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The Białowieża Forest – a UNESCO Natural Heritage Site – protection priorities

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Abstract. Despite the fact that only parts of the Białowieża Forest are protected as a national park and nature reserves, the forest is nevertheless as a whole considered a UNESCO Natural Heritage Site, Biosphere Reserve and an integrated Natura 2000 site. In the presently ongoing debate on the conservation priorities regarding the natural value of this forest and the current bark beetle outbreak, two distinct approaches can be recognized: (1) management assumed to involve considerable interference with the forest ecosystems; (2) maintenance of ecological processes and spontaneous restoration of the forest communities. The Białowieża Forest – especially its strictly protected parts – is a "bastion" where species characteristic of ancient forests (including so-called primeval forest relicts) have survived until today. This has been achieved by maintaining the forest's complexity in areas with considerably reduced human influence, but most of all by maintaining a full spectrum of forest communities, naturally developing forests diverse in age, species composition and spatial structure including stand dieback and breakdown. The following factors need to be taken into account in the protection of the Natural Heritage Site: (1) the internationally recognized value of the Białowieża Forest including its biodiversity, the level of preservation of forest communities and the ongoing natural processes; (2) existing documents and policies concerning nature conservation; (3) research findings from the Białowieża Forest and other natural forest complexes. The key priority is to limit any activities in this forest to an indispensable minimum, mostly concerning security close to roads and tourist tracks as well as collection of fire wood by locals. Without this strict protection, successive and slow anthropogenic transformation will result in the Białowieża Forest sharing the same fate as other forest complexes of the temperate climate zone in Europe or America and lose its globally appreciated value.

Keywords: natural forests, nature protection, biodiversity, natural ecological processes, forest management

1. Introduction

The Białowieża Forest (BF) includes a coherent forest complex, located on the border between Poland and Belarus. The whole Belarusian part is under legal protection as a national park. The Forest's part on the Polish side comprises an area of 62,000 ha: the Białowieża National Park (BNP), 10,500 ha; a network of nature reserves, 12,000 ha; and managed forests, 39,500 ha (Wesołowski et al. 2016).

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The uniqueness of BF nature, outstanding natural values for biodiversity conservation, representative exemplification of ongoing ecological and biological processes of great importance in ecosystem evolution and progress, as well as scientific values beyond measure have been recognised on the international forum. The BF was inscribed on the United Nations Educational, Scientific and Cultural Organisation (UNESCO) World Heritage List, as the first transboundary site (Polish–Belarusian) in Europe (on the Polish side, initially just the BNP was included in the List). In 2014, at the joint Nomination Dossier of Poland and Belarus, the whole area of the Forest was nominated the Natural World Heritage site, based on the evaluation criteria (ix) and (x). In Poland, the entry borders do not include the Forest's edges in the immediate vicinity of the village Hajnówka and villages situated along the western border of the Forest (Polski Komitet ds. UNESCO 2016a).

The BF is a member of the UNESCO World Network of Biosphere Reserves (WNBR) of the Program Man and Biosphere (MAB). According to Article 4 (Criteria) of the WNBR Statutory Framework, a designated biosphere reserve should encompass a mosaic of ecological systems that represents the main biogeographic regions in a given country. The reserve is designated with the aim to establish the sites for nature conservation, observation and research. Each reserve consists of three zones: the core zone, the buffer zone and the transition zone (Battisse 1982; UNESCO 1984; Denisiuk, Witkowski 1990; Polski Komitet ds. UNESCO 2016b). When established in 1976, the Biosphere Reserve Białowieża encompassed just the area of the BNP. Since 2005, the Reserve has embraced the areas of the Forest Districts: Białowieża, Browsk and Hajnówka, as well as the areas of the following municipalities (in part or in whole): Białowieża, Hajnówka, Dubicze Cerkiewne, Narew, Kleszczele, Narewka and Czeremcha. At the same time, the BF is protected as the Special Protection Area PLC200004 under the Natura 2000 Network (Zarządzenie 2011), the Important Bird Area (IBA PL046) (BirdLife International 2016) as well as the Area of Protected Landscape (almost entire BF area) (Rozporządzenie 2005) and the Forest Promotional Complex 'Białowieża Forest' (excluding BNP) (Zarządzenie 1994).

At the turn of 2016, in Poland, long-standing disputes between the supporters of implementation of current forest management practices in the managed parts of the BF[1] and advocates of giving the priority to the protection of natural processes in forest ecosystems reemerged (Wesołowski et al. 2016). Actually, the conflict over the scope and method of nature conservation in the BF has been lasting for years whilst it intensified for the first time in the early 1990s (Szujecki 2008; Blicharska, Angelstam 2010). The essence of the dispute is the disagreement over how the forest should be perceived and how the BF's natural values should be evaluated and protected now and in the future. The foresters responsible for the forest management in the managed part of the Forest and some scientists associated with them claim that human intervention is necessary to assure the survival of the BF. On the other hand, the majority of scientists (mainly biologists and also foresters) and numerous non-governmental organisations postulate allowing the BF ecosystems for spontaneous development, keeping the level of human intervention at minimum (amongst others, Blicharska, Van Herzele 2015; Blicharska et al. 2016; Wesołowski et al. 2016).

The aim of the paper is to demonstrate the natural values of the BF and to determine its protection priorities, based on the scientific data and in the light of the mandatory legal documents and acts regarding the protection of this area.

2. The history of the Białowieża Forest

Today's woodland of the BF is a result of ecological processes, shaping vegetation already from the beginning of the Holocene that is, for 12,000 years. The course of subsequent stages of vegetation development followed the pattern characteristic for northern regions of east-central Europe, which in the early Holocene comprised of pioneer pine-birch forests and later elm and hazel expansion (about 11, 300 and 10, 500 years ago, respectively), followed by the development of multi-species deciduous forests 9,300–3,800 years ago and then formation of multi-layer deciduous forest (*Carpinion betuli*) with dominating hornbeams (about 3,800 years ago). Climate was the main factor initiating particular stages of changes in plant communities, whilst spruce expansion that occurred relatively late in the region (1,500 years ago) was most probably a combined effect of earlier human impact in the Roman Period and climate changes (Zimny 2014; Latałowa et al. 2016).

Palynology allows for studying the long-term dynamics of forest communities and provides information for not only appraisal of the current ecological processes in view of the proper, long-term perspective but also prediction of possible scenarios of future vegetation changes under the conditions of changing climate. In recent times, declining groundwater levels have been the most important factor leading to the transformation of almost all habitats in the BF (Pierzgalski et al. 2002). The process of spruce decline caused by the European spruce bark beetle invasion under the conditions of recurring long-term droughts represents the most spectacular example of that (Keczyński 2002). Palynological data indicate that during the last millennium, spruce population fluctuated in short- and long-term periods of time (Latałowa et al. 2016). Ecological mechanisms of growth or reduction of spruce population within various habitats, because of a range of forest management methods, ground fires, excessive herbivore pressure and declining groundwater levels in hydrogenic habitats have been discussed by many authors (e.g. Faliński 1986; Keczyński 2005, 2007; Czerepko 2008; Kuijper et al. 2010; Niklasson et al. 2010;

Bobiec 2012; Bobiec, Bobiec 2012). It can also be assumed that at least some of the recurring radical reductions of spruce populations in the past, as reflected by pollen data, have been due to European spruce bark beetle outbreaks (Latałowa et al. 2016). The history of spruce in the BF shows that the species has endured in good condition both the periods of drought and unfavourable effects of other ecological factors and is still one of the main forests forming tree species in the area. Such high capability of population restitution was probably related to the broad phytocoenotic range of spruce in this region (Faliński 1986; Sokołowski 2004), which should be recognised as the positive aspect when assessing the potential ability of the species to survive the current and future outbreaks of the European spruce bark beetle.

