

# Invertebrates occurring in fruiting bodies of the pathogenic tinder fungus, *Fomes fomentarius* (Polyporales), in the different types of Polish protected forests

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## Abstract

Bracket fungi are usually considered as a cause of economic losses, while they also offer specific microhabitats and have an impact on biodiversity. However, to date this topic has not been sufficiently studied. The aim of this article is to show how the diversity of invertebrate communities, viz. spiders, harvestmen (Araneae, Opiliones), pseudoscorpions (Pseudoscorpionida), two groups of mites (Mesostigmata and Oribatida), springtails (Collembola), and insects (Insecta), inhabiting fruiting bodies of the tinder fungus, *Fomes fomentarius*, depend on specific characteristics of forests. Samples were collected in three locations: the Białowieża National Park (BNP) characterised by a high degree of forest naturalness, the Bieszczady National Park (BdNP), which was transformed by human, but has been undergoing naturalisation for several decades, and the Karkonosze National Park affected by a large-scale forest dieback in the 1980s and which for years has been under strong tourist pressure. A total of 20 fruiting bodies of *F. fomentarius* were collected at each location. In total, 9,821 individuals of invertebrates belonging to 204 species were extracted. The most numerous group was Oribatida (6,595 individuals classified to 106 species), while the most numerous species was *Carabodes femoralis* (5,216 individuals). The study sites differed in the number of species (the highest one was observed in the BdNP, 115, and the lowest one in the KNP, 88) and number of individuals (the highest one was observed in BdNP, 4,285, and the lowest one in BNP, 1,595), as well as the number of individuals per species (the highest one was observed in the BdNP, 37.26 individuals per 1 species, and the lowest in the BNP, 15.79 individuals per 1 species). A NMDS analysis revealed that the inner distribution of the samples in each of the locations was similar in the case of mountain national parks (BdNP and KNP), while the invertebrate groupings from the BNP and KNP differed the most between one another. The multilevel pattern analysis showed different, specific invertebrate species for each study sites, e.g. *Carabodes subarcticus* for the BNP, *Friesea mirabilis* for the BdNP, *Oribatella calcarata* for the KNP and *Dendrolaelaps pini* for both mountain national parks. This study shows the uniqueness of invertebrate communities inhabiting fruiting bodies of *F. fomentarius* and confirms the positive role of this pathogenic fungus in shaping biodiversity.

**Keywords:** arthropods; bracket fungi; polypores; anthropopressure; natural forest

## Introduction

Bracket fungi play an important role in forests. They cause wood rot, which is one of the most significant problems from the point of view of forest pathology, and one of the most serious defects in lumber (Kimbar 2011). On the other hand, they contribute to a greater biological diversity (e.g. Lonsdale et al. 2008) and play a vital role in the natural environment, e.g. by facilitating the process of energy flow and circulation of matter (Niemelä 2013). Bracket fungi might also affect the availability of resources for several organisms (e.g. Moore et al. 2004). Polypores offer specific

microhabitats, such as rotting wood, which has been the subject of numerous studies (e.g. Makarova 2002, Salmane 2005, Gwiazdowicz et al. 2011), or much less studied fruiting bodies. Fungal sporocarps may be termed as biological hotspots, showing high numbers of species within small volumes (Komonen 2003). They are well-researched as patches and temporary habitats that play a key role for many groups of invertebrates as a place of refuge, as well as a source of food (Hågvar and Steen 2013). The unique character of fruiting bodies of bracket fungi is evidenced among others by the occurrence of many species specialized to living in this microhabitat, such as certain mite spe-

cies from the genus *Hoploseius* (e.g. Maśán and Halliday 2016), or some insect species from the genus *Megaselia* (Disney and Pagola-Carte 2009). Studies on invertebrates found in the fruiting bodies of bracket fungi were usually faunistic in nature and concerned selected groups, such as insects (e.g. Jaworski et al. 2014) or mites (Makarova 2002). Despite the unique nature of sporocarps of bracket fungi, research on a wide spectrum of invertebrates inhabiting them and the diversity of their communities in various ecosystems is still insufficient.

*Fomes fomentarius* (L.) J.J. Kickx is a common and economically important wood-rotting fungus. It causes heart rot of wood in several tree species. Although this fungus is usually perceived in terms of losses in forestry, it is also analysed from other stand points, e.g. as a creator of microhabitats. Thus *F. fomentarius* in European beech forests has been studied in the context of the presence of arthropods in its fruiting bodies – research has proven the presence of a large number of arthropods in the fruiting bodies of this fungus, while it also showed that its sporophores represent a habitat characterized by high local variability in community composition and is colonized by species with high dispersal ability (Friess et al. 2019) for invertebrates (e.g. Matthewman and Pielou 1971).

This study is focused on biodiversity in ecosystems with varying degrees of anthropogenic impact. The adopted hypothesis assumed that there are differences in the density and structure of invertebrate communities inhabiting fruiting bodies of *Fomes fomentarius*. Those differences result from the variability of natural conditions and the degree of anthropopressure. The locations studied are three forest ecosystems: Białowieża National Park (BNP), which forests are considerably preserved, Bieszczady National Park (BdNP), transformed by human, but undergoing restoration for several decades, and Karkonosze National Park (KNP), with heavily degraded ecosystems.

This study also aimed to investigate communities of a wide spectrum of invertebrates, including those with high dispersion ability, such as insects, as well as groups with more limited mobility, i.e. mites. Among them, some groups, such as Mesostigmata, are often transmitted by phoresy, while others, such as Oribatida, are much less likely to use this mechanism. The research results are not only to provide a better understanding of that poorly researched issue but also to enable more effective protection of biodiversity.

The areas were located in national parks differing considerably in their specific character and the history of human-induced transformations. The Białowieża National Park (BNP) is the largest area of natural forests over the North European Plain, with well documented pristine features (e.g. Gutowski and Jaroszewicz 2004). To date many studies on invertebrates have been carried out in the BNP in view of its similarities to primeval forests. Only the work of Gdula et al. (2021) was devoted to invertebrate communities inhabiting fruiting bodies of fungi. The

second analysed area – the Karkonosze National Park (KNP) – was under a strong anthropogenic impact related to forest management, settlements, and the extraction of minerals (Danielewicz et al. 2002). In the 1980s the KNP was affected by the ecological disaster caused by pollution, trace metals and pests. It resulted in forest dieback over large areas (Sobik and Błaś 2008). The third location was the Bieszczady National Park (BdNP). The area marked with the remains of former forest management (overexploitation of stands, logging arrangements of forest areas inconsistent with the natural direction of silviculture), as well as pastoralism. Due to the displacement of the local population for decades following World War II, the area of today's BdNP became the site of ecosystem naturalisation processes (Winnicki and Zemanek 2003).

## Material and methods

### Study area

The Białowieża National Park (BNP) is the oldest Polish national park located near the village of Białowieża in north-eastern Poland (52°69'89" N – 52°81'89" N, 23°71'76" E – 23°93'95" E) (Figure 1). The BNP protects one of the best-preserved fragments of primeval deciduous and mixed forest in the Europe Lowland. The BNP is characterized by a great variety of plant cover, mainly the East-European oak-hornbeam forest *Tilio-Carpinetum*, as well as wetland communities such as ash-alder riparian forest *Circaeo-Alnetum*. In turn, nutrient-poor habitats are covered by subcontinental fresh coniferous forest *Vaccinio vitis-idaeae-Pinetum*, and swampy coniferous forest *Vaccinio uliginosi-Pinetum* (Jaroszewicz 2010). About 1,500 species of Macromycetes have been found



**Figure 1.** Location of the study areas (BNP – Białowieża National Park, KNP – Karkonosze National Park, BdNP – Bieszczady National Park)

(Kujawa 2009) in this area, while the inventory carried out in 2008–2012 recorded 142 species of bracket fungi (Niemelä 2013).

