Denisa Slabejová, Fedor Čiampor Jr, Zuzana Čiamporová-Zaťovičová,
Ivan Jarolímek, Mária Šibíková, Michaela Michalková**

Impact of short rotation coppice of *Populus ×canadensis* on vegetation and soil fauna diversity

Abstract: Sustainable forest management aims to preserve biodiversity while simultaneously meeting wood production demands. One of the ways to achieve this aim is by using short-rotation plantations of non-native trees. The cultivation of hybrid *Populus ×canadensis* (Canadian poplar) presents a unique case study in forest management due to its potential impact on biodiversity. This study investigates the influence of the short rotation coppice of Canadian poplar on vegetation and soil fauna, filling the knowledge gap by evaluating the multitaxa biodiversity data. The data were sampled in the Western Slovakia region. Nine vegetation plots (plot × reference plots selected and based on the forest potential vegetation in the study area) and four twin soil eDNA samples (plot × neighboring reference plot) were investigated. For vegetation data neophytes, archaeophytes, and apophytes were distinguished. The percentage number and percentage coverage were calculated for each category. In the plantation of Canadian poplar, a high number and cover of non-native species and apophytes were recorded. Metabarcoding analysis of soil fauna biodiversity using eDNA revealed a diverse community composed mainly of invertebrates, suggesting that the cultivation of Canadian poplar affects species diversity less than the composition of the soil fauna community. Overall, the findings underscore the complexity of managing Canadian poplar plantations and the importance of considering both ecological and economic factors. Different groups of organisms react differently to the replacement of alien tree species – in the vegetation, both the overall diversity and the species composition of plant communities have changed, in the soil fauna only the species composition has changed. Sustainable forest management practices must be tailored to specific local contexts to minimize negative impacts on biodiversity while maximizing economic benefits.

Keywords: Canadian poplar, plantation, biodiversity, herb synusia, soil fauna, DNA metabarcoding

Addresses: D. Slabejová, F. Čiampor Jr, Z. Čiamporová-Zaťovičová, I. Jarolímek, M. Šibíková,
M. Michalková, Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences,
Dúbravská cesta 9, 845 23 Bratislava, Slovakia; e-mails: DS denisa.slabejova@savba.sk,
MM michaela.michalkova@savba.sk;
Z. Čiamporová-Zaťovičová, Department of Ecology, Faculty of Natural Sciences, Comenius University,
Ilkovičova 6, 842 15 Bratislava, Slovakia
* corresponding authors

Introduction

Forest ecosystems host a considerable part of terrestrial biodiversity, and their sustainable management is essential for preventing biodiversity loss (Burrascano & Trentanovi, 2022). Simultaneously, forests act as an important source of wood. To combine these ecosystem services, sustainable forest management is needed. Recent projects (e.g., DENDROMASS4Europe) are focusing on establishing sustainable wood production. Some of them use native tree species, while others use non-native ones, specifically because of their better wood increment. These valuable properties are typical also for the hybrid taxon Populus ×canadensis Moench (Canadian poplar), and its planting is now widely discussed due to the missing information about the impact on biodiversity. This impact shall be assessed by monitoring focused on a diversity of multiple taxonomic groups (Burrascano & Trentanovi, 2022). Most studies on the effects of non-native tree species focus on plant diversity, especially vascular plants, while other groups receive significantly less attention (Wohlgemuth et al., 2022). The influence of hybrid poplar planting in the forest land and its impact on natural floodplain forests has been studied before (Botková et al., 2016; Genova et al., 2022), and the negative effects on vascular plant species diversity were confirmed. Multitaxa research in forest ecosystems is not widely used in Slovakia, but the first case studies (Slabejová et al., 2023) indicate a significant impact of non-native tree planting on various groups of animals. Invertebrates, especially insects, contribute to a dominant part of forest fauna diversity and are represented in every trophic level (Nageleisen & Bouget, 2009), acting as a food supply for other organisms. Fauna that depends on the microenvironment created by vegetation should be influenced as well, especially soil invertebrates.

