary study on the diversity and ecology of fungi in this area.

Keywords: natural forests ecology; fungal refuge; fungal richness estimates; fungus/plant ratio; fungal diversity; microfungi; macrofungi

1. Introduction

Primeval forests currently cover only approximately 0.7% of the total forest area in Europe [1] but have a disproportionately high value of biodiversity hotspots and refuges for many organisms in increasingly fragmented landscapes [2]. Their conservation value will certainly increase in the face of ever-increasing demand for forest-derived products and services and the recently reported significant increase in the total harvested forest area and biomass loss [3]. One such forest is the Białowieża Primeval Forest (BPF), situated in the eastern part of the Central European Lowland along the Polish-Belarusian border (Figure 1), and covering approx. 1500 km^2 in total (632 km^2 in Poland)—the only relict of the once extensive boreal-nemoral forest zone in Europe [4–6].

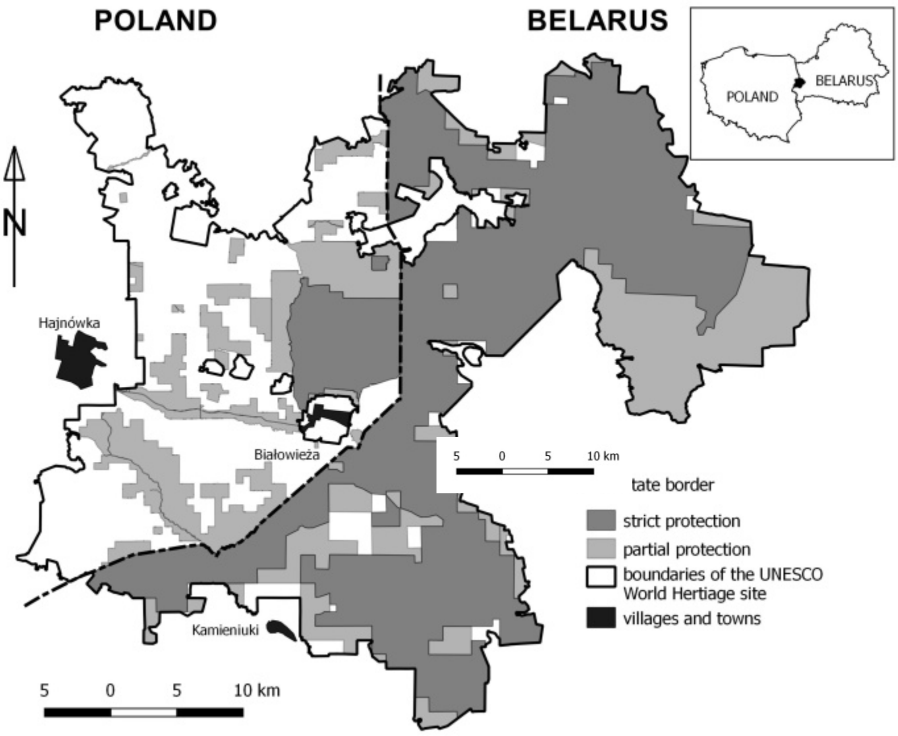

Figure 1. The location and boundaries of Polish and Belarusian parts of the Białowieża Primeval Forest (courtesy of the Institute of Forest Research, Białowieża; used with permission).

The continuous forest cover has been present there for close to 12,000 years, and substantial fragments of close-to-primeval forest have survived [6]. Natural and best-preserved forest stands show a high richness of plant species, varied age and layer structure, as well as an abundance of dead wood lying on the forest floor [1,4,7–10] (Figure 2).

The Białowieża Primeval Forest, and the Białowieża National Park, in particular, are often considered a refuge for diverse groups of organisms [4,6,7,11,12], as well as a model ecosystem for the study of the ecology of the natural temperate forest [10,13–16]. Ecological processes occur naturally and stimulate the forest's self-renewal without human intervention [17,18]. The results of the research conducted in BPF constitute a reference point for more transformed forest ecosystems. Particular attention is paid to the process of tree dieback and the role of dead wood in maintaining the high biodiversity of this area [9,19,20] (Figure 3).

After several ages of informal protection, the most valuable natural areas of BPF have been secured by national legal acts, with the first six nature reserves established in 1921. Finally, the Białowieża National Park was established in 1932 in an area with the lowest anthropogenic interference, covering 105.2 km^2 (approx. 16% of the Polish part of BPF) (Figure 4). It is the oldest national park in Poland [21–23].

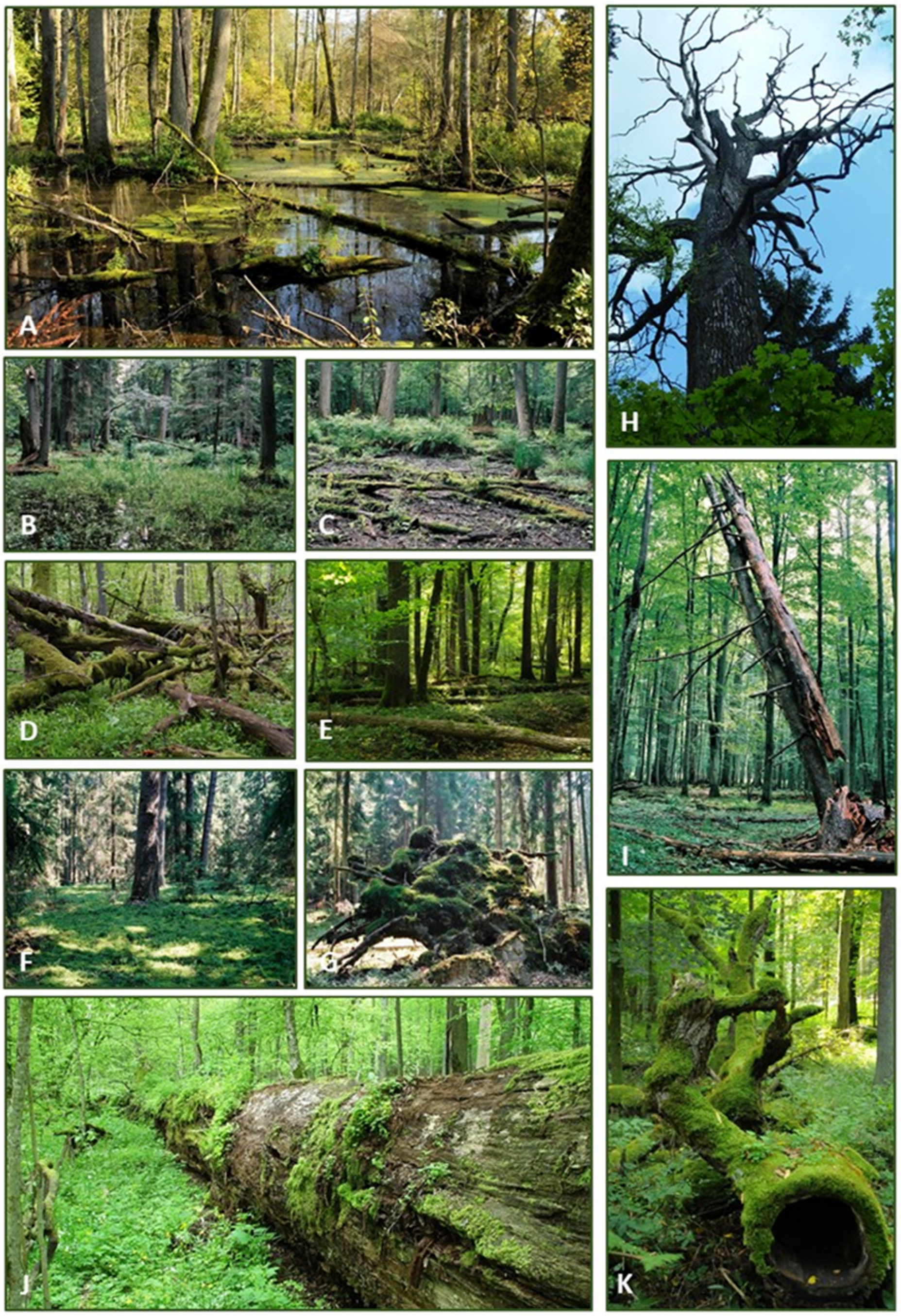

Figure 2. Deadwood in various forest communities of the Białowieża National Park. (**A**) *Circaeo-Alnetum* (ash-alder forest); (**B**,**C**) *Carici elongatae-Anetum* (black alder forest); (**D**,**E**) *Tilio-Carpinetum* (oak-linden-hornbeam forest); (**F**,**G**) *Peucedano-Pinetum* (fresh pine forest); (**H**) dead trunk of "Dąb Bartny" *Quercus robur* L. (nature monument); (**I**,**J**) dead logs of deciduous and coniferous trees in *Tilio-Carpinetum*; (**K**) dead log of "Dąb Jagiełły" *Quercus robur* (nature monument). Phot. W. Mułenko.