The Karkonosze National Park (KNP) is located in the Karkonosze Mountains in the Sudetes in south-western Poland (50°73'59" N – 50°84'10" N, 15°45'88" E – 15°82'99" E), along the border with the Czech Republic (Figure 1). Plant cover varies depending on habitat factors but also elevation above sea level. The foothill zone of the KNP is covered by Central European oak-hornbeam forest *Galio sylvatici-Carpinetum betuli*, in the lower mountain zone it is lower montane fir-spruce forest *Abieti-Piceetum (montanum)*, while in the upper mountain zone there is upper montane spruce forest *Calamagrostio villosae-Piceetum* (Danielewicz et al. 2002). To date about 250 species of Macromycetes have been identified in the KNP (Narkiewicz et al. 2013).

The Bieszczady National Park (BdNP) is the largest national park in the Polish mountains. It is located in the Western Bieszczady Mountains, in the south-eastern part of Poland, along the border with Slovakia and Ukraine (49°00'87" N – 49°14'12" N, 22°26'04" E – 22°53'38" E) (Figure 1). The BdNP protects the Eastern Carpathian mountain landscape with its unique ecosystems. The vegetation is characterized by the presence of vertical zonality: the foothill zone, lower montane zone, and "polonyna", or montane meadows. The most widely occurring forest communities in the BdNP are e.g. Carpathian beech forest *Dentario glandulosae-Fagetum*, and Carpathian alder wood *Alnetum incanae carpaticum* (Winnicki and Zemanek 2003). The research has been conducted, which identified over 1,300 species of Macromycetes fungi from the BdNP and its immediate vicinity (Kujawa et al. 2016).

### Material collection

The fruiting bodies of *Fomes fomentarius* were collected between 18<sup>th</sup>–19<sup>th</sup> July 2014 in the Karkonosze National Park, between 04<sup>th</sup>–09<sup>th</sup> August 2014 in the Białowieża National Park and between 14<sup>th</sup>–19<sup>th</sup> September 2016 in the Bieszczady National Park. A total of 60 fruiting bodies were collected from all three locations (20 in each plot). An axe was used to cut them off of tree trunks (each fruiting body was harvested from a different individual tree). The fruiting bodies were collected from the trees, where *F. fomentarius* occurred most often, i.e. silver birch, *Betula pendula*, and European beech, *Fagus sylvatica*. In order to reflect the specificity of the studied locations, the samples were taken from trees of the age and size commonly found in individual national parks. The fruiting bodies were collected from tree trunks at the height between 0 cm (ground level) and 250 cm above ground level. In order to eliminate the influence of the degree of decomposition of fruiting bodies on invertebrate assemblages, equal numbers of samples were collected from each degree of decomposition (according to the scale from the study by Gdula et al. 2021) in each of the national parks studied. A single fruiting body equals one sample.

### Laboratory procedures

In order to extract mesofauna from the fruiting bodies of *Fomes fomentarius*, they were placed for 72 hours in Tullgren funnels. The collected invertebrates were preserved in 70% ethanol, and next they were classified into seven taxonomic groups: spiders (Araneae), harvestmen (Opiliones), pseudoscorpions (Pseudoscorpionida), mesostigmatic mites (Mesostigmata), oribatid mites (Oribatida), springtails (Collembola), and insects (Insecta). Because this study showed only one species of Opiliones, and its trends were very similar to those of spiders, Araneae and Opiliones were combined to form one group. Therefore, in the further part of the paper six groups are mentioned, with spiders and Opiliones analysed and discussed jointly.

The collected Araneae and Opiliones were identified using the taxonomic keys of valid spiders and Opiliones (Roberts 1985, Rozwałka 2017, Nentwig et al. 2020).

The collected Pseudoscorpionida were examined using a stereomicroscope. For some species, temporary microslides were prepared to facilitate their examination under a compound microscope. Species were identified using the taxonomic keys of Beier (1963) and Christophoryová et al. (2011a).

For collected Mesostigmata both semi-permanent (using lactic acid) and permanent microslides (using Hoyer's medium) were prepared. The individuals of mesostigmatic mites were examined using a light microscope (Zeiss Axioskop 2) and taxonomical literature (e.g. Karg 1993, Maśán 2001, Gwiazdowicz 2007, 2010).

The collected Oribatida were identified using a light microscope, with a phase contrast and a differential interference contrast if necessary. The clearing process using concentrated lactic acid, 60% lactic acid or lactophenol was performed over a course of several days and sometimes weeks. Oribatid mites were examined using the taxonomical keys and original species descriptions (Olszanowski 1996, Weigmann 2006, Niedbała 2008). The names of the species were updated according to Weigmann (2006).

The collected Collembola were identified using a light microscope. Prior to the examination extracted individuals of springtails were mounted with Hoyer's medium and permanent microscopic slides were prepared. The individuals of Collembola were identified using the taxonomical literature (e.g. Potapov 2001, Fjellberg 2007, Dunger and Schlitt 2011).

The immature stages of collected Insecta were identified using Stehr's manuals (Stehr 2005, 2008). Adults of Coleoptera were identified using the taxonomic literature (e.g. Szymczakowski 1961, Burakowski and Ślipiński 1986, Stebnicka 1991) and a comparative collection from the Natural History Collections, AMU.

The invertebrates that were identified as higher taxonomic units, e.g. order or family, were included in the statistical analyses as separate species.

The specimens of invertebrates collected for this work were deposited in the collections at Adam Mickiewicz University, the Faculty of Biology, the Natural History Collections, Poznań, Poland (Araneae and Opiliones, Pseudoscorpionida, Insecta), the Department of Forest Pathology, the Poznań University of Life Sciences (Mesostigmata), the University of Silesia, Poland (Oribatida) and Cardinal Stefan Wyszyński University, Poland (Collembola).

**Statistics**

In order to indicate the diversity of invertebrates colonizing the samples collected in the particular national parks, an iterative non-metric multidimensional scaling method (NMDS) with the Bray-Curtis dissimilarity (McCune and Grace 2002) was used. This method provided visualization of the variability in the species composition within and among the national parks. The statistical significance of differences was calculated using a MANOVA method used for community data. Because the assumption of homogeneity of variance was not fulfilling, the nonparametric permutation analysis of similarities (ANOSIM, Clarke 1993) was applied to find statistically significant differences between the study sites. This method was based on a ranked dissimilarity matrix. The null hypothesis that similarity within groups was smaller or equal to the similarity between groups was tested using the *R* ( $-1 \leq R \leq 1$ ) statistic. *R* > 0 meant significance of the differences between groups (the null hypothesis was rejected).

When significant differences were detected (using 1,000 permutations) the invertebrates significantly influencing the differentiation in the national parks, distinguished based on their abundance and occurrence in particular studied study sites, were identified using the multilevel pattern analysis (Dufrene and Legendre 1997). The analyses were carried out for the double Wisconsin standardization data. To present differences between the parks and groups of invertebrates as regards the number

of species and the number of individuals, violin plots were applied. All testing was conducted at the significance level of 0.05. All the statistical analyses were performed in the R environment (R Core Team 2019) following the procedures of the vegan package (Oksanen et al. 2019) and the indicpecies package (De Caceres and Legendre 2009) and STATISTICA 13.3 software package (TIBCO Software 2017).

**Results**

**General information**

The total number of collected individuals of invertebrates in this study was 9,821. The most numerous group was Oribatida (6,595 indiv.), followed by Insecta (1,428 indiv.), Mesostigmata (1,264 indiv.), and Collembola (497 indiv.), while the least numerous groups were Pseudoscorpionida (26 indiv.) and Araneae and Opiliones (11 indiv.). In turn, the total number of species in the study was 204. The most numerous group in terms of the number of species was oribatid mites (106 species), followed by mesostigmatic mites (43), springtails (26), insects (20), and pseudoscorpions (5), while the least numerous group was spiders and opiliones (4 species). The number of all invertebrate individuals in the studied national parks per sample was between 1 and 1,355 (mean  $163.68 \pm 32.36$ ), whereas the number of species per sample ranged between 1 and 43 (mean  $12.85 \pm 1.18$ ) (Tables 1, 2, Appendix).