The BF did not avoid economic exploitation in the past (Faliński 1986; Samojlik 2010; Samojlik et al. 2013); nonetheless, the assessments based on palynological indices of human activities clearly indicate that an extent of human-induced transformations has been relatively low, both in the prehistory and at the historical times (Latałowa et al. 2015, 2016). This has been possible because of an underdeveloped settlement network, nearly in all the archaeological periods (Wawrusiewicz 2011; Jaskanis 2012), as well as in medieval and modern times (Mikusińska et al. 2013; Samojlik et al. 2013). The special status of a royal asset limited forest exploitation and agricultural expansion in the BF from the 15th to the beginning of the 20th century (Samojlik et al. 2013). The comparison of pollen shares of both cultivated plants and those characteristic for habitats changed because of human activities recorded in pollen diagrams from the BF sites and from other sites in northern Poland (Latałowa et al. 2016) shows a great uniqueness of the BF material. The latter is characterised by not only a considerably lower proportion of plant taxa typical for anthropogenic vegetation but also a diminutive incidence of agricultural indices. This explains the exceptional and to a high degree natural present state of forest communities in the BF. Harvesting and processing forest raw materials as well as grazing were the main forms of the BF utilization in the past (Hedemann 1939; Samojlik 2010; Samojlik et al. 2016), which allowed for maintaining continuity of forest habitats along with the successful natural regeneration processes. This contributed to the maintenance of presently best preserved fragments of deciduous and mixed forests that occur in the North European Plain, and that is why the BF has been nominated the Natural World Heritage site by UNESCO.

3. Nature conservation in the Białowieża Forest – present status and contemporary threats

The nature of the BF is protected under mandatory legal regulations regarding conservation of animal, plant and fungi species, and conservation plans comprising conservation tasks for the BNP, the nature reserves as well as the habitats and species protected under the ecological network Natura 2000 encompassing the entire area of the Forest. Furthermore, the recommendations and nature conservation priorities are accentuated in the management plan for the Forest Promotional Complex 'Puszcza Białowieska' for the years 2012–2021 (RDLP 2011) as well as in the Nomination Dossier to the UNESCO for the inscription of the BF on the World Heritage List (Krzyściak-Kosińska et al. 2012). Various informal proposals were also included in the package of projects of legislation acts on designation of the national park within the entire area of the BF. The latter was elaborated by the team appointed by the President of Poland for the duration of the works on the legal act aiming at the regulation of the status of national natural and cultural heritage of the BF (Projekty ustaw 2006). It should be stressed that the BF was inscribed on the List of UNESCO World Heritage Sites, based on the selection criteria that clearly determine the priorities – the protection of ongoing ecological and biological processes in natural habitats representative for *in-situ* conservation of biological diversity (Polski Komitet ds. UNESCO 2016a).

Even though the BF is hardly a primeval forest (never disturbed by humans), its ecosystems are best preserved in the European Lowlands. For that reason, spontaneous ecological processes ongoing here – as a consequence of numerous factors at the global, regional and local levels (i.e. the climate change, changes in water regime, nitrogen deposition, and fluctuations in large herbivore populations, as well as a cessation of livestock grazing in the managed part of the BF) – should be recognised as the a priority over economic forest functions. The frequently heard arguments about allegedly harmful effects of long-lasting (more than 90 years) strict protection on forest biotic diversity in the BNP (Brzeziecki et al. 2016) have three essential weaknesses. First of all, as stressed by Jaroszewicz et al. (2016), such conclusions are based on the observations carried out on an area of only 15.4 ha, in various types of forest communities, with diverse hydrological and edaphic conditions where the dynamics of the woody species populations operate at different scales. Hence, because of their spatial and temporal scale, the demographic processes observed by Brzeziecki et al. (2016) are not representative enough for the BF as a whole. Second, the latter study neglects the importance and absolute uniqueness of an opportunity to register the course of natural ecological processes under the conditions uninterrupted by forest management activities, which is assured exclusively by the strict protection of forest ecosystems in the Park. The observed directions and rates of natural ecological processes should not be the subject of evaluation. Hence, the statements that long-term strict protection has adverse effects on nature since it leads to biodiversity loss (Brzeziecki 2016) are not justified. In the ecological perspective, the recently observed decrease in the abundance of some tree species (e.g. oak, spruce, aspen, birch, pine, and ash) can be the combined effect of different natural factors, such as increased herbivore pressure and eutrophication, global warming, groundwater levels decline, pathogenic infections and, finally, the effect of secondary succession. Therefore, this decrease is not a result of the strict protection in the BNP. The response of individual plant species is a result of competition, which under the influence of certain factors, leads to favouring some species at the cost of others. The possibility to investigate these processes is intrinsically valuable, and for such studies, the BF is the most appropriate site within the North European Lowlands. The statements presented in scientific literature, which emphasise the great importance of forest management for the preservation of biotic diversity (Brzeziecki et al. 2016), express lack of understanding or the ignorance of the essential value of the BF, which is referred to in the UNESCO criterion IX. This criterion points out high naturalness of forests and the obligation to protect natural processes that should be accompanied by the minimisation of human interference. Furthermore, as Weiner (2016) writes, the aforesaid statements are 'a form of contestation of the view that the existence of a natural forest ecosystem is a priceless value, worth preserving' and the manifestation of 'a serious crisis of values'. The third weakness of the above-mentioned argumentation as to alleged detrimental effects of the strict protection is the identification of the observed demographic processes in tree species growing in the strict nature reserve, that is, decrease in the population numbers of certain species followed by the expansion of others, mainly hornbeam and lime, as the evidence of the homogenisation of the Forest's plant communities (Drozdowski et al. 2012; Brzeziecki et al. 2016). In the recent years, the term 'homogenisation' has been repeatedly evoked (e.g. McKinney, Lockwood 1999; Olden et al. 2004; Naaf, Wulf 2010). Nonetheless, the results of studies carried out in the BF managed forests (Drozdowski et al. 2012), referred to by Jaroszewicz et al. (2016), evidently show the same dynamic trends regarding the tree species that are observed in the protected forests in the nature reserve. Drozdowski et al. (2012) state that 'the process of forest community homogenization in old-growth forests in the managed parts of BF has not so far been as advanced as that in the BNP Strict Reserve'. As emphasised by the authors themselves, this is due to 'the forest management activities (regeneration, stock tending operations, stand structure regulation), which improved the growth conditions of the threatened tree species. Therefore, the maintenance of high tree species richness, which assures safeguarding high natural values of the managed forest stands was promoted'. Thus, as maintained by Drozdowski et al. (2012), the higher tree species richness in the managed forest stands compared to the forests released from human pressure is attributable to the effects of silvicultural treatments. In contrast, these processes should be rather explained by the intermediate disturbance hypothesis (IDH), described by Connell (1978) and widely recognised in ecology. Consistent with IDH, disturbances at an intermediate level maximise species richness. The latter decreases at both low and high level of disturbance. In the case of the BF, an increase of species richness is of no value in itself, because such an increase is often connected with the occurrence of the light-demanding species, typical for early stages of forest development (e.g. birch and common aspen), which in mature forests are successively replaced by shade-tolerant tree species. At the same time, disturbances can contribute to the penetration of a forest by alien species, including the invasive ones (Catford et al. 2012), which are a hazard to the entire forest complex. In view of the fact that disturbances, including forest management activities, are responsible for the increase in the species richness, often because of the temporal appearance of ephemeral species in the forest groundcover, lower species richness in forests free of human intervention is regularly observed when compared to forests strongly affected by management activities. Consequently, the total number of species is not sufficiently objective, or at least not the only one indicator of a forest conservation value because it often reflects the presence of disturbances affecting the local environment (Boch et al. 2013). It is worth stressing that the above-described effect is often observed in fragmented forests of small area. However, when considering the larger scale (landscape), it appears that when compared to managed forests, the number of species in protected forests is not necessarily lower. In protected forests, abundance of species populations is often lower, but the total species richness is higher. Unfortunately, empirical data on these aspects are almost non-existing, because of the fact that in Europe, besides the BF, there is a lack of extensive, large forest complexes, undisturbed by management practices that could be used in relevant comparative studies.