Figure 3. Wood-dwelling fungi in the Białowieża Primeval Forest. (**A**) *Fomitopsis pinicola* (Sw.) P. Karst. on the trunk of *Quercus robur*; (**B**) *Ganoderma* sp. and *Fomes fomentarius* (L.) Fr. on an old log of *Quercus* sp.; (**C**) *Sarcoscypha* sp. on the rotten tree remnants; (**D**) *Armillaria mellea* (Vahl) P. Kumm. s.l. on the trunk of living *Acer* sp.; (**E**) *Gyromitra sphaerospora* (Peck) Sacc. on an old hardwood log; (**F**) young fruitbody of *Fomitopsis pinicola* on the trunk of *Picea abies* (L.) H. Karst; (**G**) *Lycoperdon pyriforme* Schaeff. on the rotten roots of a fallen tree; (**H**) *Stereum* sp. on the lower side of an old stump of *Carpinus betulus* L.; (**I**) various species of fungi, lichens, and mosses on the trunk of *Carpinus betulus*; (**J**) *Xylaria polymorpha* (Pers.) Grev. on the decayed trunk of a deciduous tree. Phot. W. Mułenko.

In 1977, the Białowieża National Park was declared a Man and Biosphere Reserve, and it was inscribed on the UNESCO World Heritage List in 1979, while a whole Polish-Belarusian Białowieża Forest was nominated the Natural World Heritage site in 2014 [11].

In the years 1997–2007, it boasted an honorary European Diploma for Protected Areas, awarded by the Council of Europe to the areas of exceptional European importance that are managed in an exemplary way. Since 2008, BPF is a Special Protection Area within the "Natura 2000" network (PLC200004) [11].

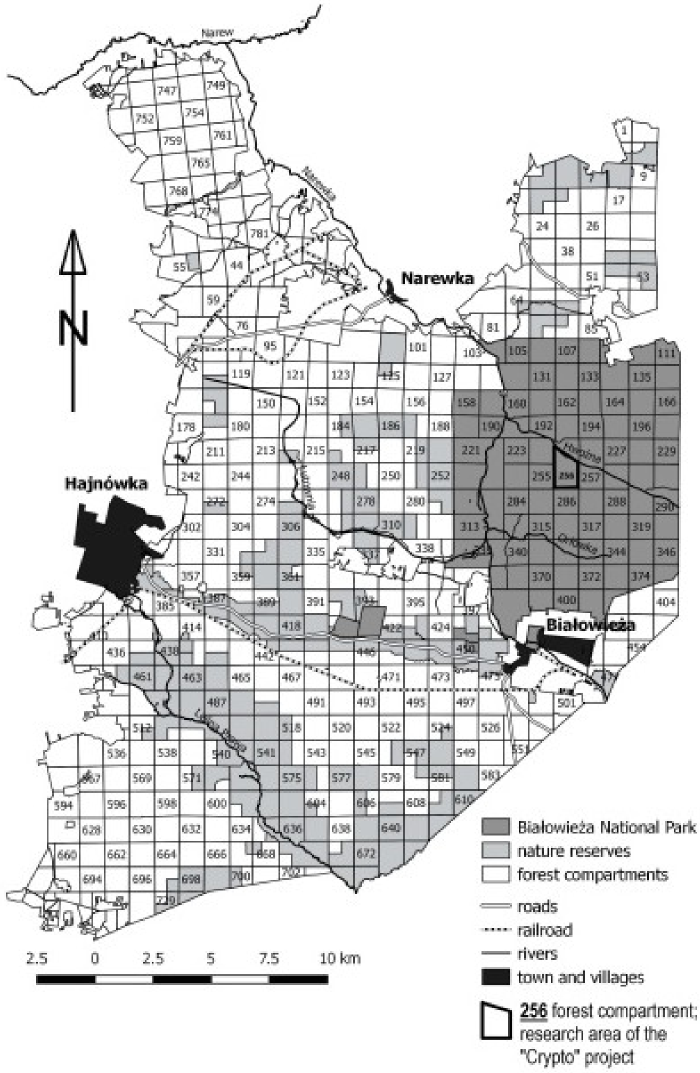

Figure 4. The location of the Białowieża National Park and other protected areas of the Polish part of the Białowieża Primeval Forest (courtesy of the Institute of Forest Research, Białowieża; used with permission).

The Białowieża Primeval Forest covers an undulating ablation moraine plain, built mainly of sands, clays, and gravels of glaciofluvial origin, and cut with numerous shallow river valleys [24]. A relatively high diversity of landforms, including vast plains, inland dunes, depressions filled with organic deposits, and short hills [24], is reflected in equally diverse vegetation, constituting of forest/shrub and non-forest communities (31 and 40, respectively) [4,17,25,26]. Due to its location close to the northern boundaries of the continental biogeographic region of Europe [27], BPF features plant communities of mixed biogeographic origin. A characteristic feature of these communities is a lack of beech (*Fagus sylvatica* L.) and a significant presence of spruce (*Picea abies*), which occurs in almost all types of forests, but also forms independent communities (spruce forests) [28]. Among more than 1000 species of vascular plants, there are 25 native and 17 introduced tree species [25], many of which reach a considerable size and impressive shape, rarely found elsewhere. Almost 1500 trees are considered nature monuments [29,30]. The flora of BPF comprises numerous rare, endangered and protected species, including relict plant species of northern origin [17,26].

Such rich and diverse flora of the primeval forests should theoretically support a high diversity of the funga [31]. Due to their extreme morphological, physiological, and ecological plasticity, fungi play an essential role in the functioning of most ecosystems on Earth as saprotrophs, parasites, and symbionts [32]. Their function is especially pronounced in forests, where they shape the interactions within plant communities as ubiquitous mycorrhizal symbionts [33], and drive carbon cycling as potent lignocellulose degraders [34,35].

Scattered reports indicate that BPF can be indeed recognized as the essential fungal refuge both in Poland and in Europe [6,10,11,36–39]. This statement is well supported by the statistics provided by Karasiński [39] and Kujawa and co-workers [11,40] for macromycetes: species listed in BPF account for ca. 25% of the European funga and 42% of the Polish funga (the term "funga" is used following the recommendation of Kuhar et al. [41]). Moreover, BPF is the only place of occurrence for almost 200 species in Poland, and for some of them, also in Europe [11].

It would seem that an area of such exceptional conservation value would have been researched in detail, but this is not so, at least not for the fungi and fungus-like organisms (FLOs). Although the history of mycological research in BPF is quite long (over 130 years), the complete checklist of fungi recorded in the area still does not exist. An earlier study estimated the already published total fungal richness in BPF to be approx. 3500–4000 species [36]. The only published checklist of non-lichenized fungi recorded in BPF covers 1761 species of microfungi, larger ascomycetes, and FLOs [42].

The knowledge of the fungal diversity in BPF is the necessary first step to more sophisticated research aimed at the general understanding of their intricate functions in the primeval forest. It is also indispensable for strengthening the conservation efforts in this area, and these are needed because logging for timber in the forests outside the BNP is a recurring problem with potentially highly negative consequences (e.g., [43]). Knowledge on the distribution of rare, endangered, and protected taxa, and the designation of umbrella species, could certainly help improve the perception of the whole BPF as an area that deserves protection.