**Invertebrate assemblages in the studied national parks**

The study assumed that both the number and the species richness of invertebrates depend on the character of the study sites. The total number of collected individuals of invertebrates was the highest in the BdNP (4,285), slightly less in the KNP (3,941), and the smallest in the BNP (1,595). The trend for the number of invertebrate species

**Table 1.** Minimum, maximum, mean number and  $\pm SE$  of invertebrate species per one sample in the study sites

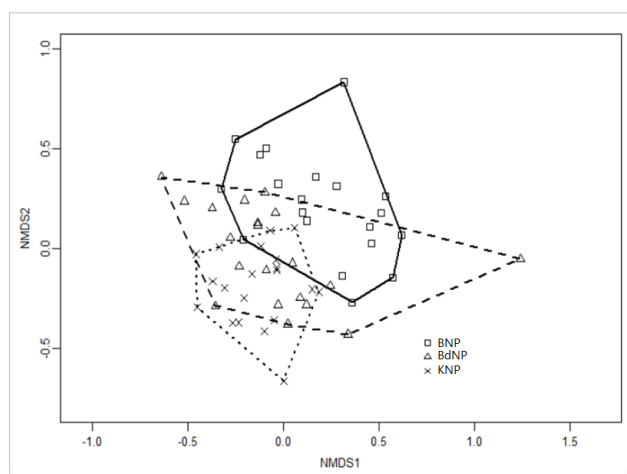
Group of invertebrates	BNP	KNP	BdNP	Total
Araneae and Opiliones	0-2 (0.20) $\pm$ 0.14	0-1 (0.10) $\pm$ 0.07	0-1 (0.10) $\pm$ 0.07	0-2 (0.13) $\pm$ 0.06
Pseudoscorpionida	0-2 (0.35) $\pm$ 0.13	0-1 (0.05) $\pm$ 0.05	0-1 (0.15) $\pm$ 0.08	0-2 (0.18) $\pm$ 0.06
Acari-Mesostigmata	0-10 (2.15) $\pm$ 0.55	0-7 (2.60) $\pm$ 0.43	0-9 (2.25) $\pm$ 0.49	0-10 (2.33) $\pm$ 0.28
Acari-Oribatida	0-21 (5.00) $\pm$ 1.30	3-15 (7.35) $\pm$ 0.76	0-26 (6.85) $\pm$ 1.45	0-26 (6.43) $\pm$ 0.70
Collembola	0-5 (1.10) $\pm$ 0.37	0-4 (1.25) $\pm$ 0.29	0-8 (3.15) $\pm$ 0.65	0-8 (1.83) $\pm$ 0.29
Insecta	0-6 (1.95) $\pm$ 0.40	0-4 (1.55) $\pm$ 0.26	0-7 (2.20) $\pm$ 0.36	0-7 (1.90) $\pm$ 0.20
Total	2-43 (10.95) $\pm$ 2.12	5-24 (12.90) $\pm$ 1.30	1-41 (14.7) $\pm$ 2.54	1-43 (12.85) $\pm$ 1.18

**Table 2.** Minimum, maximum, mean number and  $\pm SE$  of invertebrate individuals per one sample in the study sites

Group of invertebrates	BNP	KNP	BdNP	Total
Araneae and Opiliones	0-2 (0.20) $\pm$ 0.14	0-1 (0.10) $\pm$ 0.07	0-3 (0.25) $\pm$ 0.18	0-2 (0.18) $\pm$ 0.08
Pseudoscorpionida	0-7 (0.75) $\pm$ 0.37	0-1 (0.05) $\pm$ 0.05	0-7 (0.50) $\pm$ 0.36	0-7 (0.43) $\pm$ 0.17
Acari-Mesostigmata	0-62 (7.75) $\pm$ 3.25	0-188 (32.10) $\pm$ 11.21	0-90 (23.35) $\pm$ 5.99	0-188 (21.07) $\pm$ 4.49
Acari-Oribatida	0-382 (52.80) $\pm$ 23.47	6-823 (132.70) $\pm$ 45.49	0-1275 (144.25) $\pm$ 63.21	0-1275 (109.92) $\pm$ 27.17
Collembola	0-28 (4.25) $\pm$ 1.82	0-20 (3.95) $\pm$ 1.25	0-75 (16.65) $\pm$ 4.92	0-75 (8.28) $\pm$ 1.93
Insecta	0-50 (14.00) $\pm$ 3.77	0-162 (28.15) $\pm$ 9.35	0-211 (29.25) $\pm$ 12.29	0-211 (23.80) $\pm$ 5.29
Total	3-411 (80.30) $\pm$ 26.45	9-1063 (197.05) $\pm$ 61.36	1-1355 (214.25) $\pm$ 68.74	1-1355 (163.68) $\pm$ 32.36

in the study sites was slightly different: the highest number of species was collected in the BdNP (115), slightly lower in the BNP (101), and the lowest in the KNP (88). Also, the number of individuals per species clearly differs in the individual parks studied: it was 15.79 individuals per species in the BNP, 37.26 in the BdNP, and 44.78 in the KNP, respectively (Appendix). There were also differences in the share of individual groups of invertebrates between study sites, e.g. in the case of Collembola (in the KNP, there were more than two times fewer species than in the BdNP, with a very similar number of individuals). The species structure also differs between the study sites: in the BNP, the most numerous species were *Carabodes femoralis* (690 indiv.), *Cis* spp. (174 indiv.) and *Carabodes subarcticus* (129 indiv.), while in the mountain parks the most numerous species were the same: *Carabodes femoralis* (2,267 indiv. in the KNP and 2,259 indiv. in the BdNP), *Cis* spp. (543 indiv. in the KNP and 522 indiv. in the BdNP) and *Dendrolaelaps pini* (537 indiv. in the KNP and 305 indiv. in the BdNP) (Appendix). The differences between the samples from the study sites were also emphasised by non-metric multidimensional scaling (NMDS). The analysis revealed the inner distribution of the samples in each of the locations, which was similar in the case of the mountain national parks, in turn, the samples from the BNP and the KNP differing most markedly from each other. In addition, the analysis indicated a clear grouping of the bracket fungi in each location into the corresponding sets, which only slightly overlapped: the set of bracket fungi from the KNP stretched along the lower values on the NMDS2 axis, the set of samples from the BNP corresponded to higher values on the NMDS2 axis, while the set of the BdNP samples was located between the sets of the other parks (Figure 2). Moreover, the ANOSIM analysis indicated significant differences between the national parks ( $R = 0.306, p = 0.001$ ).

The differences between invertebrate communities inhabiting fruiting bodies of *F. fomentarius* in the analysed



**Figure 2.** NMDS analysis (BNP – Białowieża National Park, BdNP – Bieszczady National Park, KNP – Karkonosze National Park)