Therefore, evaluating the impact of non-native *P. ×canadensis* planted on agricultural land with short rotation on vegetation and fauna composition is important. Studies with a more comprehensive approach are few or almost completely absent (Schlick-Steiner et al., 2010; Fonseca et al., 2018). Vascular plants are among the best-known taxonomic groups in the forests (Pharo et al., 2000; Burrascano et al., 2011; Bagella, 2014; Hofmeister et al., 2022), and their affiliation to functional species groups (e.g. alien species, or species diagnostic for each forest type) has been well described (Medvecká et al., 2014; Valachovič et al., 2021; Šuvada et al., 2023). These characteristics make vascular plants ideal candidates for describing forest biodiversity (Burrascano & Trentanovi, 2022). Forest structure is a driver and result of ecosystem processes and biological diversity (Gadow et al., 2012), therefore, knowledge about the structure of each vegetation layer is crucial for understanding the development, recent condition, and future perspectives of forest ecosystems (Spies, 2004; Burrascano & Trentanovi, 2022).

The species of the poplar genus are likely to hybridize. By far the most common commercial hybrids are *Populus deltoides* × *Populus nigra* (= *P. ×canadensis* Moench), which began to hybridise when *P. deltoides* was introduced to Europe in the 17th century. By the mid-1800s, cultivated poplars became widespread in Europe. The hybrid taxon *P. ×canadensis* involves all hybrid forms of North American *P. deltoides* and Eurasian *P. nigra* (Úradníček & Chmelař, 1995; Stanturf & Van Oosten, 2014). Both of the species are from the same section *Aigeiros*. Hybridization events between species in section *Aigeiros* and also other sections are common in nature (Du et al., 2022). Euro-American hybrids usually have *P. deltoides* as the maternal parent, because the reciprocal cross is rarely successful (Stanturf & Van Oosten, 2014). Canadian poplar is very sensitive to insufficient light conditions. It needs moist soils but does not tolerate long-term soil waterlogging (Mottl & Špalek, 1961).

The impact of the *P. ×canadensis* on plants and plant assemblages remains unclear. The results of the study from Czechia (Šenkýř, 2015) suggest the stands of this tree have different species composition compared with reference plots of hardwood floodplain forests, but this change cannot be explained by the presence of the hybrid poplar itself due to forest management. The studies from Slovakia (Botková et al., 2016) and the Danube region (Gelatičová, 2021; Genova et al., 2022) showed lower plant diversity in *P. ×canadensis* plantations in comparison with willow-poplar floodplain forests. However, when plantations grow older, the plant diversity reaches a level similar to surrounding natural forests (Zedníček, 2016), which highlights the importance of rotation time. Short rotation coppices of *P. ×canadensis* on former arable land in Austria are characterized by low diversity – the mean plant species number per plot (30 m^2) was 17.5 (Pöltl & Berg, 2016). Only common, highly competitive perennials dominated the herb layer. Species richness was negatively correlated with the age of the plantation (Zedníček, 2016). A negative impact of hybrid poplar cultivation on native populations of *P. nigra* has been identified, while natural hybridization between *P. ×canadensis* and *P. nigra* was evidenced (Broeck et al., 2005; Pospíšková & Šálková, 2006).

Various forest habitats strongly differ in the level of invasion. The most invaded habitats are those with plantations of non-native tree species, especially *P. ×canadensis* and *Robinia pseudoacacia* plantations, even when cultivated tree species in the tree layer were excluded from the analyses (Chytrý et al., 2009; Medvecká et al., 2018). Higher proportions of neophytes

were found in almost all types of riparian forests including *Populus* plantations, and *Robinia* plantations. Similarly, invasive and naturalized species were most abundant in riparian forests and non-native tree plantations, especially those of *Populus* and *Robinia*. However, there were slight differences between these two groups. Forest management also plays an important role. Plantations of *P.* ×*canadensis* are usually intensively managed using topsoil removal before the planting of new trees, and this can lead to the establishment of other non-native species. However, this effect decreases after 15 years and native species start to recolonize these habitats again (Haeussler et al., 2004). Plantations on forest land are usually clearcut after 15–20 years, while short coppice plantations are often cut after less than 12–15 years. Therefore, the negative effects may be multiplied.

Interestingly, even despite intensive management, *Populus* plantations on forest land did not significantly differ in terms of non-native species occurrence from stands of riverine *Salix* woodland. These woodlands occur under the same environmental conditions but are dominated by native trees (Botková et al., 2016). This may be caused by the high total level of invasion in the whole Danube floodplain area, which eliminates differences between the plantations and *Salix* woodlands. However, *Salix* woodlands still have more native species diversity. This fact might indicate that intensive forest management plays a more significant role than the origin of planted *Populus* species.

Therefore, the aims of our study were: i) to describe the floristic structure and to evaluate the representation of the alien and apophytes species in forests and ii) to evaluate the biodiversity of the fauna sampled by the environmental DNA method.