The present study, therefore, aims to (I) review the history of the mycological research in this ecologically precious area to highlight the most valuable studies, (II) to summarize the knowledge about fungal richness, (III) to provide estimates of the potential richness to be found, and (IV) to identify the research limitations and gaps that need to be addressed. Although it focuses on the Polish part of the Białowieża Primeval Forest, a piece of short information on mycological research in its Belarusian part is also provided.

BPF is often viewed as a possible refugium for relict species. Almost 30 years ago, Cieśliński et al. [44] provided a provisional list of 35 potential macrofungal relict species from BPF, which included 13 "strictly primaeval forest relicts." Additionally, Majewski [45] proposed that at least 10 species of Laboulbeniales recorded from BPF might be considered relicts of the primeval forests. However, due to the fragmentary knowledge on the distribution of non-lichenized fungi in Poland and Europe, it is still too early to provide a reasonable list of old-growth forest relict species from BPF. The sole fact that a given species was recorded only in the BPF obviously means little if the majority of the country/region/habitat types are poorly investigated. Therefore, we resigned from any attempts to address this question in the present paper.

Information about lichenized and lichenicolous fungi is mostly omitted in the paper. These fungal groups were comprehensively studied also in recent years (e.g., [16,46,47]), and deserve a preparation of a separate survey. Microsporidia, specialised intracellular parasitic organisms classified as either protists [48] or fungi [49] were excluded from this paper, although there are a few species known from the area [50,51].

2. Data Sources and Methods

The primary sources of the data are the published papers and monographs concerning mycological studies in the Polish part of the Białowieża Primeval Forest. The data from BPF are scattered in diverse published sources from over 130 years, including old reports and checklists from regional exhibitions and forays. Many of these were written in Polish and are mostly inaccessible to the general public, also due to the lack of digital copies. The latter applies unfortunately also to the most important monumental monographs on the diversity and ecology of flora and funga in BPF resulting from the project CRYPTO [52–55]. All historical data were critically analysed, and species synonymy was agreed with modern taxonomic approaches of particular taxa [40,42]. Unfortunately, some modern papers focused on ecological questions and presenting in-depth meta-analyses (e.g., [13,56]) do not provide primary data on the species composition (missing even in supplementary files, cf. [57]).

The Web of Science [58] (accessed 23.02.2021) was searched in All Fields for all years for terms "Bialowie*" AND "funga*," "Bialovie*" AND "funga*," "Bialow*" AND "mycorrh*," which retrieved 54, 1, and 6 results, respectively. We excluded irrelevant publications (mostly related to food microbiology, trait-based broad ecological studies, and lichenological publications) based on the title, abstract, and full text. All inventories of fungi, case studies, and monographs of single fungal species were kept in the analysis.

Over 260 papers on micromycetes and larger, non-lichenized ascomycetes, and protistan and chromistan fungal analogues were found [42]. The preliminary synthesis of the bibliography on macromycetes (mainly basidiomycetes) showed about 500 items [40]. Unfortunately, many of the reports contain overlapping data, with members of Xylariales being an example of fungi classified as macro- or micromycetes. We estimate that the "overlapping data" concern 100–150 species. The precise number is unknown due to the lack of a summary list of all fungal taxa (both referred to as macro- and micromycetes) recorded in BPF.

The following databases were searched for information on genetic data (published and unpublished) on fungi and fungus-like organisms (FLOs): NCBI GenBank, UNITE, Silva, iBOL, Agricultural Research Service, Fungal Genome Size Database, Genomes OnLine Database, MycoCosm, and FungiDB [59–67]. The following phrases were entered to search: ((fungi) AND Bialowieza), ((Phytophthora) AND Bialowieza), ((molds) AND Bialowieza), ((Myxogastria) AND Bialowieza), ((Dictyostelia) AND Bialowieza), ((Protozoa) AND Bialowieza), ((Protista) AND Bialowieza), ((Chromista) AND Bialowieza), ((Oomycota) AND Bialowieza), ((Myxomycota) AND Bialowieza), (podlaskie). The variants "Białowieża," "Bialowieża," "Białowieza" (with and without Polish letters), as well as "Bialowieska" (Polish name: Puszcza Bialowieska) and "podlaskie" (podlaskie voivodeship) were also used in the above-listed queries. Whole genomes were also searched.

3. Outline of the History of Mycological Research in the Białowieża Primeval Forest

The main research findings that had shed new light on the species richness and fungal diversity of the area are outlined below. Some of them have become turning points, a key element in estimating fungi and FLOs' potential richness.

3.1. The Origins of Mycological Research—Late 19th to Early 20th Century

The first data on the fungi in BPF come from the early 19th-century paper of Brincken [68], the author of the first monograph of the Białowieża Primeval Forest. He [68] mentioned two species of hypogeous fungi: *Tuber album* (=*Choiromyces meandriformis* Vittad.) and *Tuber cibarium* (=*Tuber aestivum* (Wulfen) Spreng.), as well as three generic names (*Clavaria*, *Phallus*, and *Tremella*). For many following decades, no mycological research was conducted in this area. The papers by Błoński and co-workers [69–71] are considered to be the beginning of the actual research. Since then, the research has been carried out continuously until now. Błoński et al. [69], Błoński [70], and Błoński and Drymmer [71] listed

357 taxa of fungi in total, mostly identified to a species level, including newly described species (e.g., *Xylaria polonica* Błoński). They also provided the first data on slime moulds (19 species) in BPF, while the next information about the latter group (82 species) was given at the beginning of the 20th century [72]. During World War I, a series of five volumes entitled "*Bialowies in Deutscher Verwaltung*" (Białowieża under German administration) was published. In the 4th issue, data on fungi collected during a floristic-faunistic expedition organized by the Bayerische Akademie der Wissenschaften [Bavarian Academy of Sciences] were included. The list concerned over 70 species of fungi, mainly forming large fruitbodies [73]. The subsequent relevant publications appeared in the first half of the 20th century. In total, 209 fungal species from various taxa (asco- and basidiomycetes) were reported in five papers by Siemaszko [74–78] and by Siemaszko and Siemaszko [79,80], including the series "*Fungi bialowiezenses exsiccati.*"

In the 1940s, Karpiński [81] analysed fungi' participation in selected forest communities in a significant study entitled "*Materials for the bioecology of the Białowieża Primeval Forest.*" In total, 138 fungal genera and 247 species were listed in the paper [81].

3.2. The Second Half of the 20th Century

In the years 1950–1999, very intensive mycological research was carried out, and important results were reported. Noteworthy is the thorough and systematic research aimed at identifying fungi inhabiting linden (*Tilia cordata* Mill.), oak (*Quercus robur*), maple (*Acer platanoides* L.), hornbeam (*Carpinus betulus*), alder (*Alnus glutinosa* (L.) Gaertn.), spruce (*Picea abies*), and Scots pine (*Pinus sylvestris* L.), i.e., the main trees forming oak-hornbeam, and coniferous, alder, and riparian forests. The research was conducted by, among others, Pachlewski and Borowski [82] and Truszkowska [83–87], who provided information on over 100 fungal species (mainly ascomycetes, traditionally classified as disco- and pyrenomycetes). Mycocoenological research by Nespiak [88] should also be highlighted, as his 2-year study on the participation of fungi in forest communities of the Białowieża National Park (BNP) yielded as many as 425 macromycete species collected from 24 permanent observation plots (100 m^2 each) and in their surroundings. This significant number of species was collected from a relatively small area of approx. 0.3–0.4 ha in total. While conducting similar research in several forest types in BNP, Orłoś [89] recorded 151 fungal species (26 asco- and 125 basidiomycetes). The trip to BPF held during the 4th Congress of European Mycologists in 1966 also significantly contributed to the knowledge of this region's fungi. A post-congress paper provided data on 318 species from this area [90]. In the 1950s, also slime moulds were investigated by Krzemieniewska [91], who listed 36 species from BPF.