**Table 3.** Species characteristic for a group of sites, detected using multilevel pattern analysis

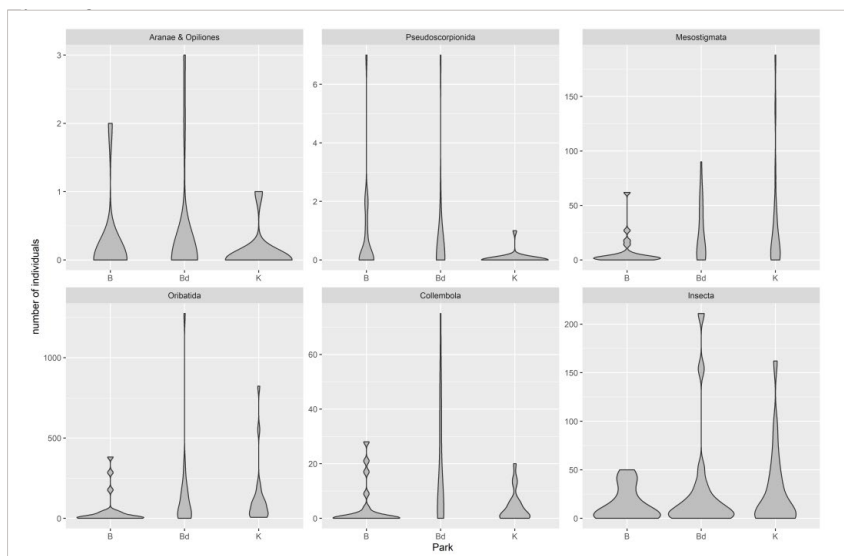
National Park	Species	Stat	Significance (p-value)
BNP	<i>Carabodes subarcticus</i>	0.362	0.0003
	<i>Pneumolaelaps lubrica</i>	0.344	0.0310
	Diptera	0.255	0.0250
BdNP	<i>Isotomurus palustris</i>	0.448	0.0017
	<i>Friesea mirabilis</i>	0.424	0.0017
	<i>Oppiella (Oppiella) spledens</i>	0.397	0.0090
	<i>Isotoma viridis</i>	0.364	0.0073
	<i>Anurophorus laricis</i>	0.361	0.0300
	<i>Willowsia buski</i>	0.348	0.0080
	<i>Schelorbates pallidulus</i>	0.305	0.0397
KNP	<i>Zercon arcuatus</i>	0.304	0.0303
	<i>Minunthozetes pseudofusiger</i>	0.225	0.0103
	<i>Carabodes reticulatus</i>	0.557	0.0003
	<i>Oribatella calcarata</i>	0.484	0.0003
	<i>Damaeus riparius</i>	0.394	0.0110
	<i>Belba corynopus</i>	0.390	0.0107
	<i>Zerconopsis michaeli</i>	0.365	0.0053
	<i>Cepheus dentatus</i>	0.345	0.0140
	<i>Nanhermannia cf. coronata</i>	0.339	0.0120
	<i>Chamobates spinosus</i>	0.336	0.0333
	<i>Carabodes coriaceus</i>	0.331	0.0230
	<i>Sminthurinus niger</i>	0.326	0.0300
	<i>Carabodes femoralis</i>	0.308	0.0367
<i>Lasioseius zerconoides</i>	0.302	0.0310	
BdNP + KNP	<i>Chamobates borealis</i>	0.293	0.0473
	<i>Dendrolaelaps pini</i>	0.304	0.0423

Note: \* – relationships significant at the level  $\alpha = 0.05$ .

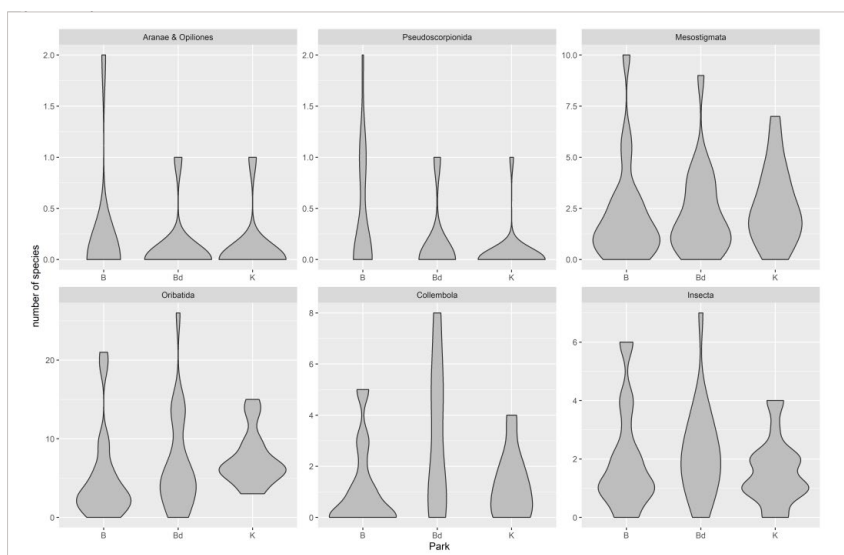
national parks were also shown by the multilevel pattern analysis. The analysis showed that *Carabodes subarcticus*, *Pneumolaelaps lubrica* and Diptera were typical species for the BNP, they were e.g. *Isotomurus palustris*, *Friesea mirabilis*, and *Willowsia buski* for the BdNP, and it was *Carabodes reticulatus*, *Oribatella calcarata* and *Damaeus riparius* for the KNP, while *Dendrolaelaps pini* was the species typical of the BdNP and KNP jointly (Table 3).

### Individual invertebrate groups in the studied national parks

The results showed also that the individual invertebrate groups differ in the study sites. In the case of spiders and Opiliones the largest number of species (3) was recorded in the BNP, while the largest number of individuals (5) in the BdNP (Appendix). The violin plots showing the distribution of the number of individuals and species depending for each study site indicate that the poorest samples were collected from the KNP (Figures 3, 4). Linyphiidae individuals were detected in the samples from all the parks studied, while *Cryphoeca silvicola* was observed only in the BdNP, and *Helophora insignis* only in the BNP (Appendix). In the case of Pseudoscorpionida both species (3) and individuals (15) were the most numerous in the BNP, while the samples from the KNP showed both the lowest numbers of species (1) and individuals (1). Some species of pseudoscorpions – *Lamprochernes chyzeri* and Chernet-



**Figure 3.** Numbers of invertebrate individuals depending on the study site (B – Białowieża National Park, Bd – Bieszczady National Park, K – Karkonosze National Park)



**Figure 4.** Numbers of invertebrate species depending on the study site (B – Białowieża National Park, Bd – Bieszczady National Park, K – Karkonosze National Park)

idae – were found in the only location, the BNP, *Chthonius (Ephippiochthonius) tetrachelatus* only in the BdNP, while Neobisiidae only in the KNP (Appendix). The violin plots for Mesostigmata showed a similarity between the studied parks in the number of recorded species, and clear differences in the number of individuals (155 in the BNP, 467 in the BdNP and 642 in the KNP) (Figures 3, 4). There are also visible differences in the number of species exclusive to particular parks: it was 11 species in the BNP, 9 in the KNP, and 7 in the BdNP. The species observed only in the samples from one park include among others: *Dendrolaelaps zwoelferi* in the BNP, *Zercon arcuatus* in the BdNP, or *Laioseius zerconoides* in the KNP. Only five mesostigmatic mite species (e.g. *Lasioseius ometes*) were found in all the study sites, while many more were recorded in the samples from two or one park. Some species, such as *Dendrolaelaps pini*, showed a tendency to be most abundant in the mountain parks (Appendix). In the analysed material Oribatida were the most numerous invertebrate group both in terms of the number of species and the number of indi-

viduals. In the case of this mite group, notable differences were observed in the number of individuals collected in particular study sites (BNP – 1056, BdNP – 2885, KNP – 2654), while the differences between the number of species were slightly less marked (BNP – 49, BdNP – 58, KNP – 48) (Figures 3, 4). Also, for this group of mites it is apparent that very few (only 11 out of 104 recorded) species occurred in all the localities. In the studied national parks there was a similar number of oribatid mite species exclusive to only one study site: in the BNP and BdNP there were 23 species (e.g. *Carabodes subarcticus* in the BNP and *Minunthozetes pseudofusiger* in the BdNP), and in the the KNP, 22 species (e.g. *Carabodes reticulatus*), while there were 12 species that occurred only in the mountain parks (e.g. *Cepheus dentatus*) (Appendix). The results concerning Collembola also showed clear differences in trends between the parks studied – in the BdNP there were definitely more individuals (333) and species (20) than in the BNP (85 individuals belonging to 11 species) and the KNP (79 indiv. belonging to 7 species) (Figures 3, 4). In

the BNP and KNP two species exclusive to each of these study sites were recorded (i.e. *Pseudachorutella assigilata* in the BNP and *Ptenotrix atra* in the KNP), while in the BdNP there were definitely the most exclusive species, as many as 12 (i.e. *Friesea handschini*) (Appendix). The violin plots for Insecta, in turn, showed the scarcity of individuals in the BNP (280) compared to the mountain parks (BdNP – 585, KNP – 583), with a simultaneous tendency to similarity between the number of species in the individual parks (BNP – 13, BdNP – 13, KNP – 8) (Figures 3, 4). The number of exclusive species was the highest (5) in the BdNP (e.g. *Neomida haemorrhoidalis*), slightly lower (4) in the BNP (e.g. *Trixagus* sp.), and the lowest (2) in the KNP (e.g. *Anisotoma* sp.) (Appendix).