4. Evaluation of the conservation status of Natura 2000 sites designated within the area of the Białowieża Forest and recommendations on their protection

In accordance with the Standard Data Form (SDF) for the site Natura 2000 Puszcza Białowieska (BF), 10 habitats are protected here (5 non-forest and 5 forest habitats) (Table.1). Forest habitats encompass 67.53% of the area of the Natura 2000 site (63, 147.58 ha) that was designated in the complex with forest plant communities characteristic of primeval plant associations (Matuszkiewicz 2007a), much better preserved and more stable compared to other regions. In the area, deciduous forests (9170 *Galio-Carpinetum*, *Tilio-Carpinetum* oak-hornbeam forests), which cover 39, 814.56 ha (91.54% of the total area of Natura 2000 habitats), prevail. The conservation status of this habitat is assessed as excellent, based on the parameters such as 'specific structure and functions' (serves to define the typical nature of habitat development and conformity with specific species composition) as well as 'habitat conservation prospects' (SDF 2014). Similar overall assessments are reported for habitats 91E0 and 91F0 (riparian forests) (Table 1). However, it must be emphasised that in the case of deciduous forests, plant communities in the BNP or the nature reserves considerably differ from those of managed forests. In the latter, high diversity of actual vegetation is observed, which is associated with plant species occurring after tree harvesting and different stages of forest regeneration (Kwiatkowski 1994). Managed forests considerably differ from the forests of BNP in terms of stand age structure, proportions of deciduous species, amount of deadwood and biomass. The protected and managed deciduous forests also differ in terms of biogeochemical cycles. In managed deciduous forests, the cycle is disturbed as a result of changes in species composition (e.g. spruce domination). Continuous losses of mineral nutrients caused by timber removal are observed; water retention is altered, and surface runoff is enhanced within harvesting areas (Kwiatkowski 1994). According to Matuszkiewicz (2007b), the majority of tree stands within the BNP entered the decomposition stage, and this instigates natural fluctuations in deciduous forest, that is, the processes of regeneration ongoing within small areas connect with those of degeneration linked to tree falls because of natural factors. Slow changes in the Park's stands are associated with an increasing dominance of hornbeam and lime trees and the reduction in the shares of other tree species (especially spruce, birch and aspen) (Matuszkiewicz 2007b).

In line with the conservation action plan for the Natura 2000 site PLC200004 Puszcza Białowieska (Zarządzenie 2015), the conservation tasks rule out management activities in forest habitats 91D0 and 91E0. In the case of habitat 9170, all the stands with more than 10% share of trees older than 100 years are to be excluded from forest management activities (Table 2). It needs to be highlighted that the only conservation task proposed for the non-forest habitats (except for 3150) is improvement in knowledge through inventories aiming at recognition of all the habitat sites and monitoring of their conservation status with the use of methods established by the Chief Inspectorate of Environmental Protection, Poland.

Forest management is classified as a potential threat (Table 2) and not as an existing threat, and this is probably due to the standpoint of the Minister of Environment (document DP-074-60/30110/15/JJ of 13 August, 2015), which states that the fundamental method of conservation of Natura 2000 habitats is sustainable management of nature resources. As only unsustainable forest management threatens protected habitats, and the principles of forest management in Poland are perceived as sustainable, the forest activities may only be classified as the potential threat for the BF.

Recommendations for the majority of the BF habitats (i.e. riparian, oak-hornbeam, coniferous and boggy forests), which have not yet been transformed as a result of forest management, clearly point out to the need for exclusion of such forests from management activities. In the case of transformed stands (on deciduous forest sites), slow stand restoration is recommended towards adjusting species composition to site conditions.

5. Species diversity in the Białowieża Forest – selected examples

The BF is a 'hot spot' of Poland's species diversity (Jaroszewicz 2010). Habitat mosaic and diversity, the presence of old trees together with hollow and dying trees and deadwood abundance provide good life conditions for numerous species, including relict species characteristic for the old primeval forests. Some of these have been preserved only in the BF. It is impossible to completely describe biotic biodiversity of the BF; therefore, only selected groups of organisms are described in the following sections.

5.1. Macrofungi

In the BF, macrofungal species diversity has been thus far recognised at a range of levels. For the most part, the area of the BNP has been studied in this respect. In the years 1987–1991, the project CRYPTO was conducted in this region, and in one forest division (no. 256), 913 species of macrofungi (Faliński, Mułenko 1997) were found. Data on fungal species diversity in the BF (mainly BNP) were gathered by many mycologists, amongst others, Pilát (1950), Nespiak (1959), Orłoś (1960), Skirgiełło (1960, 1998), Domański (1967), Bujakiewicz (1994) and Karasiński et al. (2009). The results of mycological studies carried out in the Forest were in some measure reviewed by Karasiński et al. (2010) during the works on the nature management plan for the BNP. Outside the Park's borders, research on fungi was carried out only in selected areas, and particularly, in the nature reserves (Bujakiewicz 2002, 2003; Bujakiewicz, Kujawa 2010). In the BF as a whole, most detailed studies concerned polyporoid fungi (Niemelä 2013; Karasiński, Wołkowycki 2015). Up to date, 1,850 species of macrofungi have been described in the BF (Kujawa, unpublished), that is, 43% of fungal species reported from Poland. More than half (933) of the fungal species in the BF are rare (included in Poland's Red List or found in one to three sites in the country or just lately described – thus, not included in the lists of critical species) or under legal protection. The group of rare species comprises almost 200 species of fungi that have never been found on other sites in the country (Kujawa, unpublished). The Forest's mycobiota has not yet been fully recognised and potentially will be broader, which is confirmed by the fact that new species of macrofungi are reported every year during the cyclic exhibition of fungi, held in the Białowieża village (e.g. Szczepkowski et al. 2008, 2011; Gierczyk et al. 2013, 2014, 2015).

Table 1. List of natural habitats which are the objects of protection according to the Standard Data Form for the Natura 2000 the Białowieża Forest

No	Habitat code	Habitat name	State of preservation	Habitat area [ha] / share in the total Nature 2000 area [%]
Non-forest habitats				
1.	3150	Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition* - type vegetation	C	12.63 / 0.02
2.	6230	Species-rich *Nardus* grasslands, on silicious substrates in mountain areas (and submountain areas in Continental Europe)	B	132.61 / 0.21
3.	6510	Lowland hay meadows (*Alopecurus pratensis, Sanguisorba officinalis*)	B	524.13 / 0.83
4.	7140	Transition mires and quaking bogs	B	18.94 / 0.03
5.	7230	Alkaline fens	C	157.87 / 0.25
In total:				**849.18 / 1.34**
Forest habitats				
6.	9170	*Galio-Carpinetum* and *Tilio-Carpinetum* oak-hornbeam forests	A	39 814.56 / 63.05
7.	91D0	Bog woodland	B	2 746.92 / 4.35
8.	91E0	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion, Alnion incanae, Salicion albae*)	A	12.63 / 0.02
9.	91F0	Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)	A	63.15 / 0.10
10.	91I0	*Euro-Siberian* steppic woods with *Quercus* spp.	C	6.31 / 0.01
In total:				**42 643.57 / 67.53**
Natural habitats in total:				**43 492.75 / 68.87**

Explanations: A – excellent, B – good, C – medium or degraded

With regard to the species richness of polyporoid fungi, the BF stands out from the rest of European forests. From the group of 394 species of polyporales known in Europe, as many as 210 have been observed in the BF. This is almost 90% of all polyporoid fungi known in Poland (Karasiński, Wołkowycki 2015).

The above results demonstrate the uniqueness of the BF. At the same time, the aggregation of many habitats of fungi, especially those associated with declining trees and deadwood, in the areas under strict protection (mainly in the BNP) proves that the passive protection of forest ecosystems is efficient for safeguarding high diversity of fungal species associated with forests. This especially concerns hemerophobic species, sensitive to ecosystem changes because of management activities carried out by man. There is a need for further research on the status of species diversity of macrofungi in the BF.

5.2. Lichenised fungi (lichens)

The biota of lichenised fungi that occurs in the BF has been quite well recognised. Information has been provided by numerous studies carried out from the 1800s. A review of earlier works (e.g. Błoński 1888; Krawiec 1938; Lecewicz 1954; Rydzak 1961) and wide-ranging information on the distribution and ecological preferences of 309 species of lichens occurring in the BF are available in the paper by Cieśliński and Tobolewski (1988). The study area V-100 of the Project CRYPTO conducted in the BNP (Protected Nature Reserve, forest unit no. 256) was best described in terms of the biota of lichenised fungi. Within the area of one forest unit (140 ha), 164 species of lichens were identified (Cieśliński et al. 1995; Cieśliński, Czyżewska 1997).

In the register of lichenised fungi occurring in the BF (Cieśliński 2010 and references), 450 lichen species are listed (including 268 observed in BNP).