In the 1960s, intensive research on plant-parasitic micromycetes was started in BNP: T. Majewski studied obligatory plant parasites' participation in 8 forest communities [92]. The three-year study provided data on 193 species from three groups of true fungi: powdery mildews (Erysiphaceae), rust fungi (Pucciniales), smut fungi (Ustilaginales s.l.), and fungus-like organisms (FLOs)—downy mildews (Peronosporales and Albuginales). It should be emphasized that, for the first time, research on this group of fungi was conducted with the use of permanent observation plots, which resulted in comprehensive ecological data. The research methodology designed by Majewski [92] was used in many subsequent field studies in Poland [93]. At the same time, prof. Majewski has started long-term research on Laboulbeniales (insect parasites) in BNP. The results were being published successively for almost 30 years (a series entitled Rare and new Laboulbeniales from Poland), and their culmination was the monographic study Laboulbeniales of Poland [94]. Later, a comprehensive study on laboulbenialean fungi in the Polish part of BPF and the Atlas of the geographical distribution of Laboulbeniales in Poland were prepared [45,95].

The last two decades of the 20th century brought new, fundamental data on fungal richness, diversity, and ecology. In 1987, interdisciplinary research was initiated to study the role of spore organisms: fungi (including lichens), mosses, liverworts, slime moulds, and algae in the structure of the natural forest communities of BPF. The research was proposed by prof. W. Wojewoda (Institute of Botany of the Polish Academy of Sciences), and it was implemented under the supervision of prof. J.B. Faliński, head of the Białowieża Geobotanical Station of the University of Warsaw. This research is known as project CRYPTO [52]. The study was conducted for four seasons (1988–1991) in a single forest division of a total area of ca. 1.5 km^2 (plot no. V-100 BSG UW) (Figure 4) divided into 144 one-hectare squares. The study area had excellent geobotanical documentation that facilitated interdisciplinary research. The basic assumption was to adopt the same research method for all groups of organisms, which allowed comparative analyses. In this relatively small area, 1878 species of cryptogams (including 1380 species of fungi) and 286 species of vascular plants were confirmed. The results were presented in four monographs [52–55] and over 50 original papers. Species new to science were described during project CRYPTO: e.g., *Kainomyces rehmanii* T. Majewski, *Stigmatomyces minilimosinae* T. Majewski, *Siemaszkoa ramificans* T. Majewski, *S. valida* T. Majewski [96,97], and *Entylomella sii-latifolii* (Sacc.) U. Braun and Mułenko [98]. Moreover, many species of fungi new to Poland, rare or associated with new host species were found, e.g., *Gyoerffyella oxalidis* Vanev, *Erysiphe gorlenkoi* (F.T. Chien) Giril and Gulis, *Plasmopara ribicola* J. Shröt. [99,100]. Some participants of the project CRYPTO continued mycological research in BPF, and their results were presented only in the 21st century. The research on microscopic plant parasites was continued in the years 1992–1995 on a much smaller, one-hectare area (plot no. 40 BSG UW) with one forest community (the oak-linden-hornbeam forest, *Tilio-Carpinetum*) [101]. A total of 226 species of fungi associated with the above-ground shoots of 30 herbaceous plant species were identified (on average, seven fungal species per one vascular plant species) and analysed in connection with the rhythm of host phenology. This study's results are mainly unpublished: only the analysis of fungi on *Stellaria holostea* L. has been reported [102]. Other CRYPTO participants took part in a pan-European initiative to monitor the fungi in oak forests [103]. The research, carried out on two observation plots in the oak-linden-hornbeam forest (*Tilio-Carpinetum*), resulted in a significant number (215) of macromycete species [104].

3.3. The 21st Century and Genetic Advancements

Another CRYPTO participant, macromycologist, prof. A. Bujakiewicz for many years organized the **Exhibition of Fungi**. This long-term initiative was launched in 1966 (during the 4th Congress of European Mycologists) and has been regularly organized since 1993 at the Educational Center of the Białowieża National Park by Dr. A. Kujawa and co-workers [40]. Exhibited macrofungal specimens are provided mainly by the students of the local forestry college and visiting mycologists, but they also include specimens collected and brought by the local people and identified by the curators of the exhibitions. The significant involvement of the non-professionals adds to this enterprise a dimension of a citizen-science approach. The exhibitions play an important role in exploring the BPF's funga as the reports (11 published until now) presenting the lists of collected species have been published, the first in 1996 [105] and the last only recently [106]. The summary of the six exhibitions (in the years 2012–2017) mentioned a total of 865 species (72 asco- and 793 basidiomycetes) collected in BPF [40], being, in fact, the third most important source of data on fungal diversity in BPF after the project CRYPTO [52–55] and studies by Nespiak [88].

Prof. T. Majewski extended his research to cover the entire Polish part of the Białowieża Primeval Forest and its extensive foreground and published a comprehensive study of Laboulbeniales [45]. The paper lists 240 species collected on 282 invertebrate host species at 722 sites, making BPF and its surroundings the best-studied area in Poland in terms of laboulbenialean fungi.

The arthropod-pathogenic fungi were also investigated by prof. S. Bałazy and his Polish-Belarusian team [107] in both parts of BPF. They reported 36 species from

Entomophthorales (26), Hypocreales (7), and Eurotiales (3) isolated from insects, soil, and leaf-litter samples from the Polish part of BPF.

In the 2010s**,** some previously initiated research yielded important syntheses, and a few new mycological projects have begun. The specimens collected during the preparation of the Exhibitions of Fungi were included in the papers concerning particular species (*Buglossoporus quercinus* (Schrad.) Kotl. and Pouzar and *Pluteus albineus* Bonnard) and genera (*Coprinus* and *Lepiota*) [108–112], as well as in the ecological studies [40,113]. Some fragmentary data from BPF have also been reported or discussed in other papers (i.e., [114–116]).

Some essential data on diverse fungal groups were collected in Białowieża forests in 2019 during the rapid biodiversity inventory called bioblitz designed for quick collection of site-specific survey data, held during the 18th Congress of European Mycologists [117]. The numerous mycologists, including the renowned specialist in some taxa, have identified 233 species (561 records), including four species new to Poland and eight new to BPF [118].

As the result of older and new projects, some taxa have been recently newly described based on specimens originating from BPF, e.g., *Aporpium macroporum* Niemelä, Spirin and Miettinen [119], *Aurantiporus priscus* Niemelä, Miettinen and Manninen [120], *Hebeloma aanenii* Beker, Vesterh. and U. Eberh. [121], *Lecanicillium praecognitum* Gorczak and Kisło [122].

Since 2017, ectomycorrhizae have been investigated in more detail in the frame of two projects [123–125]. One of them concerns ectomycorrhizal fungi investigated using mycorrhizal root examination and fruitbodies. The preliminary results have been reported only recently [123,124]. About 490 ectomycorrhizal taxa have been identified using the fungal barcoding region (rDNA ITS). The most numerous taxa observed as mycorrhizae include *Cortinarius* (48), *Tomentella* (32 species new for BPF), *Russula*, and *Lactarius*. For the first time, some hypogeous fungi, e.g., *Pachyphlodes* (3 species), *Melanogaster* (3 species), and *Tuber* (5 species) have been confirmed in BPF. Moreover, Leski et al. [123] and Wilgan et al. [124] reported *Lentaria albovinacea* (Pilát) Pilát, and *Russula intermedia* P. Karst.—the species considered to be extinct in Poland [126] and 63 other species red-listed in Poland.

In another study, the effects of coarse woody debris (presence and stage of decay) on species composition of ectomycorrhizal fungi associated with *Quercus robur* have been studied [125]. In 120 soil samples from the vicinity of 60 investigated trees at three study sites in BPF, 18 species of fungi have been detected using DNA barcoding. Most of them belong to basidiomycetes (13 species), and one out of five ascomycetes is classified as a dark septate endophyte (*Phialocephala fortinii* C.J.K. Wang and H.E. Wilcox). The most abundant ectomycorrhizae have been identified as formed by *Tomentella* sp. and *Pachyphlodes nemoralis* Hobart, Bóna and Conde. The research confirmed that coarse woody debris supported ectomycorrhizae development, stimulating mainly the species with contact or short-distance exploration types of mycelium [125].