## Discussion and conclusions

### Invertebrate assemblages in the studied national parks

The results of this study showed clear differences between the fauna inhabiting fruiting bodies of tinder fungus in the studied national parks. The Białowieża National Park in its nature and intensity of anthropopressure and a unique natural structure presents a vast abundance of invertebrate species (e.g. Olszanowski and Błoszyk 1998). For several decades the undergrowth of the Bieszczady National Park has been regenerating. Despite relatively few studies, a number of rare species have been found (e.g. Rozwałka 2010). Effects of forest dieback and strong anthropopressure in the Karkonosze National Park were evident also in the case of the invertebrate fauna (e.g. Mazur et al. 2007). These differences are apparent both in the species composition (the mountain parks were more similar in this aspect and had a common characteristic species detected using the multilevel pattern analysis), and in the number of individuals and species of invertebrates (in the BNP, although the number of individuals observed was markedly lower than in the other study sites, the samples collected in this park were much richer in terms of species). The differences between the invertebrate communities colonizing the samples in the particular study sites, especially between the samples from the BNP and KNP, were confirmed also by the NMDS analysis. The results might be a consequence of the specific diversity of the analysed parks. A few factors had a significant impact: character (lowland vs. mountain), the level of micro- and macrohabitat diversity (possibility of colonization by invertebrates), a different history of forest management implemented in these areas and their subsequent protection (influencing, among others, the diversity of plant communities). The species poverty in the KNP may also be related to the environment polluted with harmful chemical compounds, including trace metals, also researched by Marko-Worłowska et al. (2013). Pedofauna analyses showed that in the environment polluted with trace metals the abundance and diversity of invertebrates are much lower than in unpolluted soils (Błoszyk et al. 2002).

This study showed that a greater abundance of invertebrates was found in the study sites more transformed by humans. It was also demonstrated in other publications on invertebrates (e.g. Graham et al. 2004). This correlation might be justified by abiotic factors common to disturbed habitats, such as higher light availability or increased temperature (Feinsinger et al. 1988).

### The ecology of the species

The obtained results show similarities with previous publications examining invertebrates in sporocarps of *F. fomentarius*. *Proctolaelaps pygmaeus* was observed by Makarova (2002), while Gwiazdowicz and Łakomy (2002) collected 14 species from *F. fomentarius* fruiting bodies (including *Lasioseius muricatus*, *L. ometes* and *Trichouropoda ovalis*). Those studies also showed similarities to our results. Insects identified in fruiting bodies of this species of fungus included *Bolitophagus reticulatus*, while species from the family Ciidae were previously known (Hågvar 1999, Kaczmarczyk-Ziemba et al. 2019).

To date some of the listed species, such as *Hoploseius oblongus*, have been shown only from polypore fungi (Maśan and Halliday 2016, Gdula et al. 2021). They might prefer this microhabitat – as in the case of beetles from the Ciidae family that live, feed and reproduce inside basidiomes of polypore fungi (Oliveira et al. 2013). *Hoploseius oblongus* is an obligate inhabitant of fruiting bodies of *Fomitopsis pinicola* (Andrianov et al. 2022); however, it has also been found in large numbers in other species of bracket fungi (Gdula et al. 2021). The most numerous species of invertebrates recorded in this study were also observed in other microhabitats. *Carabodes femoralis* is the most numerous invertebrate species in all the studied national parks – it is a common forest (Weigmann 2006) and mycophagous species (Schneider et al. 2005). This species is known from various microhabitats, e.g. litter, soil (e.g. Manu and Honciuc 2010), nests of *Formica rufa* ants (Sell 1990), deadwood (Siira-Pietikäinen et al. 2008), and guano (Maślak and Barczyk 2011). Also, the most numerous found invertebrate taxa from groups other than Oribatida are shown from substrates other than fruiting bodies. Spiders from the Linyphiidae family are observed in various habitats, such as forests (Wiśniewski et al. 2018), farmland (Schmidt and Tschardtke 2005) and grass (Thomas and Jepson 2003). The most numerous pseudoscorpions in this study – *Chernes cimicoides* – has also been found in tree hollows, under tree bark (Krajčovičová and Christophoryová 2014), at the bark and trunk eclectors (Muster and Blick 2015), and in bird nests (Christophoryová et al. 2011b). The most frequently recorded mesostigmatic mite, *Dendrolaelaps pini*, is known from fruiting bodies of polypores (Salmane 2005), rotting wood (Gwiazdowicz et al. 2011), galleries of *Ips typographus* (Khaustov et al. 2018), pine stumps, as well as under wing covers of bark beetles (Karg 1993). To date the most numerous species of springtails, *Friesea mirabilis*, has been found in soil (Jucevica

and Melecis 2006), leaf litter (Cox 1982), litter of meadows and lichen heath (Fjellberg 1975). In the case of the most numerous insects, beetles of the genus *Cis*, their representatives are observed primarily in fruiting bodies of bracket fungi, rarely in other microhabitats, such as under the bark or in rotting wood (Lawrence 2016). Some of the recorded species, such as *Carabodes femoralis* and *Dendrolaelaps zwoelferi* in the BNP, or *Zercon curiosus* and *Lasioseius ometes* in the KNP, were previously reported from these parks (Gabryś et al. 2008, Gdula et al. 2021). The results for the first time showed the occurrence of some species, e.g. large numbers of *H. oblongus* and *Carabodes areolatus* in the BdNP, or *Dendrolaelaps pini* and *Entomobrya corticalis* in the KNP.

Despite numerous studies and increasing knowledge concerning the biology of invertebrates, for many of the species shown in this study there is still a lack of data on their relationship with bracket fungi, related to e.g. the potential spread of fungi by their spores being transported on bodies of invertebrates.

It is also worth noting that the studied areas differed significantly in terms of being beneficial for invertebrates inhabiting fungi. The BdNP, which had been undergoing renaturalisation for several decades, offered favourable conditions for the most numerous groups to live in. However, in terms of species richness the most distinguished park was the BNP with the highest degree of naturalness. The KNP subjected to strong anthropopressure turned out to be the least conducive to the development of invertebrate species diversity. In this park, despite a much larger number of invertebrates than in the BNP, the lowest number of invertebrate species was found among all the study sites.

The results of this study shed light on the poorly understood issue of invertebrate biology. The obtained results could be useful in the context of sustainable forest management, by showing the role of bracket fungi in shaping biodiversity. However, this is a complex problem and requires further research, among other things aimed at studying the mechanisms of fruiting body colonization and providing better understanding of the biology of individual invertebrate species inhabiting them.

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**Appendix.** Invertebrates occurring on fruiting bodies of tinder conk *Fomes fomentarius* (L.) J.J. Kickx in Białowieża National Park (BNP), Bieszczady National Park (BdNP) and Karkonosze National Park (KNP), Poland. Abu – abundance. Fre – frequency. Dom – Dominance