The updated list of about 500 species of lichenised fungi and about 50 species of fungi living on lichens known from the BF also comprises the information published in the recent years (e.g. Matwiejuk, Bohdan 2011; Kukwa et al. 2012a,b; Łubek, Jaroszewicz 2012; Guzow-Krzemińska et al. 2016; Łubek, Kukwa 2016), as well as data on lichens obtained in the project KlimaVeg (http://www.klimaveg.eu/), conducted in V-100 study area (Łubek, Kukwa unpublished). Lichen

Table 2. Selected conservation activities resulting from the plan of protection tasks for forest habitats and identified threats

Habitat code	Protection tasks	Potential threats*
9170	exclusion from the economic use all forest stands with the species in the composition of 10% at the age of 100 years or more on the habitat of oak-hornbeam subcontinental forest;	B02.04 – removal of dead and dying trees B02 – forestry and tree plantation, use of forests and plantations
	adjusting the composition of the tree stands to the composition in accordance with the natural habitat; in the tree stands with domination of aspen, birch, pine and less frequently spruce – in stands less than 100 year old	
	renaturisation of tree stands	
	elimination of invasive species	
91D0	preventing the degradation of habitats by exclusion from economic activities patches of habitat 91D0	
	reducing of maintenance and renewal of drainage ditches, except as necessary for the maintenance of road and railway infrastructure	
91E0	exclusion from the economic use all forest stands on the habitat 91E0	B02.04 – removal of dead and dying trees
	monitoring and removing of invasive species	
91F0	maintenance of proper water conditions in the catchment areas of forest rivers using artificial rapids	
91I0	cuttings, limiting shading of the forest floor	

* According to the "Reference list of pressures, threats and activities" included in the annex 5 of the Instruction for the Natura 2000 Standard Data Form, version 2012.1, prepared by the General Directorate for Environmental Protection, available at http://natura2000.gdos.gov.pl/strona/nowy-element-3

species that have been so far identified in the BF represent about 30% of the biota of lichenised fungi reported from Poland and about 20% of the biota of non-lichenised fungi living on lichens (e.g. Fałtynowicz 2003; Czyżewska, Kukwa 2009).

Back in the 1930s, the biota of lichenised fungi occurring in the BF was characterised by the great abundance of foliose macrolichens, such as *Lobaria pulmonaria*, that formed giant thalli with fruiting bodies, overgrowing tree trunks and branches, including those of spruces. Also, thalli of fruticose and filamentous species of the genus *Bryoria* and *Usnea* and those of the species such as *Ramalina thrausta* and *Evernia divaricata* hung down from tree branches, creating a 'primeval landscape' (Krawiec 1938). *Usnea longissima* specimens with 1-m long thalli were observed in the BNP still in the 1950s (Lecewicz 1954). Unfortunately, the end of the 20th century brought a very strong change in the lichen biota across Poland and many other European countries, as a result of increased air pollution (e.g. Hawksworth et al. 1973; Kiszka 1977; Czyżewska 2003). Lichens of the BF also suffered, despite of the considerable distance from large industrial centres and main roads. Owing to the impact of the long-range pollutions and contamination derived from the small local sources (Malzahn 2009; Malzahn et al. 2009 and cited references), the species most sensitive to acid rain and gaseous SO_2 disappeared here (many species from the genera *Bryoria* and *Usnea)* or their occurrence got strongly reduced, for example, previously luxuriant *Lobaria pulmonaria* was described as a very rare species, forming small thalli without fruiting bodies (Cieśliński, Tobolewski 1988; see also Gauslaa 1995 and cited references). In spite of these losses, lichen biota of the BF is extremely rich in very rare species, including those endangered in Poland (Cieśliński et al. 2006) and protected by law (Rozporządzenie 2014). Thanks to the presence of strictly protected forest areas in the Park, as well as older forests in the nature reserves, this biota has a very large share of red-listed lichens (52%), with approximately 40% of the species in the highest threat categories (CR, EN, VU) (Cieśliński 2010). The BF is the most important refuge in Poland for majority of these species. Amongst them, especially important are the epiphytic and epixylic lichens, which are regarded as primeval relicts (Cieśliński et al. 1996).

Relicts (species, indicators) of primeval forests are the remnants of larger groups of species, typical components of previously widespread forest ecosystems, characterised by the continuity of natural ecological processes, in which a key role was played by generational turnover of tree species, shaping the internal structure of forest community and habitats available for lichens (Faliński 1986; Peterken 1996; Cieśliński et al. 1996). The occurrence of primeval forest lichens depends on the presence of specific microniches, which are old and very old trees of various species and wood in varying degrees of decomposition and forms (dead standing or broken trunks without bark, lower stumps, fallen logs, exposed root systems of fallen trees and lying branches). The continuity of microclimate conditions (especially high humidity) is very important for these species (Cieśliński et al. 1996).

The distinguishing feature of the biota in the BF is a very large group of such primeval forest micro- and macrolichens, as well as local high frequency of many of them. Still quite common are species such as *Arthonia byssacea*, *Calicium adspersum*, *Loxospora elatina*, *Opegrapha vermicellifera* and *Pertusaria flavida* that belong to the category of endangered species in the country (EN). It should be noted, however, that their localities are concentrated mainly in the BNP and other protected areas with the highest naturalness (Cieśliński, Czyżewska 2002; Cieśliński 2003; Czyżewska, Cieśliński 2003a, b; Cieśliński 2009).

Data collected in the recent years (Golubkov et al. 2011; Popławska 2012; Zalewska, Bohdan 2012, Bohdan 2014; Matwiejuk, Bohdan 2014; Bohdan – unpublished; Zalewska et al. – unpublished) indicate that populations of some macrolichens critically endangered in Poland (Cieśliński et al. 2006) are slowly regenerating in the BF, but almost exclusively within the areas of the Park and nature reserves. A fairly large number of the localities of *Bryoria capillaris* as well as fewer localities of lichen species such as *Ramalina thrausta, Usnea ceratina* and *Lobaria amplissima* (previously reported as *L. virens* – see Kukwa et al. 2008) were observed. For the latter three species, the BF is the last refuge, not only in Poland but also in the lowlands of Central Europe. Furthermore, several other lichens from the threat category CR, for example, *Evernia divaricata*, *Usnea glabrescens* and *U. florida* (recently often included to the species *U. subfloridana* – Articus et al. 2002; Kukwa 2005; Kościelniak 2007) have the greatest populations in the BF at the country level. Some other species endangered in Poland are locally quite common, for example, *Menegazzia terebrata* (CR), *Thelotrema lepadinum* (EN) and representatives of the genus *Cetrelia* (EN), as well as *Lobaria pulmonaria* (EN) – sometimes forming large thalli (Ryś 2007; Paluch 2009).

Nearly all of the taxa described above have been placed on the list covering a total of 71 species that are regarded as indicators of primeval forests in the Polish Lowland (Czyżewska, Cieśliński 2003c). The occurrence of species from this list is applied in Poland in assessing the natural values of forests, as in the case of indicator species used in other countries (e.g. Rose 1976, Arup 1997, Coppins, Coppins, 2002; Rose, Coppins, 2002; see also Kubiak 2013a,b, with references).

The main threat to rare, specialised forest lichens are changes in the structure of forest communities and the discontinuity of microclimatic conditions related to timber acquisition and regeneration of tree stands, regardless of the method used (e.g. Rose 1992; Czyżewska 2003; Pykälä 2004; Scheidegger, Werth 2009; Nascimbene et al. 2013 and cited references).

These rare lichen species can be best preserved when the continuity of ecological processes is protected, that is, maintaining the natural turnover of tree generations, which ensures spontaneous fluctuation of available substrates, along with the natural dynamics of small, short-term gaps, which bring no dramatic changes in microclimate conditions inside the forest. In case of natural disturbances, such as windthrow or insect outbreak, open spaces of different sizes are formed. In such areas, the processes of slow, natural regeneration of forest communities are accompanied by equally slow regeneration of the biota of the specialised forest lichens. The condition for the effectiveness of this process is the continuity of undisturbed areas around the sites with damaged communities. Thalli of rare forest lichens inhabiting undisturbed areas serve as a source of propagules for recolonisation of regenerated, mature phytocoenoses (Scheidegger, Werth 2009). The additional source, mainly for epixylic species, may be the thalli of lichens growing on snags (dead broken trees), which usually occur in the damaged and regenerating forest communities (Czarnota 2012; Czarnota et al., unpublished).