In the last years, mycologists' attention has been particularly attracted by fungi preferring deadwood—the substrate present in the BPF in great abundance and a wide variety of tree species, age, and size. Papers on taxonomy and ecology of *Pluteus fenzlii* (Schulzer) Corriol and P.-A. Moreau, and two species complexes (*Postia caesia* (Schrad.) P. Karst., *Skeletocutis nivea* (Jungh.) Jean Keller) have also been published based on specimens gathered in BPF [127–129]. The papers by Holec et al. [10,127,130] and Szczepkowski et al. [112], devoted to the ecology of wood-inhabiting fungi (associated with fallen oak trunks), included the discussion on the threat factors to the stenobiontic fungi species. Important information about the species richness of wood-inhabiting macromycetes was also provided by Holec et al. [10]: during a single field visit, they collected as many as 187 macroscopic fungi species (seven asco- and 180 basidiomycetes) on 32 logs of *Quercus robur*. Kowalski et al. [20] provided a list of 51 fungal species (40 asco- and 11 basidiomycetes) isolated from trunks of dying trees of spruce *Picea abies*.

The projects in progress include the experiment on the effect of various biotic and abiotic factors on the decomposition of deadwood of four tree species (oak *Quercus robur*, hornbeam *Carpinus betulus*, spruce *Picea abies*, and Scots pine *Pinus sylvestris*) [131,132]. It started in 2011 with the settling of 720 tree logs in three forest communities (deciduous and coniferous) in three different manners: logs have been either fastened to trees at 1.5 m above ground, set on the ground, or buried 5 cm underground. Based on morphological traits, Jaroszewicz and co-workers [133] distinguished 93 morphotypes on 716 logs of wood of the four tested tree species, and half of them was identified to the species level. The host wood identity and the degree of contact with the soil were the most important factors shaping the communities of deadwood-inhabiting macrofungi, while the forest type appeared to be less important. After seven years, the first samples were also studied using the Next Generation Sequencing method to provide the metabarcoding data for 30 *Picea abies* logs buried in the ground. The resulting operational taxonomic units represent yeasts, white and brown rot fungi, mycorrhizal taxa, and others. According to Wrzosek and co-workers [132], the preliminary results confirm the biocoenotical significance of the buried wood.

Wood-associated fungi are also currently studied in terms of their medicinal properties. The specimens from BPF are successfully screened for biologically active compounds with anticancer potential and other promising applications by the team of M. Wołkowycki and Dr. E. Zapora [134–136].

One of the less-studied groups of micromycetes in BPF is water-associated fungi. Only scarce information was available until the late 2000s: 37 species of aquatic fungi and fungus-like organisms (FLOs) were isolated from the Narewka river's water and natural ponds in the Białowieża village by Kiziewicz [137,138] and Orłowska et al. [139]. Further studies [140–142] increased their number to 155 species confirmed in rivers and water bodies of BPF. Moreover, Górniak et al. [143] investigated the fungal biomass in Narewka and other rivers in the region. The latter study did not provide data on species richness and diversity of fungi and fungal analogues.

Only in the second decade of the 21st century, intensive research on slime moulds was undertaken. The observations were carried out on permanent observation plots located in BNP in 2013 and in other regions of BPF in 2014 by Dr. A. Drozdowicz [144,145]. The synthesis of literature and the author's data revealed 127 species [145], which accounts for almost half of all myxomycete species recorded in Poland [146].

The 21st-century studies are also the first source of molecular data on fungi and FLOs in BPF (Supplementary Table S1). The INSDC database (GenBank) [59] provides only one RefSeq of *Lecanicillium praecognitum* based on 18S rRNA [122]. Two barcodes based on mitochondrial DNA are available for rust fungus (*Chrysomyxa ledi* (Alb. and Schwein.) de Bary): one of cytochrome c oxidase subunit III (*CO3*) coding gene, and the second of dehydrogenase subunit 6 (*nad6*) gene [147]. The vast majority of sequences belong to genomic DNA and RNA sequences. There are 295 genomic barcodes: 16S rRNA, 5.8S rRNA coding gene, ITS1/ITS2, and 26S rRNA, or 28S rRNA genes that code large subunits D1 and D2 of ribosomal ribonucleic acid (LSU). Four other genes, i.e., *Mcm7* (DNA replication licensing factor), *tub2* (beta-tubulin), *EF1-α* (translation elongation factor 1-α), and *RPB2* (DNA-dependent RNA polymerase second largest subunit), were sequenced less frequently. In total, 41 species are represented in the GenBank dataset [59], including 25 basidiomycetes, ten ascomycetes, and six FLOs species from the *Phytophthora* genus [122,130,147–150]. The detailed information on molecular data is given as a supplementary material (Table S1).

Table 1. The current number of species of fungi and FLOs from the BPF according to published and unpublished data [20,42,107,118,122,125,137–142,147–155].

FUNGI	**3221**
Ascomycota	1245
Basidiobolomycota	1
Basidiomycota	1907
Blastocladiomycota	4
Chytridiomycota	8
Entomophthoromycota	45
Mortierellomycota	2
Mucoromycota	7
Zoopagomycota	2
CHROMISTA	**159**
PROTOZOA	**124**
Total	**3504**

The search in the iBOL (BOLD) [62] database retrieved only two sequences of *Chrysomyxa ledi*, i.e., 28S rRNA and ITS2 [147].

3.4. Mycological Research in Belarusian Part of the Białowieża Primeval Forest

Concluding the history of mycological research in BPF, one should also mention its Belarusian part (ca. 58% of the entire BPF complex), the second part of the UNESCO Biosphere Reserve, which is also partially protected as the National Park "Belovezhskaya Pushcha." However, a summary of mycological activity in the Belarusian part of BPF is lacking [156]. Moreover, information about the research is scattered in a variety of often unsearchable and inaccessible sources, including books from the 1960s (often only in Russian) and scientific journals (e.g., Микология и Фитопатология (Mycology and Phytopathology) published by the Russian Academy of Sciences). The first piece of information comes from the XIX century from papers of Polish naturalists [70,71], but for the following decades, fungi were studied sporadically only [157]. The most recent information about macromycetes provided by Shabashova et al. [157] indicates that they are very poorly studied compared to the Polish part of BPF. The studies of macromycetes were undertaken twice: the first in 1950–1970 (159 aphyllophoroid and over 300 agaricoid species) and a second time in 2015–2018 (140 species of aphyllophoroid fungi) [157]. The scarce online papers available concerning micromycetes in the National Park "Belovezhskaya Pushcha" present incomplete data, e.g., seven anamorphic species associated with seven plant species from Ranunculaceae [158], 27 anamorphic, plant-parasitic species [159], 66 species of Erysiphales [160], and 67 species of plant-associated anamorphs [161]. Moreover, the limited data on entomopathogens were reported by Sosnowska and co-workers [107], who listed 13 species isolated from soil samples and infected insects, including common fungi—*Beauveria bassiana* (Bals.) Vuill., *Metarhizium anisopliae* (Metsch.) Sorok., and *Paecilomyces fumosoroseus* (Wize) Brown and Smith. Both a synthesis of existing data and further intensive research are essential for recognizing the fungal richness and diversity in the Belarusian part of BPF.

4. The Known—A Synthesis

Over centennial efforts to explore the diversity of fungi and fungus-like organisms (FLOs) in the Białowieża Primeval Forest (BPF) yielded information highly diverse in terms of scientific value and accuracy. It is evident from Figure 5 that there are only three relatively recent milestones in the history of the mycological research in BPF that provided the most significant number of newly reported fungal taxa: the research by Nespiak [88], the project CRYPTO [52–55], and the most recent mycological activities including mainly the Exhibitions of Fungi [40,106], and the preparation of the micromycete checklist by Kozłowska et al. [42]. A significant contribution of the Exhibitions of Fungi emphasizes the growing role of citizen science, which to some extent buffers the paucity of the scientific projects on the fungal diversity in the BPF, but often at a price of lower quality metadata (e.g., mostly the species identity is recorded and not the habitat, substrate, or precise locality, etc.).