Species	BNP			BdNP			KNP			ALL		
	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom
<b>Araneae &amp; Opiliones</b>	4	0.10	0.00	5	0.10	0.00	2	0.10	0.00	11	0.10	0.00
<i>Cryphoeca silvicola</i>	0	0.00	0.00	2	0.05	0.00	0	0.00	0.00	2	0.02	0.00
<i>Helophora insignis</i>	1	0.05	0.00	0	0	0	0	0	0	1	0.02	0.00
Linyphiidae	2	0.10	0.00	3	0.05	0.00	1	0.05	0.00	6	0.07	0.00
<i>Lophopilio palpalis</i>	1	0.05	0.00	0	0.00	0.00	1	0.05	0.00	2	0.03	0.00
<b>Pseudoscorpionida</b>	15	0.30	0.01	10	0.15	0.00	1	0.05	0.00	26	0.17	0.00
<i>Chernes cimicoides</i>	5	0.15	0.00	8	0.10	0.00	0	0.00	0.00	13	0.08	0.00
Chernetidae	9	0.15	0.01	0	0.00	0.00	0	0.00	0.00	9	0.05	0.00
<i>Chthonius (Ephippiochthonius) tetrachelatus</i>	0	0.00	0.00	2	0.05	0.00	0	0.00	0.00	2	0.02	0.00
<i>Lamprochernes chyzeri</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
Neobisiidae	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<b>Mesostigmata</b>	155	0.80	0.10	467	0.85	0.11	642	0.90	0.16	1264	0.85	0.13
<i>Celaenopsis badius</i>	0	0.00	0.00	4	0.05	0.00	0	0.00	0.00	4	0.02	0.00
<i>Dendrolaelaps armatus</i>	0	0.00	0.00	16	0.15	0.00	0	0.00	0.00	16	0.05	0.00
<i>Dendrolaelaps cornutus</i>	0	0.00	0.00	5	0.10	0.00	3	0.05	0.00	8	0.05	0.00
<i>Dendrolaelaps pini</i>	18	0.20	0.01	305	0.40	0.07	537	0.65	0.14	860	0.42	0.09
<i>Dendrolaelaps acornutus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Dendrolaelaps cornutulius</i>	3	0.10	0.00	0	0.00	0.00	0	0.00	0.00	3	0.03	0.00
<i>Dendrolaelaps euarmatus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Dendrolaelaps punctatulus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Dendrolaelaps</i> sp.	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Dendrolaelaps zwoelferi</i>	11	0.05	0.01	0	0.00	0.00	0	0.00	0.00	11	0.02	0.00
<i>Dinychus arcuatus</i>	5	0.10	0.00	7	0.10	0.00	0	0.00	0.00	12	0.07	0.00
<i>Dinychus perforatus</i>	29	0.10	0.02	0	0.00	0.00	5	0.05	0.00	34	0.05	0.00
<i>Gamasellodes bicolor</i>	3	0.05	0.00	0	0.00	0.00	0	0.00	0.00	3	0.02	0.00
<i>Gamasellus montanus</i>	1	0.05	0.00	2	0.05	0.00	5	0.15	0.00	8	0.08	0.00
<i>Geholaspis mandibularis</i>	0	0.00	0.00	0	0.00	0.00	4	0.05	0.00	4	0.02	0.00
<i>Geolaelaps brevipilis</i>	0	0.00	0.00	0	0.00	0.00	3	0.05	0.00	3	0.02	0.00
<i>Holoparasitus calcaratus</i>	0	0.00	0.00	0	0.00	0.00	5	0.10	0.00	5	0.03	0.00
<i>Hoploseius oblongus</i>	43	0.20	0.03	2	0.05	0.00	0	0.00	0.00	45	0.08	0.00
<i>Lasioseius inconspicuus</i>	0	0.00	0.00	11	0.05	0.00	0	0.00	0.00	11	0.02	0.00
<i>Lasioseius muricatus</i>	0	0.00	0.00	17	0.15	0.00	0	0.00	0.00	17	0.05	0.00
<i>Lasioseius ometes</i>	4	0.20	0.00	5	0.10	0.00	16	0.20	0.00	25	0.17	0.00
<i>Lasioseius zerconoides</i>	0	0.00	0.00	0	0.00	0.00	15	0.20	0.00	15	0.07	0.00
<i>Lysigamasus vagabundus</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
Parasitidae	0	0.00	0.00	1	0.05	0.00	6	0.10	0.00	7	0.05	0.00
<i>Pergamasus rühmi</i>	0	0.00	0.00	0	0.00	0.00	2	0.10	0.00	2	0.03	0.00
<i>Pergamasus</i> sp.	0	0.00	0.00	13	0.15	0.00	7	0.10	0.00	20	0.08	0.00
<i>Pneumolaelaps lubrica</i>	7	0.20	0.00	0	0.00	0.00	6	0.05	0.00	13	0.08	0.00
<i>Proctolaelaps pygmaeus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Sejus polonicus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Sejus togatus</i>	3	0.10	0.00	0	0.00	0.00	0	0.00	0.00	3	0.03	0.00
<i>Thenargamasus</i> sp.	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Trachytes aegrota</i>	0	0.00	0.00	1	0.05	0.00	1	0.05	0.00	2	0.03	0.00
<i>Trichouropoda ovalis</i>	7	0.15	0.00	18	0.20	0.00	0	0.00	0.00	25	0.12	0.00
<i>Uroobovella vinicolora</i>	0	0.00	0.00	5	0.10	0.00	3	0.10	0.00	8	0.07	0.00
<i>Veigaia</i> sp.	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00

## Appendix (continued)

Species	BNP			BdNP			KNP			ALL		
	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom
<i>Veigaia nemorensis</i>	3	0.05	0.00	2	0.05	0.00	1	0.05	0.00	6	0.05	0.00
<i>Veigaia transisale</i>	3	0.05	0.00	0	0.00	0.00	0	0.00	0.00	3	0.02	0.00
<i>Zercon arcuatus</i>	0	0.00	0.00	16	0.20	0.00	0	0.00	0.00	16	0.07	0.00
<i>Zercon curiosus</i>	8	0.20	0.01	0	0.00	0.00	1	0.05	0.00	9	0.08	0.00
<i>Zercon storkani</i>	0	0.00	0.00	0	0.00	0.00	3	0.10	0.00	3	0.03	0.00
<i>Zercon triangularis</i>	0	0.00	0.00	4	0.10	0.00	0	0.00	0.00	4	0.03	0.00
<i>Zerconopsis michaeli</i>	0	0.00	0.00	0	0.00	0.00	16	0.25	0.00	16	0.08	0.00
<i>Zerconopsis remiger</i>	1	0.05	0.00	32	0.10	0.01	1	0.05	0.00	34	0.07	0.00
<b>Oribatida</b>	1056	0.85	0.66	2885	0.90	0.67	2654	1.00	0.67	6595	0.92	0.67
<i>Acrogalumna longipluma</i>	0	0.00	0.00	0	0.00	0.00	3	0.05	0.00	3	0.02	0.00
<i>Achipteria nitens</i>	0	0.00	0.00	4	0.10	0.00	0	0.00	0.00	4	0.03	0.00
<i>Achipteria coleoptrata</i>	3	0.10	0.00	0	0.00	0.00	0	0.00	0.00	3	0.03	0.00
<i>Achipteria</i> sp.	19	0.10	0.01	0	0.00	0.00	0	0.00	0.00	19	0.03	0.00
<i>Adoristes ovatus</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Anachipteria deficiens</i>	21	0.05	0.01	15	0.15	0.00	0	0.00	0.00	36	0.07	0.00
<i>Autogneta longilamellata</i>	0	0.00	0.00	1	0.05	0.00	5	0.05	0.00	6	0.03	0.00
<i>Banksinoma lanceolata</i>	1	0.05	0.00	1	0.05	0.00	1	0.05	0.00	3	0.05	0.00
<i>Belba corynopus</i>	0	0.00	0.00	0	0.00	0.00	7	0.25	0.00	7	0.08	0.00
<i>Berniniella bicarinata</i>	0	0.00	0.00	4	0.05	0.00	0	0.00	0.00	4	0.02	0.00
<i>Caleremaeus monilipes</i>	2	0.10	0.00	2	0.05	0.00	0	0.00	0.00	4	0.05	0.00
<i>Carabodes areolatus</i>	5	0.10	0.00	112	0.35	0.03	73	0.50	0.02	190	0.32	0.02
<i>Carabodes femoralis</i>	690	0.65	0.43	2259	0.80	0.53	2267	1.00	0.58	5216	0.82	0.53
<i>Carabodes labyrinthicus</i>	2	0.10	0.00	10	0.30	0.00	1	0.05	0.00	13	0.15	0.00
<i>Carabodes marginatus</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Carabodes reticulatus</i>	0	0.00	0.00	0	0.00	0.00	44	0.50	0.01	44	0.17	0.00
<i>Carabodes</i> sp.	0	0.00	0.00	16	0.15	0.00	0	0.00	0.00	16	0.05	0.00
<i>Carabodes tenuis</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Carabodes coriaceus</i>	27	0.25	0.02	0	0.00	0.00	31	0.30	0.01	58	0.18	0.01
<i>Carabodes ornatus</i>	6	0.10	0.00	0	0.00	0.00	4	0.15	0.00	10	0.08	0.00
<i>Carabodes subarcticus</i>	129	0.65	0.08	0	0.00	0.00	0	0.00	0.00	129	0.22	0.01
<i>Cepheus cepheiformis</i>	8	0.15	0.01	28	0.25	0.01	2	0.10	0.00	38	0.17	0.00
<i>Cepheus dentatus</i>	0	0.00	0.00	27	0.20	0.01	16	0.35	0.00	43	0.18	0.00
<i>Cepheus latus</i>	0	0.00	0.00	0	0.00	0.00	2	0.05	0.00	2	0.02	0.00
<i>Cepheus</i> sp.	0	0.00	0.00	6	0.15	0.00	0	0.00	0.00	6	0.05	0.00
<i>Ceratoppia quadridentata</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Chamobates borealis</i>	0	0.00	0.00	15	0.35	0.00	19	0.35	0.00	34	0.23	0.00
<i>Chamobates cuspidatus</i>	22	0.20	0.01	22	0.05	0.01	3	0.10	0.00	47	0.12	0.00
<i>Chamobates</i> sp.	0	0.00	0.00	4	0.05	0.00	0	0.00	0.00	4	0.02	0.00
<i>Chamobates spinosus</i>	0	0.00	0.00	0	0.00	0.00	41	0.20	0.01	41	0.07	0.00
<i>Chamobates voigtzi</i>	0	0.00	0.00	1	0.05	0.00	9	0.15	0.00	10	0.07	0.00
<i>Cultroribula bicultrata</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Cymbaeremaeus cymba</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Damaeus (Adamaeus) onustus</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Damaeus (Paradamaeus) clavipes</i>	2	0.05	0.00	4	0.05	0.00	0	0.00	0.00	6	0.03	0.00
<i>Damaeus riparius</i>	0	0.00	0.00	0	0.00	0.00	6	0.25	0.00	6	0.08	0.00
<i>Damaeus (Epidamaeus) bituberculatus</i>	3	0.05	0.00	0	0.00	0.00	0	0.00	0.00	3	0.02	0.00
<i>Damaeus</i> sp.	2	0.10	0.00	0	0.00	0.00	0	0.00	0.00	2	0.03	0.00
<i>Dameobelba minutissima</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Dissorhina ornata</i>	4	0.10	0.00	23	0.15	0.01	1	0.05	0.00	28	0.10	0.00
<i>Eniochthonius minutissimus</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Epidamaeus bituberculatus</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Eueremaeus oblongus</i>	2	0.05	0.00	7	0.15	0.00	0	0.00	0.00	9	0.07	0.00
<i>Eupelops</i> sp.	0	0.00	0.00	3	0.05	0.00	0	0.00	0.00	3	0.02	0.00
<i>Eupelops major</i>	2	0.10	0.00	0	0.00	0.00	0	0.00	0.00	2	0.03	0.00
<i>Eupelops subulinger</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Euphthiracarus cribrarius</i>	1	0.05	0.00	2	0.05	0.00	1	0.05	0.00	4	0.05	0.00
<i>Furcoribula furcillata</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Galumna lanceolata</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Globozetes longipilus</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Graptoppia foveolata</i>	1	0.05	0.00	1	0.05	0.00	0	0.00	0.00	2	0.03	0.00
<i>Lagenobates lagenulus</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00