Only large-area passive protection through a very long period of time can assure regeneration of the natural lichen biota in disturbed forest areas. The crucial role of the passive protection in set-aside areas for the maintenance of rare forest lichens is emphasised in many studies (Cieśliński 2008; Kościelniak 2008; Zalewska 2012; Kubiak 2013b, Nascimbene et al. 2013 – with cited references).

5.3. Vascular flora

The first floristic notes on the vascular plant species of the BF appeared in the monograph by Gilbert, dated 1791. The 19th century brought another development, amongst others, by Brincken (1828), Gorski et al. (1829), Eichwald (1830) and, finally, Paczoski (works carried out in 1897–1900) as well as Błoński, Drymmer and Ejsmond (1888–1889). During the World War I and after, much data about flora of this region were provided by German and Polish botanists, and particularly by J. Paczoski, the author of a masterpiece publication 'Forests of Białowieża' dated from 1930 (Sokołowski 1995). The flora of vascular plants occurring in the Polish part of the Forest was most fully recognised by Sokołowski (1995), conducting his research between 1961 and 1993, who recorded the presence of 1,017 species, representing 93 families and 428 genera. This number is about the half of the vascular plant species occurring in the Polish lowlands. From 1,017 species recorded by Sokołowski, 664 are the components of natural plant communities occurring in the Forest, whereas the remaining 353 penetrated here as a result of human activity (synanthropic species), counting those ecologically (apothytes) or geographically alien.

The compactness of the BF complex and its high degree of naturalness are reflected in the number of the ancient woodland indicator species. From 664 plant species determined by Sokołowski (1995) as associated with natural plant communities, 115 are those that show the affinity to ancient forests. These represent 17% of the vascular plant species that are present in natural plant communities in the BF and 74% of all the species of this category (as described by Dzwonko and Loster 2001) that occur in Poland. This proportion is considerably high, given that many of the plant species included in the Polish list of ancient woodland indicator species are plants occurring in mountainous regions, as well as those whose geographical range does not cover the area of the BF. Plants of this group can, therefore, be a good indicator of the naturalness and continuity of centuries-old forest habitats (*sensu* Peterken 1974) in large parts of the BF. Their affinity to forests is a result of long-lasting evolution/adaptation to habitats with low level of disturbance, operating in small scale and with low frequency. Living under such conditions caused that typical forest species did not evolve life history traits that would allow them to for a quick escape, either in space or in time (Hermy et al., 1999; Dzwonko, Loster 2001; Whigham 2004). Hence, many of the so-called forest specialists did not develop the ability to disperse over long distances, because about one-third of plant species of the herb layer are autochores, myrmecochores (with seeds dispersed by ants) or barochores (spread because of gravity) (Hermy et al. 1999; Dzwonko, Loster 2001). Most herb layer species produce short-lived seeds (longevity of less than 1–5 years) and, in contrast to non-forest plants, do not form permanent seed banks (Thompson et al. 1997). An expression of plant adaptation to forest conditions is their longevity (the average lifespan of forest perennials is 64 years – Ehrlén, Lehtilä 2002) and ability to clonal growth – typical for more than 80% of herb layer species (Klimeš et al. 1997). These features are of great importance in the case of large-scale disturbances with high frequency and intensity, because after some time, these may lead to permanent loss of many forest groundcover species. The adverse effects of disturbances caused by human intervention in forest ecosystems, mainly due to the activities related to forest management, may occur after several decades after the disturbance. At this stage, stopping the progress of forest plant species loss may be impossible (Tilman et al. 1994; Vellend et al. 2006).

Flora of the BF embraces many rare species, including those of relict northern origin. The interim, subboreal nature of the flora of this area is expressed by the presence of plant species with a circumboreal distributional range, mostly representing chorological Euro-Siberian and Central European elements, although the representatives of sub-Atlantic and sub-Pontian flora have also been observed here. Furthermore, several plant species reach their eastern, south-western, western or north-western limits of their ranges in this region (Adamowski 2009).

According to Sokołowski (1995), about 35% of vascular flora of the BF represents the previously mentioned synanthropic species. Some of them appeared here spontaneously, others were introduced intentionally. Humans significantly alter habitats through their activities and create conditions for the encroachment of plant species characteristic for places completely transformed, such as clear-felled areas, mid-forest roads, fields, meadows and glades. Amongst them, there are native species (apophytes) and also geographically alien species, including those from other regions of the country (e.g. *Carex brizoides* and *Acer pseudoplatanus*) or dragged/introduced from outside of Europe (e.g. *Acer negundo*, *Quercus rubra*, *Impatiens parviflora*) (Sokołowski 1995; Adamowski 2009). This certainly increases the overall species diversity of vascular plants in the BF. Nevertheless, it also poses a huge threat to native flora, as some alien species displace native ones, changing the original species composition of plant communities of this forest complex (Faliński 1998).

5.4. Insects

Up to date, nearly 10,000 species of insects have been observed in the BF (Gutowski, Jaroszewicz 2001, 2004; Gutowski et al. 2009; Gutowski unpublished) from 26,000 of species known from the Polish territory (Chudzicka, Skibińska 2003; Razowski 1990, 1991a, 1991b, 1997a, 1997b). Most probably, many more insect species occur here, as every year brings new discoveries.

The orders such as true bugs, Hemiptera (652 species, representing 29% of Poland's entomofauna); beetles, Coleoptera (3,199 species, 51%); wasps, Hymenoptera (2,005 species, 33%); butterflies and moths, Lepidoptera (1,609 species, 51%); flies, Diptera (1,772 species, 26%) are outstanding in terms of species richness. Given that the best identification concerns the orders Coleoptera and Lepidoptera – as a result of more studies carried out on these groups both at the country and the BF levels – as well as the fact that these orders are represented in the Forest by more than half of the species known in Poland, we can assume similar proportions with regard to the majority of other insect orders. The best-known Coleoptera families include Apionidae (65% of Poland's fauna in this group), jewel beetles (Buprestidae, 55%), longhorn beetles (Cerambycidae, 65%), ladybirds (Coccinellidae, 68%), weevils (Curculionidae, 53%), false click beetles (Eucnemidae, more than 70%) and sap beetles (Nitidulidae, 65%). These data were compiled by Gutowski and Jaroszewicz (2001, 2004), Gutowski et al. (2009) and Jędryczkowski and Gutowski (2014). The results obtained by these authors as well as summarised in their studies as result of years of research carried out by numerous authors place the BF at the forefront of not only Polish but also European refuges of biodiversity of forest insects.

Saproxylic insects represent a group most typical for forests, which is exceptionally species rich and most vulnerable to forest management (Grove 2002). A substantial part of their life is directly associated with dying or dead trees (in various forms and decomposition stages) or with diverse fungi and insects colonising deadwood (Speight 1989). Apart from outstanding insect species richness, when compared to other natural forests, and especially those located within the European Lowlands, the entomofauna of the BF is characterised by the distinctively high representation of species considered relicts of natural forest habitats, often referred to as relicts of primeval forests. This term denotes the species that have disappeared from the majority of European forests, as a result of their anthropogenic transformations because of considerable depletion of forest ecosystems, attributable to the planned forest management (in a relatively short period of time, i.e. 200–250 years of development of notional forest management principles, and implemented with varying intensity in different places in Europe, including Poland). The impoverishment of natural forests mainly refers to

- natural age structure of forest stands (currently, in most managed forests, a significant shortage, and sometimes the lack of old trees, i.e. those achieving the age that individual species can potentially reach, is observed – the assumed cutting age of a given tree species, accepted in forestry practice, has effectively eliminated the possibility of the formation of forest natural age structure);
- natural spatial structure of forest stands, with the mosaic of forests affected by all kinds of disturbances, and the areas covered with abundant herbaceous vegetation blocking fast regeneration of tree stands or surfaces 'held' by large herbivores 'at the no-stand stage' or the areas covered by highly dispersed trees (currently, in the majority of managed forests, such spaces do not occur or occur for a short time – the existing forest management principle for the full use of habitat productive potential through rapid regeneration has actually eliminated the possibility of the formation of natural spatial structure of forest stands);
- natural species structure of forest stands, dynamically changing at different rates, depending on the local factors altering habitats that allow for the renewal and development of various tree species – often undesirable from the economic point of view – including hornbeam, aspen and lime (currently, in most managed forests, the accepted silvicultural and forest utilization principles rule out the possibility of spontaneous formation of such a structure);
- abundance of deadwood, which is naturally present in the forest – depending on its specific character and stand fluctuation stage – in a full range of forms (standing, lying, suspended), as well as on the phase of wood decomposition in a complete range of its dimensions, and the amount of sunlight available – which all also refers to very old trees (currently, in the majority of managed forests, sanitary, harvest or tending cuttings, by definition have eliminated the possibility of a steady stream of deadwood; dying or fallen trees are removed from forests, which effectively reduces or completely eliminates the creation of saproxylic microhabitats).