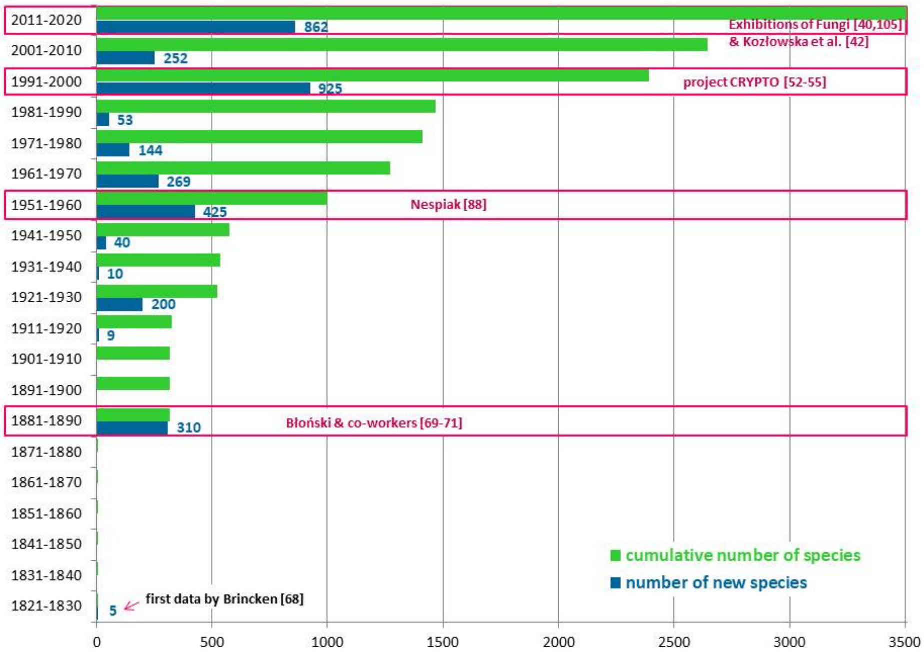

Figure 5. Total number of new species of fungi recorded in decades from the Polish part of BPF. The cumulative number of new species is also provided. The milestone works, contributing the most significant numbers of species, are highlighted. The calculations include only taxa identified at a species level.

The total number of fungal and FLOs species presented in Table 1 is the result of a compilation of data from 510 published papers and a number of unpublished data; the latter mainly limited to molecular information from the databases available online (cf. Supplementary Table S1). The list prepared by Kozłowska and co-workers [42] was the main source of data on species traditionally classified as micromycetes (diverse taxa of fungi and FLOs) and larger non-lichenized ascomycetes. The list covered 1667 species [42]. It has been further supplemented with data from a few earlier omitted papers, and the resulting current number of fungi and FLOs species is 1777. This number is further extended with critically revised and compiled data concerning taxa of larger basidiomycetes [151]. This group accounts for 1719 taxa (including 1689 species, one subspecies, 27 varieties, and four forms).

Therefore, the current total number of fungal taxa (species and subspecific taxa of macro- and micromycetes) found in BPF and its immediate vicinity is 3504. This finding adequately supports the claims that the taxonomic diversity and species richness of fungi observed in BPF are the greatest among all the protected areas and forest complexes hitherto studied in Poland [11,151,162–164].

Only the existing checklist of micromycetes and larger non-lichenized ascomycetes [42] can be provided with more detailed information on the diversity of species collected in the forests of the Polish part of BPF and its man-transformed areas, e.g., clearings, arable fields, meadows, and roads. The highest number of species (1266 species) from the two above-mentioned groups was reported from the forests located within the Białowieża National Park, the most mycologically studied area of BPF. Far fewer species were collected in the forests outside the national park (727 species), while 359 species were recorded in the above-mentioned man-transformed areas.

According to Kozłowska and colleagues' checklist [42], the most frequently inhabited substrates in BPF include:

- Vascular plants—fungi were hosted by 473 species, which constitute almost 50% of the flora of the Polish part of BPF and over 60% of the national park flora. Particularly significant numbers of fungal species were found in association with some tree species: *Carpinus betulus* (139 fungal species), *Quercus robur* (112), *Picea abies* (90), *Populus tremula* L. (86), *Alnus glutinosa* (83), *Tilia cordata* (54), *Betula pendula* Roth (45), *Fraxinus excelsior* L. (30), and *Betula pubescens* Ehrh. (23).
- Cryptogamous plants—13 species (mosses, ferns, clubmosses, and horsetails) hosted 19 fungal species.
- Other plant substrates—wood (244 fungal species), bark (12), small twigs (130), dead stems of herbaceous plants (76), tree trunks (60), and boughs and branches (41).
- Invertebrates—270 species hosted 163 fungal species altogether (126 from Laboulbeniales and 37 from Entomophthorales).
- Soil—68 species were isolated.
- Water and plant remnants submerged in water—149 species were isolated from streams, rivers, and water bodies (permanent and periodic).
- Fungi—66 fungal species hosted 38 taxa of mycoparasites, including six species of hyperparasites.

The dominant plant community in the area, the oak-linden-hornbeam forest (*Tilio-Carpinetum*), is the best-studied in terms of the amount of research, and it is the most species-rich community (726 fungal species) [42] of fungi recorded: black alder forest (*Carici elongatae-Alnetum*)—365, high mixed coniferous forest (*Pino-Quercetum*)—229, fresh coniferous forest (*Peucedano-Pinetum*)—207, and low mixed coniferous forest (*Querco-Piceetum*)—215. Mycologists rarely investigated non-forest communities (rushes, herbs, pastures, etc.), and the greatest number of fungi was recorded in grassland communities, including fresh meadows of *Arrhenatherion* alliance—24 species.

In contrast, the data on macromycetes cited below are much less detailed. Even though the research on the participation of Agaricomycotina and Pezizomycotina in BPF's forest communities was conducted more often than on micromycetes, no comprehensive list has ever been published, and the metadata are often missing from the oldest studies and those resulting from citizen-science-related activities. Until the end of 2020, at least 2187 species were confirmed in BPF (summarized data from [40,106,165]), which accounts for approx. 46% of the biota of larger asco- and basidiomycetes in Poland. Among them, 32 species are under legal protection, and almost 500 out of 963 species are red-listed in Poland (according to [126]), including the highest threat categories (extinct and endangered) [151].

5. Estimations of Potential Fungal Richness

The total species richness of fungi in the world has attracted the interest of scientists for many years or even centuries, but it was rarely defined precisely. Carolus Linnaeus (1707–1778) defined the number of fungi as "very large," and Elias Magnus Fries (1794–1878) defined it as at least equal to the number of insect species (approx. 250,000 known at that time). Later on, the number of fungal species was also most often referred to as the number of other groups of organisms [31]. Only the early 21st century sources gave the species number instead of estimates: Kirk et al. [166] indicated 97,330 scientifically described species, while currently, this number is one and a half times greater, ca. 148,000 species [167].

In the early 1990s, Hawksworth [31] started a contemporary discussion about the potential species richness of fungi living on Earth. He [31] estimated that the number of fungal species in a given area is at least six times greater (on average) than the number of its plant species. Assuming this pattern and the number of known plant species (then ca. 270,000), the predicted number of fungal species in the world was over 1.5 million (1,620,000). The subsequent estimates showed that the ratio fungi: plants could be considered as being even higher. Hawksworth [168] estimated it as 8.2:1, while Hawksworth and Lücking [169] proposed it as equal 7.9:1 to 10.7:1, and the number of expected fungal species as ca. 2.3 million to even over 3 million (2.2–3.8 million), respectively.

Further discussion of the richness of BPF's funga is based on the model proposed by Hawksworth [31]. In addition to published data, we also used the unpublished or partially published information from other studies conducted in BPF (e.g., [101]).

F. Błoński, the first researcher interested in BPF's macromycetes, while publishing a list of 350 identified species, estimated that their number might range from 1200 to 2000 [71]. His predictions now appear to be valid for macromycetes alone.

The results of the project CRYPTO [52–55], despite the limited research time (4 seasons), acreage (140 ha, cf. Figure 4), and the number of studied plant communities (6), indicated a proportion close to 5:1 (1380 macro- and micromycete species and 303 plant species). The results of the subsequent research [101] indicated a 7.6:1 ratio (227 fungal species and 30 plant species), even though it was carried out for three years, on a smaller area (1 ha), in a single plant community (oak-linden-hornbeam forest, *Tilio-Carpinetum*), and was limited to micromycetes on above-ground organs of herbaceous plants. However, the total number of fungi was certainly underestimated, as no culturing and molecular identification methods were used. Still, the single plant species were confirmed to host numerous fungi species, e.g., *Urtica dioica* L. (26 fungal species), *Stellaria nemorum* L. and *Mycelis muralis* (L.) Dumort. (25 each), *Galium odoratum* (L.) Scop. and *Oxalis acetosella* L. (22 each), *Moehringia trinervia* L. (21), *Ranunculus lanuginosus* L., and *Rubus idaeus* L. (20 each) [101]. Additionally, the single sampling of fungi on 32 logs of a single tree species (*Quercus robur*) done by Holec et al. [10] revealed a high richness of fungi (187 species).