Appendix (continued)

Species	BNP			BdNP			KNP			ALL		
	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom
<i>Liacarus coracinus</i>	1	0.05	0.00	6	0.20	0.00	0	0.00	0.00	7	0.08	0.00
<i>Liebstadia longior</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Liebstadia similis</i>	0	0.00	0.00	0	0.00	0.00	4	0.05	0.00	4	0.02	0.00
<i>Melanozetes mollicomus</i>	0	0.00	0.00	3	0.05	0.00	0	0.00	0.00	3	0.02	0.00
<i>Metabelba propexa</i>	0	0.00	0.00	1	0.05	0.00	1	0.05	0.00	2	0.03	0.00
<i>Metabelba pulverosa</i>	0	0.00	0.00	2	0.05	0.00	0	0.00	0.00	2	0.02	0.00
<i>Metabelba</i> sp.	3	0.10	0.00	1	0.05	0.00	0	0.00	0.00	4	0.05	0.00
<i>Micropopia minus</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Minunthozetes pseudofusiger</i>	0	0.00	0.00	51	0.25	0.01	0	0.00	0.00	51	0.08	0.01
<i>Moritzoppia unicarinata</i>	10	0.10	0.01	0	0.00	0.00	0	0.00	0.00	10	0.03	0.00
<i>Mycobates bicornis</i>	0	0.00	0.00	5	0.05	0.00	0	0.00	0.00	5	0.02	0.00
<i>Nanhermannia cf. coronata</i>	0	0.00	0.00	2	0.05	0.00	19	0.35	0.00	21	0.13	0.00
<i>Nanhermannia</i> sp.	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Nanhermannia nana</i>	10	0.10	0.01	0	0.00	0.00	0	0.00	0.00	10	0.03	0.00
<i>Neoribates aurantiacus</i>	16	0.05	0.01	0	0.00	0.00	0	0.00	0.00	16	0.02	0.00
<i>Oppia nitens</i>	2	0.05	0.00	0	0.00	0.00	0	0.00	0.00	2	0.02	0.00
Oppidae	0	0.00	0.00	8	0.10	0.00	1	0.05	0.00	9	0.05	0.00
<i>Oppiella (Moritzoppia) keilbachi</i>	0	0.00	0.00	3	0.05	0.00	1	0.05	0.00	4	0.03	0.00
<i>Oppiella (Moritzoppiella) splendens</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Oppiella (Oppiella) maritima</i>	0	0.00	0.00	3	0.05	0.00	1	0.05	0.00	4	0.03	0.00
<i>Oppiella (Oppiella) nova</i>	0	0.00	0.00	5	0.10	0.00	0	0.00	0.00	5	0.03	0.00
<i>Oppiella (Oppiella) spledens</i>	0	0.00	0.00	89	0.25	0.02	0	0.00	0.00	89	0.08	0.01
<i>Oribatella calcarata</i>	1	0.05	0.00	9	0.10	0.00	32	0.55	0.01	42	0.23	0.00
<i>Oribatella quadricornuta</i>	0	0.00	0.00	2	0.05	0.00	3	0.15	0.00	5	0.07	0.00
<i>Oribatella similesuperbula</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Oribatella</i> sp.	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Oribatella superbula</i>	0	0.00	0.00	0	0.00	0.00	2	0.05	0.00	2	0.02	0.00
<i>Oribatella sexdentata</i>	2	0.05	0.00	1	0.05	0.00	0	0.00	0.00	3	0.03	0.00
<i>Oribatula tibialis</i>	1	0.05	0.00	1	0.05	0.00	0	0.00	0.00	2	0.03	0.00
<i>Oribatula (Zygoribatula) exilis</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Parachipteria punctata</i>	3	0.10	0.00	0	0.00	0.00	0	0.00	0.00	3	0.03	0.00
<i>Pergalumna nervosa</i>	2	0.05	0.00	1	0.05	0.00	0	0.00	0.00	3	0.03	0.00
<i>Phauloppia nemoralis</i>	2	0.10	0.00	0	0.00	0.00	0	0.00	0.00	2	0.03	0.00
<i>Phthiracarus bryobius</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Phthiracarus longulus</i>	5	0.10	0.00	21	0.15	0.00	4	0.20	0.00	30	0.15	0.00
<i>Phthiracarus compressus</i>	2	0.05	0.00	0	0.00	0.00	0	0.00	0.00	2	0.02	0.00
<i>Pilogalumna tenuiclava</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Platynothrus peltifer</i>	0	0.00	0.00	10	0.15	0.00	17	0.05	0.00	27	0.07	0.00
<i>Porobelba spinosa</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Quadropia quadricarinata</i>	0	0.00	0.00	8	0.05	0.00	0	0.00	0.00	8	0.02	0.00
<i>Ramusella clavipectinata</i>	1	0.05	0.00	0	0.00	0.00	2	0.10	0.00	3	0.05	0.00
<i>Rhinoppia subpectinata</i>	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Scheloribates (Hemileius) initialis</i>	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Scheloribates latipes</i>	14	0.10	0.01	30	0.15	0.01	0	0.00	0.00	44	0.08	0.00
<i>Scheloribates pallidulus</i>	2	0.05	0.00	31	0.35	0.01	10	0.15	0.00	43	0.18	0.00
<i>Scheloribates</i> sp.	0	0.00	0.00	3	0.15	0.00	0	0.00	0.00	3	0.05	0.00
<i>Spatiodamaeus boreus</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Steganacarus (Atropacarus) striculus</i>	0	0.00	0.00	0	0.00	0.00	4	0.15	0.00	4	0.05	0.00
<i>Subiasella quadrimaculata</i>	15	0.15	0.01	10	0.05	0.00	0	0.00	0.00	25	0.07	0.00
<i>Suctobelba trigona</i>	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Suctobelba atomaria</i>	2	0.05	0.00	0	0.00	0.00	0	0.00	0.00	2	0.02	0.00
<i>Trichoribates novus</i>	0	0.00	0.00	3	0.10	0.00	0	0.00	0.00	3	0.03	0.00
<i>Xenillus tegeocranus</i>	2	0.05	0.00	0	0.00	0.00	0	0.00	0.00	2	0.02	0.00
<i>Zygoribatula exilis</i>	0	0.00	0.00	1	0.05	0.00	4	0.15	0.00	5	0.07	0.00
<b>Collembola</b>	<b>85</b>	<b>0.45</b>	<b>0.05</b>	<b>333</b>	<b>0.80</b>	<b>0.08</b>	<b>79</b>	<b>0.65</b>	<b>0.02</b>	<b>497</b>	<b>0.63</b>	<b>0.05</b>
<i>Anurophorus laricis</i>	0	0.00	0.00	8	0.20	0.00	0	0.00	0.00	8	0.07	0.00
<i>Desoria propinqua</i>	0	0.00	0.00	8	0.10	0.00	0	0.00	0.00	8	0.03	0.00
<i>Entomobrya corticalis</i>	35	0.25	0.02	0	0.00	0.00	31	0.30	0.01	66	0.18	0.01
<i>Folsomia quadrioculata</i>	2	0.05	0.00	5	0.10	0.00	0	0.00	0.00	7	0.05	0.00
<i>Friesea handschini</i>	0	0.00	0.00	24	0.10	0.01	0	0.00	0.00	24	0.03	0.00
<i>Friesea mirabilis</i>	0	0.00	0.00	82	0.30	0.02	0	0.00	0.00	82	0.10	0.01