Methods

Study area

The study was conducted in the Western Slovakia region (Fig. 1). The localities with the short rotation coppice (SRC) of Canadian poplar were selected (Fig. 2). The vegetation data from Canadian poplar plantations (9 phytosociological relevés) were sampled in 2022 from June to November. Soil samples (4 samples) and its neighboring reference plot (4 samples – mixed forests) for fauna analysis were taken
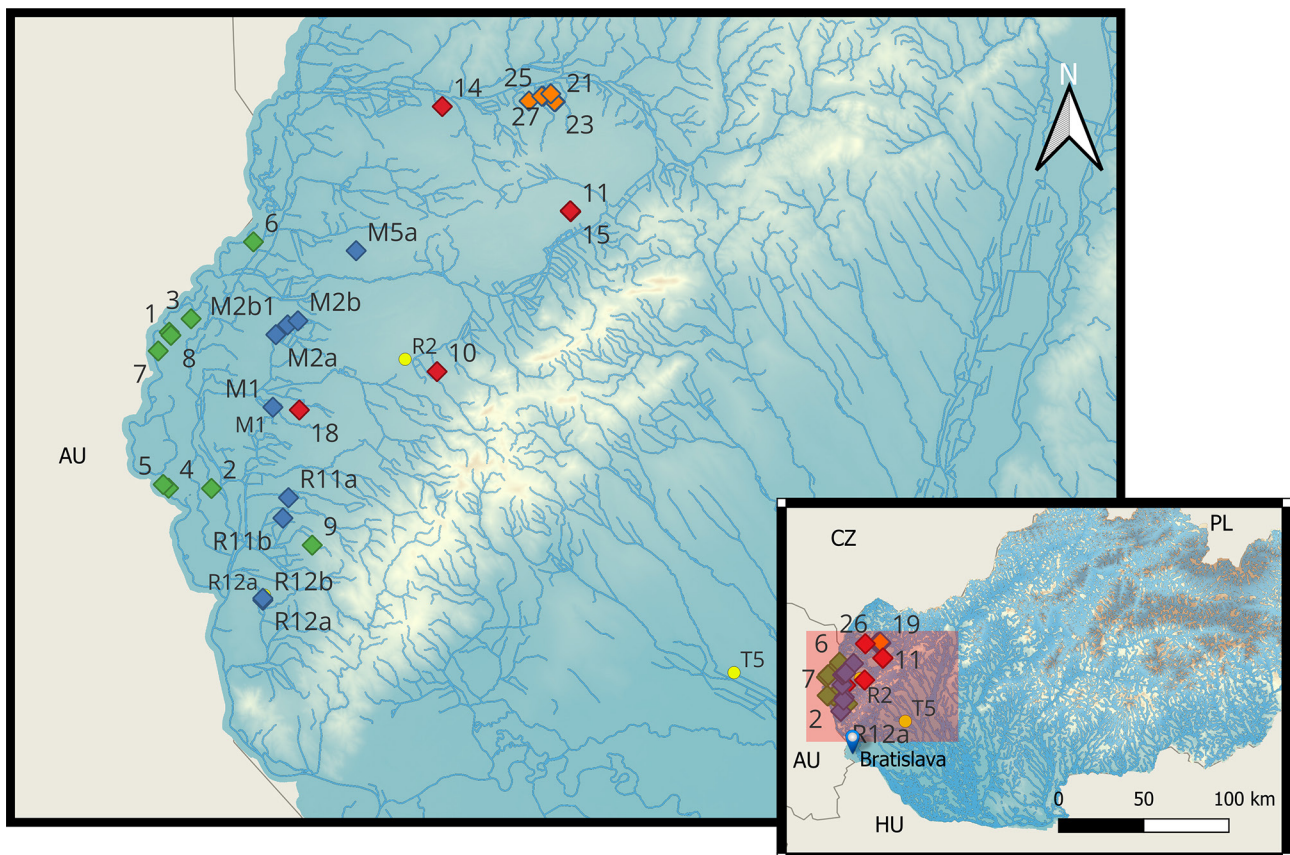

Fig. 1. Distribution map of 9 sampled phytosociological relevés from *Populus* ×*canadensis* coppices (blue diamonds) plus reference plots in hardwood floodplain forests (green diamonds), oak forests (red diamonds), and *Pinus* forests (orange diamonds) and four soil samples for soil fauna (yellow dots together with the reference neighbouring plots in the Western Slovakia region

Fig. 2. Sampled short rotation coppice of Canadian poplar and neighbouring reference sites for soil fauna (photos by F. Čiampor, 2022)

from the four locations also in western Slovakia, with three of them located west and one located east of the Small Carpathians, on 26th October = 2022.