The presence of unique entomofauna in forests is directly associated with the occurrence of the above-described elements of the ecological structure with its full diversity – typical for natural forest ecosystems. Amongst forest saproxylic insects that endured in the BF's numerous sites with preserved elements of natural ecological structure, as relicts of primeval forests or the species associated with development of natural forest microhabitats (e.g. old trees with the of hollows shaped by lasting many decades processes of humification), the following ones deserve a special attention: *Boros schneideri* (Boridae), *Buprestis splendens* (Buprestidae), *Leptura thoracica*, *Stictoleptura variicornis* (Cerambycidae), *Ampedus melanurus*, *Lacon lepidopterus* (Elateridae), *Otho sphondyloides* (Eucnemidae), *Lopheros lineatus* (Lycidae), *Phryganophilus ruficollis* (Melandryidae), *Pytho kolwensis* (Pythidae), *Rhysodes sulcatus* (Rhysodidae), *Bius thoracicus* (Tenebrionidae) and *Mycetoma suturale* (Tetratomidae). These Coleoptera species represent the ecological group of saproxylic beetles that comprises more than 1,000 species observed in the BF. This demonstrates that the Forest is the main refuge of relict forest fauna in the North European Plain (Gutowski, Jaroszewicz 2004; Gutowski et al. 2009). Amongst saproxylic beetles observed here, as many as 12 species included in Annexes II and IV of the EU Habitats Directive occur here. Several species from other ecological and systematic groups are also enlisted in the Directive's Annexes, for example, insects inhabiting aquatic habitats and terrestrial open areas (e.g. dragonflies, butterflies). Two hundred beetle species occurring in the BF are included in the 'Red List of threatened animals in Poland' (Pawłowski et al. 2002).

There has been observed the presence of many species of insects for whom the BF is one of a few or even the only site in Central Europe. These are, amongst others, taiga species of beetles (boreal and Siberian): *Carphoborus cholodkovskyi*, *Polygraphus punctifrons*, *Pityogenes saalasi*, *Orthotomicus starki*, *Cryphalus saltuarius*, *Pityophthorus morosovi* (Curculionidae: Scolytinae); *Acmaeops angusticollis*, *Evodinus borealis*, *Stictoleptura variicornis*, *Leptura thoracica*, *Xylotrechus ibex*, *Mesosa myops* and *Monochamus sartor urussovii* (Cerambycidae). In the BF, insect species from other zoogeographic regions have been observed, for example, *Aulonothroscus laticollis* (Throscidae), *Buprestis splendens*, *Eurythyrea quercus*, *Agrilus pseudocyaneus* (Buprestidae), *Nematodes filum* (Eucnemidae), *Pseudanostirus globicollis* (Elateridae), *Alosterna ingrica* (Cerambycidae) and *Pachytychius sparsutus* (Curculionidae) (Gutowski, Jaroszewicz 2004). The Forest represents a unique refuge for rare Le-

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pidoptera species, especially boreal ones – associated with bogs, for example, *Colias palaeno*, *Vacciiniina opilete*, *Boloria eunomia*, *Euphydryas maturna* and *E. aurinia*.

The occurrence of unique primeval entomofauna in the BF is conditional on the continuous (from prehistoric times) presence of standing dead trees and lying deadwood, as well as the occurrence of natural stand fluctuation stages, including those of decay and regeneration. The latter is related to slowly progressing secondary succession hindered by intense coverage of herbaceous vegetation on the areas affected by natural disturbances (with weaker or stronger effects) (e.g. Buchholz, Burakowski 1992). This is a result of limited management of considerable portions of forest ecosystems, including those not yet taken under protection within the nature conservation system. Entomofauna species richness, as well as the occurrence of species closely related to the effects of spontaneously running ecological processes, clearly indicates positive effects (for forest biodiversity) of the exclusion or substantial reduction of forest management based on the principles adopted in modern forestry.

Despite relatively good knowledge on the Forest's entomofauna when compared to other European forests, species new to this area are still being discovered, including those previously unknown in Poland, such as *Acmaeops angusticollis* (Cerambycidae) (Gutowski 1988), *Isorhipis marmottani* (Eucnemidae) (Buchholz, Burakowski 1989), *Ampedus melanurus* and *A. suecicus* (Elateridae) (Buchholz, Ossowska 1998), *Mordellochroa milleri* (Mordellidae) (Kubisz 2000), *Euplectus tholini* (Staphylinidae) (Jałoszyński et al. 2005), *Nacerdes carniolica* (Mordellidae) (Gutowski et al. 2012) and *Sepedophilus wankowiczi* (Staphylinidae) (Szujecki 2014). The BF is *locus typicus* for more than a dozen species of Coleoptera, Diptera, Hymenoptera, Lepidoptera and Mallophaga – recognised as new for the science (Disney, Durska 1998; Okołów 2015; Gutowski unpublished).

In addition to the most valuable group of saproxylic insects, a comparatively species-rich group of hygrophilous insects – associated with waters and peat bogs – also occurs in the BF, for example, dragonflies (Odonata) are represented by 60 species (83% of Poland's dragonfly fauna). The group of xerophilic insects is of slightly lower importance and less species rich (with some exceptions) (Wanat 1994, 1999; Gutowski et al. 2009).

5.5. Birds

In the past decades, 153 breeding bird species were recorded in the BF (Pugacewicz 1997), and these represent 67% of contemporary breeding avifauna in Poland (Chodkiewicz et al. 2015). Breeding avifauna of the BF comprises 30 species listed in Annex I of the EU Birds Directive (Rowiński 2010).

The stands of the BF are exceptional in terms of extremely rich, unique assemblage of forest and forest edge birds. Breeding bird communities recorded here resemble the structure of avifauna inhabiting undisturbed tropical forests (a large number of species, low density, high levels of nest predation) (Walankiewicz, 2002; Tomiałojć, Wesołowski, 2005; Czeszczewik et al. 2015). The number of species nesting on sample plots established in 1975 on the area of only 187.5 ha is more than 80 (although for individual seasons and plots this number is indeed smaller) (Tomiałojć et al. 1984; Wesołowski et al. 2015). Almost all European species of woodpeckers nest in the Forest. The condition of the BF avifauna is primarily due to a very large share of stands close to primeval or old stands – originating from natural regeneration in forest areas disturbed or cut down nearly 100 years ago (with many dead trees, including spruces and pines).

More than 40-year-long research on the assemblage of birds in the BF has proved that it is an inherent 'window to the ecological past' of European forests (Wesołowski, Fuller 2012). The ecology of many bird species under the BF conditions distinctively differs from the ecology of the same species in heavily fragmented managed forests (Tomiałojć, Wesołowski 2005; Wesołowski 2007). Studies conducted in the BNP have shown that certain ways of nesting, unknown or regarded as exceptional in other parts of the country and Europe, are relatively common here, and thus, our views on evolution of the selection of a breeding site must have been modified. This regards, for example, blackbird *Turdus merula* and song thrush *T. philomelos*, frequently nesting on naturally fallen trees (Tomiałołojć et al. 1984), as well as robin *Erithacus rubecula* and blackbird – nesting in tree cavities (Walankiewicz unpublished; Rowiński oral communication). Wesołowski and Fuller (2012) published a long list of differences between the BF and the UK forests with regard to habitat preferences/nesting site choices of the same bird species. This issue is of great importance, as in ornithological literature, the presented depiction of ecology of many European forest bird species has been shaped by the results of numerous studies conducted on bird populations in British, Dutch or Swedish forests and wooded lands heavily transformed by man (Wesołowski 2007, Wesołowski, Fuller 2012; Jędrzejewska, Jędrzejewski 1998). Therefore, the BF and the research conducted here is now the most important point of reference for studies on ecology of birds in forests of temperate Europe, as well as those in North America.