Potential hosts/partners for fungi include over 14,600 species from main eukaryotic groups (Table 2) occurring in BPF [25,170–176]. If only vascular plants are included in the estimate, the number of fungal species expected to be present in the BNP alone varies from ca. 4000 to 7800, and in the whole Polish part of BPF from ca. 5000 to over 10,000 (Table 3). Given that the total fungal richness recorded in BPF so far is ca. 4000, one could therefore ask where is the rest of this diversity.

Table 2. The number of species of diverse groups of organisms in BPF.

Group	Number
vascular plants (Białowieża Primeval Forest)	1020
vascular plants (Białowieża National Park)	786
cryptogams	286
algae	156
lichens	400
animals (diverse groups in total)	12,000
mammals	59
birds	260
spiders	331
insects	9482
Total	**14,648**

Table 3. The estimates of fungal numbers in BPF and BNP according to the presumed fungus: plant ratio.

Number of Fungi Species: Number of Plants Species
5:1
Białowieża Primeval Forest → 5 × 1020 = **5100**
Białowieża National Park → 5 × 786 = **3930**
8:1
Białowieża Primeval Forest → 8 × 1020 = **8160**
Białowieża National Park → 8 × 786 = **6288**
10:1
Białowieża Primeval Forest → 10 × 1020 = **10,200**
Białowieża National Park → 10 × 786 = **7860**

6. Where to Look for Undiscovered and Undescribed Fungi?

6.1. Taxonomic Groups

The history of mycological research conducted in the Białowieża Primeval Forest (BPF) shows that, as in any other research area, the best, scientifically robust results are achieved by studies carried out by experts in specific taxa. In this regard, intensive studies worth noting (cited in detail in the "history" section) were carried out by (i) W. Truszkowska (pyrenomycetes on woody plants), (ii) T. Majewski (obligatory plant parasites—rusts, smuts, powdery and downy mildews, and insect parasites—Laboulbeniales), (iii) M. Chmiel (discomycetes), (iv) A. Bujakiewicz, B. Gierczyk, D. Karasiński, A. Kujawa, M. Lisiewska, A. Skirgiełło, and A. Szczepkowski, and J. Holec and his co-workers, (diverse macromycete taxa), (v) S. Bałazy, A. Chlebicki, M. Kozłowska, and W. Mułenko (diverse micromycete taxa).

However, what draws attention is the lack of information about some fungal taxa or their inadequate exploration in BPF. It applies to the three groups monographed in Poland relatively recently: (i) ubiquitous endomycorrhizal fungi from Glomeromycota—no data from BPF [177], (ii) arthropod-parasitic fungi from Entomophthorales—46 species from BPF in total [107,118,178], and (iii) saprotrophic dematiaceous anamorphs—12 species from BPF [179]. The latter group was planned to be studied during the project CRYPTO, but unfortunately, the designated specialist resigned.

Additionally, the specialists in corticioid and polyporoid fungi did not participate in the project CRYPTO, which significantly influenced the completeness of the species list. Information about these fungi was later supplemented by various authors, including D. Karasiński, M. Wołkowycki, T. Niemelä, as well as A. Kujawa, A Szczepkowski, B. Gierczyk, T. Ślusarczyk, and other co-workers with data gathered during the preparation of the annual fungal exhibitions in Białowieża [40].

The species richness of fungi from basal clades (Basidiobolomycota, Chytridiomycota, Blastocladiomycota, Mortierellomycota, Mucoromycota, and Zoopagomycota) is also barely known (Table 1). The complete lack of data applies to other, relatively poorly known taxa in Poland, e.g., Neocallimastigomycota, Cryptomycota, and Rozellomycota.

6.2. Terrestrial and Aquatic Habitats

Only six out of over 30 forests and scrub communities [17,180] and over 40 non-forest, terrestrial communities [26] have been thoroughly investigated under the project CRYPTO and later by Kozłowska [101]: *Tilio-Carpinetum*, *Fraxino-Alnetum*, *Carici elongatae-Alnetum*, *Peucedano-Pinetum*, *Pino-Quercetum*, and *Querco-Piceetum*. Five other forest and peatland communities were investigated sporadically (*Potentillo albae-Quercetum*, *Piceo-Alnetum*, *Vaccinio uliginosi-Pinetum*, *Molinio-Pinetum*, and *Sphagno girgensohnii-Piceetum*). The least known in terms of fungi are open peatlands and non-forest communities—meadows, fens, rushes and pastures, as well as ruderal and synanthropic habitats. Even though they comprise a significant number of plant species (potential hosts of fungi), they have been almost completely ignored in previous research of plant-associated fungi. Similarly, only a few species of fungi were recorded on arable crops. The list of litter-associated fungi, i.e., those found on dead remnants of plants, animals, and fungi lying on the forest floor, is still incomplete. Most of the data on this group concerns discomycetes and come from forest communities studied on plot no. V-100 BSG UW during project CRYPTO [181–183]. Elsewhere, only species forming large fruitbodies (e.g., *Peziza* spp., *Helvella* spp., *Sarcoscypha* spp.) were noticed. Additionally, small basidiomycetes were collected very rarely, and there is no information about non-fruiting species massively overgrowing the forest litter.

It is worth emphasizing that there is little information on soil microfungi and species associated with the plant rhizosphere (excluding ectomycorrhizal species). So far, the isolation of saprobic microfungi from BPF soils has not been carried out on a larger scale, and 68 species are known only from forest soils [42].

The total number of fungi and FLOs found in or isolated from water (aquatic and aero-aquatic fungi) in BPF is considerable and accounts for 162 species. However, this number originates from a few studies, which were limited in scope and time. Saprotrophic hyphomycetes, potentially very numerous in freshwaters, are greatly underrepresented. Data on yeasts and yeast-like fungi, and species related to aquatic micro-organisms, e.g., algicolous or rotifer-associated fungi, are entirely lacking. There is no information on the spores of airborne fungi (part of aeroplankton) originating from different types of habitats and substrates.

6.3. Diverse Substrates and Hosts

While there is an enormous richness of potential substrates in BPF, the data on the fungi associated with them vary greatly in quality and number. Most of the information comes from the studies on fungi inhabiting plant material, most importantly living or dead trees, and, to a lesser extent, also herbaceous plants. The synthesis of the results from the CRYPTO project [52–55] revealed that epixylic and litter-inhabiting fungi were dominant in terms of species richness, followed by parasitic micromycetes and epigeous fungi. This pattern might be true also for the whole BPF—the wood-inhabiting fungi producing large fruitbodies prevail in the inventories with about 250 species of ascomycetes [42] and several hundred species of larger basidiomycetes (from Agaricomycotina) recorded. However, these records still represent only a small fraction of the fungi associated with multi-species and different-aged wood, which are expected to occur in the BPF's forests.

Herbaceous plants, mainly native (ca. 1000 species in BPF), are the second relatively well-studied group of micromycetes' hosts in BPF [54,92,101]. The data on obligatory parasites and facultative saprotrophs growing on living herbaceous plants mostly come from a few plant communities, among which most meadow, rushes, synanthropic and ruderal phytocoenoses are missing. Only a small percentage of hosts are spore plants (mosses, ferns, clubmosses, and horsetails)—19 species of fungi were recorded from only 13 species from this numerous group of hosts.