Vegetation sampling

Together 36 phytocoenological relevés were processed. All of them were recorded according to the Zürich-Montpellier school (Barkman et al., 1964; Braun-Blanquet, 1964; Westhoff & van der Maarel, 1978) on 400 to 600 m² plots. Nine of them were newly recorded in 2022 in Canadian poplar coppices plantations. In all stands Canadian poplar dominated (more than 50% coverage, with an average of 75%) in the tree or shrub layer. According to the potential vegetation map of Slovakia (Michalko et al., 1987) these relevés were localised at places of former floodplain forests, and forests dominated by *Pinus sylvestris* or *Quercus petraea* agg. Relevés representing these types of vegetation were fulfilled by own relevés from previous years (floodplain forests) and by relevés from the Central database of phytocoenological relevés of Slovakia (https://ibot.sav.sk/cdf/) (*Pinus* and *Quercus* forests).

All relevés were stored in the TURBOVEG database program (Hennekens & Schaminée, 2001) and subsequently processed and analysed using the JUICE 7.0.207 program (Tichý, 2002). Plant taxa nomenclature follows Euro+Med (Euro+Med, 2006). Non-native species (specifically neophytes and archaeophytes) for Slovakia were selected according to Medvecká et al. (2012). Apophytes were selected according to their affinity to synanthropic vegetation classes, expert estimation, and field experience. The percentage number, percentage coverage and diversity indexes for the herb layer were counted in the JUICE software. Analysis of the data was done using the ggplot2 package (v3.3.3; Wickham, 2016) and the R software (R Core Team, 2023). The synoptic table was created by using JUICE software (Tichý, 2002). Frequency and cover thresholds were set at 40 to 60%.

Soil fauna sampling

Soil fauna analysis was conducted using environmental DNA extracted from 4 twin samples, i.e. coppice plot and neighbouring sites with natural vegetation (Fig. 1). To conclude about soil fauna communities, we used DNA present in the soil as a "trace" of the presence of particular species. At each sampling point, soil was collected from multiple locations, mixed in a clean plastic bag, and then two replicates were taken from the mixture. The samples were stored for analysis in a freezer at −25 °C.

In the laboratory, the DNA was released from the soil using saturated phosphate buffer (Taberlet

et al., 2012) and the solution was subsequently filtered through a syringe filter with pores of 0.22 μm. From filters, DNA was extracted and purified using the DNeasy blood & tissue kit (Qiagen), following the manufacturer's protocol. PCRs were conducted with 2 replicates per extract. A 418 bp fragment of the mitochondrial cytochrome c oxidase subunit 1 (COI) gene was targeted in a two-step PCR using BF3/BR2 primers (Elbrecht & Steinke, 2019). For the second PCR, each sample was amplified using BF3/BR2 uniquely tagged fusion primers (Elbrecht & Steinke, 2019) and 1 μL of the respective first PCR product as a DNA template. The second PCR products were pooled equimolarly based on fluorometric quantification (Quantus™ Fluorometer, QuantiFluor® ONE dsDNA System, Promega) and purified using 0.8× SPRIselect beads (Beckman Coulter). The final 15 pM sequencing library included 10 % PhiX, and was analyzed on Illumina MiSeq with Reagent Kit v3, 2 × 300 bp at the Institute of Chemistry, Slovak Academy of Sciences. Raw sequence data was filtered and processed in the mBrave application (www.mbrave.net), in which determination also took place (i.e., blasting against the reference barcode database BOLD – Barcode of Life Data Systems, www.v4.boldsystems.org). To increase the confidence of subsequent analyses, operational taxonomic units (OTUs) represented by <5 reads were removed from the resulting list of detected OTUs (putative species). The total number of identified species, proportional representation of higher taxa (families, orders, subclasses, classes) at individual sites, and non-metric multidimensional scaling (nMDS) ordination based on Jaccard dissimilarity matrices to illustrate the composition variations of communities were done in Taxontabletools (Macher et al., 2021).

Results

Vegetation

The whole dataset consisted of 36 relevés and 336 species. Specifically, there were 17 neophytes, 31 archaeophytes, 38 facultative apophytes (native species dominated in native habitats), and 21 obligate apophytes (native species dominated in anthropogenic habitats). The 229 species did not fall into any category (others, usually the forest or forest edge species (Table 1). The average number of species in Canadian poplar stands was 25.7 species per plot (SD = 7.3), in hardwood floodplain forests it was 36.8 species per plot (SD = 8.5), in *Quercus* plots 35.8 (SD = 9.4) and in *Pinus* stands just 21.8 species per plot (SD = 7.4) (Table S1).