The protection of spontaneous ecological processes ongoing in bird assemblage is the most important priority in research on ecology and behaviour of birds in the BF. Forty-year-long studies on avifauna conducted here enabled, for example, description of a substantial increase in the total bird densities in 1985–2001, followed by a downward phase (Tomiałojć et al. 1984; Wesołowski et al. 2015). The results obtained by Walankiewicz (2002, 2006) showed that in hornbeam and oak seeding years, the numbers of rodents and predators fluctuated, which caused changes in bird population numbers. The ecological processes described above can be studied only when as large as possible areas of naturally disturbed old stands (e.g. by spruce bark beetle and other insect outbreaks) remain free from human interference (Wesołowski, 2005; Wesołowski, Rowiński 2006; Czeszczewik et al. 2015).

The major threat to the BF avifauna and its 'primeval ecology' is the transformation of fragments of natural or primeval, as well as the ones affected by bark beetles (disturbed) tree stands, which have endured in managed parts of the Forest, into a 'simplified' production forest. Forest management involves the removal of old and dead trees and establishment of fenced reforestation areas with one or two dominant tree species, which leads to the development of managed forest plantations typical for Europe. The removal of individual dead trees (e.g. spruces and pines) also constitutes a threat. Cavities in dead standing tree trunks are important nesting sites for birds, sometimes used for decades (Walankiewicz et al. 2014).

The strictly protected area within the BNP (less than 50 km^2) is too small to sustain biologically viable populations of woodpeckers, such as white-backed woodpecker *Dendrocopos leucotos* and three-toed woodpecker *Picoides tridactylus* (Wesołowski 2005). The negative impact of forest management on tree stands and associated avifauna was demonstrated by comparing the groups of birds inhabiting the BNP, nature reserves and managed parts of the Forest (Czeszczewik et al. 2015). Likewise, the indicators of the white-backed woodpecker population's status have been decreasing with the increasing intensity of forest management activities performed in the Forest's stands (Walankiewicz et al. 2011). As emphasised in the current recommendations in the nature management plan of the BNP (Regulation 2014b), hollow, dead and dying trees, as well as those fallen as a result of natural reasons, play an imperative role in the life of numerous protected species of birds.

In conclusion, the best way to safeguard the ecological processes along with the whole, extremely valuable assemblage of breeding birds is the passive protection of the whole Polish part of the BF.

5.6. Mammals

A distinct gradient in mammal species numbers has been observed in Poland – from the greatest abundance in the south to the lowest in north-eastern parts of the country (Ciechanowski, Bogdanowicz 2014). Despite the location on Poland's northern outskirts, the BF is remarkable in terms of species-rich mammal community (approximately 60 species) (Stachura et al. 2004; Rachwald, Ruczyński 2015). In addition to numerous species of the temperate zone, mammals characteristic for the boreal zone occur here (whilst at the same time they are absent in the central and southern parts of the country), such as snow hare *Lepus timidus* (Gryz, Krauze-Gryz 2014) and Laxmann's shrew *Sorex caecutiens* (Pucek 2001b) – both considered as the post-glacial relicts. The BF is the south-western limit of *L. timidus* range (Zbyryt et al. 2014), and in the case of *S. caecutiens*, the Forest constitutes an islet in the far south, beyond the continuous range of the species (van der Kooij et al. 2015). Notwithstanding the long-term protection and good maintenance of forest habitats, BF mammal fauna has not been able to resist the negative effects of human activities and has been depleted of several species, including brown bear *Ursus arctos* and European mink (*Mustela lutreola*) (Stachura et al. 2004), in the past centuries.

In the BF, the protection of European bison *Bison bonasus* is one of the main conservation objectives, as the Forest is the most important refuge for this species. This is mainly a consequence of its history – the last exterminated wild individuals used to live here, and European bison population was reintroduced here, first – thanks to breeding, and then as free-living herds (Krasińska, Krasiński 2004). Modern scientific research has challenged earlier beliefs, according to which bisons were perceived as the animals strongly associated with forests. The evolution of the species, dental morphology, behaviour, food intake and microhabitat preferences indicate that it is a ruminant species, associated with grassy open areas, rich in plant species (Kerley et al. 2012; Bocherens et al. 2015). This is reflected, amongst others, in the BNP nature management plan, which emphasises preservation of non-forest ecosystems as feeding sites for European bisons (Regulation 2014b).

Thanks to considerably high proportion of stands of natural character, as well as the presence of numerous dead and dying trees in various stages of decomposition, both standing and lying, mammals in the BF have numerous natural shelters that are not present or available in limited numbers within managed forests. Such shelters are crucial for protected arboreal rodents, such as red squirrel *Sciurus vulgaris*, common dormouse *Muscardinus avellanarius*, forest dormouse *Dryomys nitedula* and fat dormouse *Glis glis* (Ściński, Borowski 2006, 2008; Czeszczewik et al. 2008). In Poland, the two latter species have the status of near-threatened (Pucek 2001a; Pucek, Jurczyszyn 2001).

Hollows, spaces under the protruding bark and cracks formed in decaying trunks of standing dying trees are also key shelters for many species of bats – strictly protected Poland. Fifteen bat species have been recorded in the BF (Stachura et al. 2004; Rachwald, Ruczyński 2015). Shelter preferences of common noctule *Nyctalus noctula* and lesser noctule *N. leisleri* – species at high risk of extinction in Poland (Voloshin 2001) – have been studied in detail. Noctules inhabit both the hollows carved out by woodpeckers as well as the holes in tree trunks formed as a result of wood decomposition processes (as a rule, in oak and ash trees; less frequently, in alders, maples, hornbeams, pines and lime trees). The trees with bat hiding places have a significantly greater diameter at breast height (DBH) (on an average 84 cm) when compared to those growing nearby – not inhabited (average DBH of 40 cm). The inhabited trees are also characterised by a much older age, usually more than 160 years. Noctules prefer to hide in dying trees (80%), over those alive or completely dead. Unlike birds, bats chose the hollows situated high, on an average 18 m above the ground level (Ruczyński, Ruczyńska 2000; Ruczyński, Bogdanowicz 2005, 2008). Similar preferences for hiding places – mostly slots in protruding bark, located in high dying trees – were observed in western barbastelle *Barbastelle barbastellus* – one of the species protected under Natura 2000. This bat species usually chooses hiding in the stands where forest management is limited or absent (Russo et al., 2004), and individuals specimens return year after year to their favourable patches of forest and even to the same trees (Hillen et al. 2010). For this reason, in the nature management plan for the BNP, one of the conditions to ensure the favourable conservation status of *B. barbastellus* is the preservation of forest areas with a high proportion of old trees as well as the presence of old trees with hollows (Zarządzenie 2014b).

Dead or dying trees (including lying deadwood) play a crucial role also in the life of larger mammal species. Decayed stumps of naturally fallen trees are often used by badgers *Meles meles* as a temporary shelter (Kowalczyk et al. 2004). In 95% cases, pine martens *Martes martes* use hiding places situated on trees; the females prefer the hollows and cracks in the trunks to hide their offspring (Zalewski 1997). Wolves *Canis lupus* – the priority species according to the Habitats Directive – give birth to their young not only in burrows but also in windthrows (Schmidt et al. 2008).

In turn, lynx (*Lynx lynx*) – also subject to the protection under Natura 2000 – hunt most often in forest patches with numerous fallen and wind-thrown trees that provide them cover whilst approaching the prey (Podgórski et al. 2008). Therefore, to protect this wild cat threatened with extinction in Poland (Wolsan, Okarma 2001), it is crucial to safeguard forest diversity and assure the presence of a large number of dead trees, in particular – lying trunks and windthrows (Schmidt et al. 2007). Hence, in the BF as a whole, preservation of the mosaic diversification of forest habitats structure, typical for natural forests (fallen or broken trees, woodland glades, along with natural regeneration with deadwood at a level above 10% of stand stock) should be promoted in line with the current recommendations of the nature management plan for the BNP (Rozporządzenie 2014b). Protective measures for large carnivores in the Forest cannot be implemented solely within the BNP, as lynx home ranges and territories of wolf family groups are much larger than the area of the Park (Jedrzejewska, Jędrzejewski 1998).