The mycorrhizal and endophytic symbioses are among the least studied plant-fungus relationships. Historical data on species richness and taxonomic diversity of ectomycorrhizal fungi are known in BPF mainly from research on fruitbodies, while studies of mycorrhizae based on the actual examination of roots have started only in the 2010s and are not numerous [123–125]. Data on species richness and diversity of endophytes are very limited. The presence of a single species of systemic endophytes (*Epichloë typhina* (Pers.) Brockm.) was confirmed [42], and three dark septate endophytes (*Acephala applanata* Grünig and T. N. Sieber, *Phialocephala fortinii* and *P. europaea* Grünig and T.N. Sieber) were observed recently in association with tree roots [153,154]. However, there is little information on species belonging to a large and highly taxonomically diverse group of non-systemic endophytes, although some of the so-far-recorded plant parasites presumably belong to this group.

Among the animal hosts, the arthropods inhabited by Laboulbeniales (126 species, hosted mainly by carabids and staphylinids) and, to a lesser extent, Entomophthorales (45 species) and Hypocreales (8), are the best-studied [45,107,118,178]. However, the number of known hosts of these fungi constitutes less than 3% of ca. 9800 species of insects and spiders known from BPF [173]. Data on parasites of vertebrates and animal endosymbionts are mostly lacking.

The vegetative and generative structures of fungi are among the least known as hosts and substrates. Information on their occurrence in BPF is limited to 38 species (including six species of hyperparasites) found on 66 species of fungi from a few taxa. No data are available on myxomyceticolous fungi, and the exact number of lichenicolous fungi species found in BPF is unknown, although it is estimated at 50 species [6,11].

7. Limitations of the Data

Methods used in the mycological research in the Białowieża Primeval Forest (BPF), and the corresponding quality of collected data, are another, perhaps most important, limitations to the full recognition of the fungal diversity in this area. Long-term, multidisciplinary studies conducted on fixed observation plots were carried out only once in BPF because such research is a highly demanding endeavour in terms of time, money, and logistics. In fact, they are limited to the single effort in the frame of the project CRYPTO in the 1990s [52–55]. In the last decade, citizen-derived data became a major source of information on fungal diversity in BPF [11,118].

Almost all pre-2010 studies were based on observations of fruitbodies, rarely also on isolation and culturing. Molecular, metagenomic studies should be included as a standard in the further exploration of the funga, as the genetic data from BPF currently available in GenBank [59] and iBOL [62] databases cover only 41 species of fungi and fungus-like organisms (FLOs). The majority of sequences are the barcodes based on ITS1, ITS2, SSU, and LSU, while others are rare (Table S1). There is a lack of diverse sequences that are widely used in fungal taxonomy or phylogenetics, e.g., fungal-specific translation elongation factor 3 (*tef3*), DNA topoisomerase I (*top1*), phosphoglycerate kinase (*pgk*), or fungal hypothetical protein Lipin/Ned1/Smp2 (*LNS2*).

Given that the majority of fungal taxa were recorded during only a few scientific projects (all pre-2010), and that the only other significant share of the taxon list was contributed by basically a citizen-science endeavour (i.e., Exhibitions of Fungi [11]) supplemented by ad hoc initiative (i.e., bioblitz 2019 [118]), the quality of the data is a serious problem in any broader analysis of fungal diversity and ecology in BPF. While even the identity of taxa recorded in older works often remains questionable, the metadata, including precise location, substrate, season, habitat, host, etc., are mostly missing from the oldest and anecdotal reports, as well as from a significant share of the data collected during the Exhibitions of Fungi (2012–2019). This means that any ecological meta-analyses are currently feasible only on the data from a project CRYPTO and a few other studies—

projects covering only a small fraction of the BPF area (cf. Figure 4), conducted over a short time period, and/or focusing on only selected fungal groups. Several preliminary analyses were already published [53–55] and revealed interesting phenomena, e.g., constant proportions of species numbers of vascular plants and pteridophytes, fungi, lichens, mosses, and hepatics irrespectively of the forest community type [54], or an increase in fungal species richness in the ecotones of specific forest communities [55]. However, to what extent their results are still valid for BPF, and whether they can be extrapolated to other non-forest ecosystems within BPF or other primeval forests in Europe remains an open question. The answer requires a modern, broad-scaled, and long-term project. The calls to repeat the multidisciplinary investigations taken under a CRYPTO project using the up-to-date approach remain, as for now, unanswered [184].

8. Conclusions

Despite 130 years of mycological research in the Polish part of the Białowieża Primeval Forest (BPF), the picture of the fungal diversity in this area is still surprisingly far from complete. A high proportion of the data was contributed during short-term scientific activities and forays organised by the non-scientific community. The plant-associated fungi and fungus-like organisms (FLOs) belong to the best-explored taxa, while animal-related species have attracted much less attention from researchers. Species associated with fungi are mostly underexplored, and taxa accompanying myxomycetes and algae remain unexplored. Forest-dwelling fungi are obviously best-studied, while fungal diversity in the diverse non-forest communities is largely unexplored.

Cautious predictions lead to the conclusion that:

- Considering the current knowledge of fungi and FLOs in BPF (3504 species), the number of ca. 5000 species (5:1 fungus: plant ratio) should be treated as a minimum number that can be found in the Białowieża Primeval Forest, even if only the existing, traditional research methods are maintained. However, based on the list of hosts, habitats, substrates, or taxonomic groups that have not been studied so far (or have been studied insufficiently), it is very likely that the number of species could exceed 8000 (8:1 fungus: plant ratio).
- The intensification of research, the use of molecular identification methods on a larger scale, and also conducting research well-prepared in terms of methodology (permanent research plots, interdisciplinary long-term research, and the extension of research to previously omitted types of habitats and plant communities) should result in finding much larger numbers of fungal and FLOs species, exceeding the values corresponding to proportion 1:10 (i.e., about 10,000–15,000 species).
- The expected numbers of fungal and FLOs species would be even greater if the estimates were corresponding to the biodiversity of the entire area of the Białowieża Primeval Forest, including its greater Belarusian part. Thus, the holistic approach and the future, joint Polish-Belarusian studies of funga in the entire complex of BPF are greatly needed.

Our review of the richness and diversity of fungi and FLOs and their factual and presumed complex interactions with other organisms is yet another argument supporting the conservation of the natural resources in the Białowieża Primeval Forest, including the deadwood, a substrate scarce in man-managed forests. Since BPF regularly gains some wider attention in the popular and scientific literature, in the context of the controversies surrounding the loggings in its area, we feel that our paper would add a valuable point to this general discussion. Our paper clearly highlights the existing and the potential diversity of fungi in BPF, which calls for both appropriate conservation/management strategies and a more comprehensive investigation. We also emphasize the need for collaborative, interdisciplinary research on the diversity and function of fungi in this area and the formulation of easy-to-implement metadata collection guidelines to aid the increasingly popular citizen-science-based inventories of fungi and improve the overall quality of the data collected in BPF.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/12/5/518/s1, Table S1: Molecular data on fungi and FLOs from BPF available in GenBank and iBOL databases.

Author Contributions: W.M. conceived the idea and led the writing of the manuscript together with M.R.-M. and M.W. All authors wrote specific parts of the manuscript (introduction: W.M., source queries and methods: M.W., M.R.-M. and K.J.-S.; history: M.K. and W.M., recent and molecular studies: M.R.-M., M.W. and K.J.-S., estimates: W.M. and M.K., conclusions: W.M., M.K., M.R.-M., M.W. and K.J.-S.) and contributed critically to the drafts of the whole manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: The research was funded by the Polish Ministry of Science and Education: subvention for the Institute of Biological Sciences of Maria Curie-Skłodowska University in Lublin, Poland. M.W. was funded by the National Science Centre grant no. 2019/35/D/NZ9/03212.

Acknowledgments: We are grateful to Anna Kujawa, (Institute for Agricultural and Forest Environment of Polish Academy of Sciences in Poznań, Poland) for critical remarks on the manuscript and for providing unpublished data on the numbers of macrofungi in BPF, which were essential for the presented synthesis. We also thank Robin Wilgan, (Institute of Dendrology of Polish Academy of Sciences in Kórnik, Poland), Julia Pawłowska, and Michał Gorczak, (University of Warsaw, Poland) and Anna Biedunkiewicz, (University of Warmia and Mazury in Olsztyn, Poland) for information on current projects in the Białowieża Primeval Forest and helping to complete the literature.

Conflicts of Interest: The authors declare no conflict of interest. The funder had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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