## Appendix (continued)

Species	BNP			BdNP			KNP			ALL		
	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom	Abu	Fre	Dom
<i>Isotoma viridis</i>	0	0.00	0.00	14	0.25	0.00	0	0.00	0.00	14	0.08	0.00
<i>Isotomiella minor</i>	13	0.15	0.01	2	0.05	0.00	16	0.25	0.00	31	0.15	0.00
<i>Isotomurus palustris</i>	2	0.05	0.00	49	0.35	0.01	0	0.00	0.00	51	0.13	0.01
<i>Lepidocyrtus lanuginosus</i>	0	0.00	0.00	6	0.10	0.00	0	0.00	0.00	6	0.03	0.00
<i>Lepidocyrtus cyaneus</i>	17	0.15	0.01	33	0.35	0.01	0	0.00	0.00	50	0.17	0.01
<i>Neanura muscorum</i>	0	0.00	0.00	5	0.15	0.00	0	0.00	0.00	5	0.05	0.00
<i>Orchesella bifasciata</i>	1	0.05	0.00	5	0.05	0.00	0	0.00	0.00	6	0.03	0.00
<i>Parisotoma notabilis</i>	0	0.00	0.00	2	0.05	0.00	0	0.00	0.00	2	0.02	0.00
<i>Pogonognathellus flavescens</i>	0	0.00	0.00	14	0.15	0.00	0	0.00	0.00	14	0.05	0.00
<i>Proisotoma minuta</i>	0	0.00	0.00	4	0.10	0.00	0	0.00	0.00	4	0.03	0.00
<i>Pseudachorutella assigilata</i>	3	0.10	0.00	0	0.00	0.00	0	0.00	0.00	3	0.03	0.00
<i>Pseudanophorus binoculatus</i>	2	0.05	0.00	4	0.10	0.00	0	0.00	0.00	6	0.05	0.00
<i>Pseudisotoma sensibilis</i>	2	0.05	0.00	0	0.00	0.00	6	0.10	0.00	8	0.05	0.00
<i>Ptenotrix atra</i>	0	0.00	0.00	0	0.00	0.00	2	0.05	0.00	2	0.02	0.00
<i>Schoetella ununguiculata</i>	0	0.00	0.00	28	0.10	0.01	0	0.00	0.00	28	0.03	0.00
<i>Sinella coeca</i>	2	0.05	0.00	0	0.00	0.00	0	0.00	0.00	2	0.02	0.00
<i>Sminthurinus niger</i>	0	0.00	0.00	5	0.20	0.00	10	0.25	0.00	15	0.15	0.00
<i>Tetracanthella pilosa</i>	0	0.00	0.00	0	0.00	0.00	2	0.05	0.00	2	0.02	0.00
<i>Tomocerus minor</i>	6	0.15	0.00	22	0.10	0.01	12	0.25	0.00	40	0.17	0.00
<i>Willowsia buski</i>	0	0.00	0.00	13	0.25	0.00	0	0.00	0.00	13	0.08	0.00
<b>Insecta</b>	<b>280</b>	<b>0.85</b>	<b>0.18</b>	<b>585</b>	<b>0.90</b>	<b>0.14</b>	<b>563</b>	<b>0.85</b>	<b>0.14</b>	<b>1428</b>	<b>0.87</b>	<b>0.15</b>
<i>Anisotoma</i> sp.	0	0.00	0.00	0	0.00	0.00	2	0.05	0.00	2	0.02	0.00
<i>Aspidiphorus</i> sp.	0	0.00	0.00	0	0.00	0.00	1	0.05	0.00	1	0.02	0.00
<i>Bolitophagus reticulatus</i>	1	0.05	0.00	7	0.20	0.00	0	0.00	0.00	8	0.08	0.00
<i>Cerylon</i> sp.	2	0.10	0.00	0	0.00	0.00	3	0.05	0.00	5	0.05	0.00
Ciidae	0	0.00	0.00	3	0.10	0.00	0	0.00	0.00	3	0.03	0.00
<i>Cis</i> spp.	174	0.65	0.11	522	0.80	0.12	543	0.85	0.14	1239	0.77	0.13
Coleoptera	51	0.15	0.03	6	0.10	0.00	5	0.25	0.00	62	0.17	0.01
Dermestidae	2	0.10	0.00	0	0.00	0.00	0	0.00	0.00	2	0.03	0.00
Diptera	32	0.30	0.02	5	0.20	0.00	1	0.05	0.00	38	0.18	0.00
Elateridae	8	0.15	0.01	6	0.15	0.00	0	0.00	0.00	14	0.10	0.00
<i>Ennearthron</i> sp.	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
Hemiptera	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
Hymenoptera	2	0.10	0.00	2	0.10	0.00	0	0.00	0.00	4	0.07	0.00
<i>Neomida haemorrhoidalis</i>	0	0.00	0.00	2	0.05	0.00	0	0.00	0.00	2	0.02	0.00
<i>Orthoperus</i> sp.	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
Ptinidae	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00
<i>Ropalodontus</i> sp.	2	0.05	0.00	19	0.10	0.00	5	0.10	0.00	26	0.08	0.00
Staphylinidae	3	0.15	0.00	10	0.25	0.00	3	0.15	0.00	16	0.18	0.00
Thysanoptera	0	0.00	0.00	1	0.05	0.00	0	0.00	0.00	1	0.02	0.00
<i>Trixagus</i> sp.	1	0.05	0.00	0	0.00	0.00	0	0.00	0.00	1	0.02	0.00