6. Future of the Białowieża Forest – Conclusions

The protection of natural processes (either strict or active conservative) should predominate in the BF, because it allows for, amongst others, preservation of adequate quantity and quality of deadwood and old trees, indispensable for the survival and development of numerous organisms (including species endangered in Europe) (amongst others: Cieśliński et al. 1996; Gutowski, Buchholz 2000; Czyżewska, Cieśliński 2003c; Gutowski et al. 2004; Cieśliński 2009; Kujawa 2009; Bohdan 2014; Karasiński, Wołkowycki 2016). It is also important that the area of diverse protected environments should be sufficiently large to comprise all fluctuation stages of tree stands, thus providing microhabitats suitable for the development and survival of organisms with very different ecological requirements. Within the large forest, where the protection of spontaneous natural processes is the main concern, there are always open or semi-open areas, appearing as a result of the natural disturbances (e.g. death of old trees, insect outbreak, damage to hurricane winds, and frost or flood). Animal species (in particular many invertebrates and birds), plants and fungi are associated with these areas that give them an opportunity to find suitable niches. It is obvious that in such forests, species populations do not reach large numbers, but species richness is at least the same as that in forest areas exploited economically, where there is always more open space available. The main reason behind this is evolutionary adaptation of organisms associated with mid-forest open areas to rapid detection and colonisation of such habitats. Open habitats within forests, which once covered almost the entire continent, often appeared for a relatively short time, in different places, sometimes distant from each other.

The lack of a solid, comprehensive management plan to protect this precious area, along with recommendations in the relevant documents regarding the protection of the Forest (see Section 3), as well as currently existing threats to its nature, resulting, amongst others, from the fact that in many managed parts of the Forest, timber harvest, 'the protection with the use of the methods of ecological engineering' and 'reconstruction of deciduous oak-hornbeam forests' are planned, all these underline the urgent need for a coherent approach based on the following principles/priorities:

- the protection (strict or active conservative) of natural processes taking place in forest communities. This approach should include forest stands growing in deciduous habitats with incompatible tree species composition (in particular, excessive representation of spruce) as a result of former forest management activities. Reconstruction of such tree stands should be performed by forces of nature. The above recommendations should not apply to heliophilous oak communities, the degenerated patches of which endured in the BF on the area of few hectares. In order to preserve the floristic composition of this anthropozoogenic habitat (resulting from cattle grazing), continuation of cattle grazing is required in the forest. Abandonment of grazing leads to decrease in species richness, hornbeam regeneration and natural return of species composition characteristic for oak-hornbeam forest;

- the active protection of some non-forest communities and enclaves created by man, which are now habitats of protected species (clearings, previous repositories of wood, gravel pits, etc.), in line with the recommendations of the protection action plan for Natura 2000 site;
- limiting the timber harvesting to small areas, in order to provide wood for local communities (as suggested in the legislation projects proposed in 2006);
- lessening management activities in the Forest (also in the aforementioned stands with species composition incompatible with the site); in accordance with the recommendations of the plan of protection tasks for Natura 2000 site as well as those in the renomination dossier submitted to UNESCO.

In the debate about the future of the BF, the proponents of its economic use have raised arguments that much of this forest complex is already covered by different forms of protection. In addition to the BNP, there is a dense network of nature reserves, where forests with ongoing natural processes are protected. Hence, the advocates of this approach believe that the existing network of protected areas (i.e. the BNP and the nature reserves) is sufficient to protect all the natural values of the Forest as a whole, and for that reason, the remaining part can be used economically. Furthermore, they emphasise the fact that the strict protection of no more than 20% of the Forest is sufficient to study the natural processes occurring in the Forest (Brzeziecki 2016). Assuming the need for sustainable management of forests, some scientists, including Jan Marek Matuszkiewicz, make an allowance for artificial regeneration of the sites with removed spruce stands with various species of trees (Hilszczański 2016). However, a cursory analysis of the maps of the distribution of protected areas in the BF shows that the continuation of the economic use of the rest of the Forest will lead over time to a significant isolation of the currently preserved most valuable areas. Such a fate has befallen many Polish forest complexes as well as those in the world. Most of them are nameless forests while others, like those famous situated in the state of Wisconsin in the United States (Curtis 1956; cit. after Burgess and Sharpe 1981) are a key example of human folly and greed. For decades, scientific literature has been full of examples of research on the fragmentation of forest cover and its consequences for various organisms as well as ecological processes (e.g. Helliwell 1976, Burgess, Sharpe 1981, Burgess 1988; Harris, Silva-Lopez, 1992; Honnay et al. 2005). The popular web search service Web of Science gives 26,090 results for 'forest fragmentation' (access date June 21, 2016). In addition to climate change and biological invasions, habitat fragmentation is one of the three main factors causing the loss of the world's biotic diversity (Jackson, Sax 2010). This is the effect of shrinking the area of the habitats suitable for survival along with increasing the isolation of populations of various species living in forests. This leads to a reduction of genetic variation and an increase of genetic differentiation between populations from different patches of the same forest (because of the genetic drift, increased inbreeding and decreased gene flow between populations spatially isolated from each other) (Honnay et al. 2005). Forest habitat fragmentation may adversely affect abundance and diversity of various groups of organisms present in the isolated forest patches. It can also cause an increase in forest perimeter to forest area ratio, in other words: an enhancement of the so-called edge effects. The area affected by the latter will grow at the expense of the internal (core) forest area, which is as a rule free of the edge of effect, and has different microclimate that determines the existence of many forest species. With the increasing range of edge effects and changes in microclimate in the forest, the risk of invasion of interior forest habitats by alien species (which naturally either do not occur there or occur only temporarily and less frequently) increases. Microclimate changes may in fact give invasive species additional chances to compete with forest species (Honnay et al. 2005 and cited references).

The processes described above, caused by forest cover fragmentation and followed by intensified disturbances, adversely affect the reproductive success of many forest species. Some of these processes are initiated after a short time, whilst the consequences of others are revealed after many years. For certain groups of organisms, including herb layer plants, the effects taking place in their disturbed environments, including those related to forest fragmentation, become apparent after many decades. Forest plants, owing to their longevity and clonal growth, outwardly show a reduced sensitivity to habitat fragmentation, but in fact their response is delayed in time. Consequently, currently observed distribution of forest plants is not in equilibrium with the present level of habitat fragmentation and disturbances in their environment (Eriksson, Ehrlen 2001). Some species will become extinct in the future, once a new equilibrium is established in response to the disturbance in their habitats. This phenomenon was described by Tilman et al. (1994) as the extinction debt. It was demonstrated in the case of herb layer species (Kolk, Naaf 2015; Naaf, Kolk 2015), epiphytic forest lichens (Berglund, Jonsson, 2005; Ellis, Coppins 2007), meadow plants (Lindborg, Eriksson 2004) and some animal species (Hanski, Ovaskainen 2002). In the case of forest herb layer species of the temperate zone, the estimated duration of the extinction debt 'payoff', that is, successive species loss after the occurrence of disturbances, is estimated to be about 100–250 years (Vellend et al. 2006).

Exploitation of the currently managed forests of the BF triggers many not fully understood processes, some of which may be irreversible in their consequences for wildlife. Undeniably, the slow and gradual transformation of subsequent parts of the BF will lead to the situation that it will share the fate of other temperate climate forests of Europe and North America. The continuation of silvicultural techniques used in commercial forests is destructive for the nature of this region. The undesirable changes that have occurred here as a result of forest management can sometimes be reversible once the management activities are abandoned. The future of the BF primarily depends on the changes in the way we think about it. The endurance of this unique forest for future generations, in the condition the least altered by humans, can only be assured if we stop perceiving just the economic dimension of it (as the value obtained from wood raw material) and start appreciating the value of its ecosystem services, and if we limit the Forest's use to the minimum satisfying no more than the needs of the local community.

Conflict of interest

The authors declare no potential conflicts.

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Authors' contributions

All authors – the concept, assumptions, work system; A.K. – coordination, writing, editing the whole manuscript; A.K., A.O., M. B., M.F., J.M.G. – general chapters (Introduction, Species Diversity in the Białowieża Forest – selected examples, Conclusions).

Other chapters:

M.L. – history of the Białowieża Forest; M.F., A.O., A.K. – nature conservation in the Białowieża Forest – current status and threats; M.F. – evaluation of the conservation status of Natura 2000 habitats in the Białowieża Forest and recommendations on their protection; A.K. – macrofungi; A.Z., AB – lichens; A.O. – vascular flora; J.M.G., L.B. – insects; P.Ch., W.W. – birds; S.N., R.W.M. – mammals.

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