In the short rotation coppices of Canadian poplar was recorded the high percentage number and

Table 1. Shortened synoptic table with frequency (%) and cover range (expressed by minimum and maximum cover class in modified Braun-Blanquet's scale) across studied groups of forests.

Group	Canadian poplar		Hardwood plain forests		*Quercus petraea* agg. forests		*Pinus sylvestris* forests	
No. of relevés	9		9		9		9	
Cirsium arvense	89	+−a	.	.	.	.	.	.
Setaria pumila	89	+−b	.	.	.	.	.	.
Taraxacum sect. *Ruderalia*	89	+−1	22	r−+	.	.	.	.
Erigeron canadensis	89	1−3	.	.	.	.	.	.
Ambrosia artemisiifolia	78	1−4	.	.	.	.	.	.
Populus ×canadensis	78	4	.	.	.	.	.	.
Solidago gigantea	78	+−3	11	+	11	+	.	.
Geranium pusillum	56	+−a	.	.	.	.	.	.
Elymus repens	56	1−5	.	.	.	.	.	.
Erigeron annuus	56	+−a	11	r	.	.	.	.
Aster lanceolatus	44	+−b	33	a−b	.	.	.	.
Capsella bursa-pastoris	44	+−a	.	.	.	.	.	.
Trifolium pratense	44	+−a	.	.	.	.	.	.
Carex hirta	44	+−1	.	.	11	+	11	1
Acer campestre	.	.	100	+−b	.	.	.	.
Ranunculus ficaria ssp. *bulbilifera*	.	.	100	+−4	.	.	.	.
Viola reichenbachiana	.	.	100	+−b	11	r	.	.
Geum urbanum	11	+	100	+−a	.	.	.	.
Alliaria petiolata	.	.	89	+−b	.	.	.	.
Geranium robertianum	.	.	89	r−b	.	.	.	.
Fraxinus angustifolia	.	.	89	b−5	.	.	.	.
Veronica sublobata	22	+−1	89	+−4	.	.	.	.
Impatiens parviflora	.	.	78	+−a	.	.	.	.
Chaerophyllum temulum	.	.	78	+−a	.	.	.	.
Crataegus monogyna	22	r−+	78	+	.	.	.	.
Euonymus europaeus	.	.	78	+−a	.	.	.	.
Fraxinus angustifolia	.	.	78	r−a	.	.	.	.
Acer campestre	.	.	67	+−3	.	.	.	.
Rubus caesius	11	+	67	+−b	.	.	.	.
Quercus robur	.	.	67	b−3	33	a−4	.	.
Glechoma hederacea	11	a	67	1−3	.	.	.	.
Acer campestre	.	.	67	1−3	.	.	.	.
Ulmus laevis	.	.	67	+−1	.	.	.	.
Lysimachia nummularia	.	.	56	+−1	.	.	.	.
Ulmus laevis	.	.	56	1−b	.	.	.	.
Anemone ranunculoides	.	.	56	+−b	.	.	.	.
Ulmus laevis	.	.	56	+−3	.	.	.	.
Stachys sylvatica	.	.	56	1−a	.	.	.	.
Sambucus nigra	22	r−+	56	r−b	.	.	.	.
Urtica dioica	33	r−1	56	+−4	.	.	.	.
Carex remota	.	.	44	+−1	.	.	.	.
Carpinus betulus	.	.	44	+−b	.	.	.	.
Carex sylvatica	.	.	44	+−a	.	.	.	.
Convallaria majalis	.	.	44	+−1	11	3	.	.
Viola hirta	.	.	44	+−b	.	.	.	.
Cornus sanguinea	.	.	44	+	.	.	.	.
Ajuga reptans	.	.	44	+−1	22	r	11	+
Rumex sanguineus	.	.	44	r−1	.	.	.	.
Galanthus nivalis	.	.	44	+−b	.	.	.	.
Galeopsis pubescens	.	.	44	r−1	.	.	11	+
Hieracium murorum	.	.	.	.	89	+	11	+
Sorbus aucuparia	.	.	.	.	78	r−1	22	+
Quercus petraea	.	.	11	4	78	3−5	22	+−4

Group	Canadian poplar		Hardwood plain forests		*Quercus petraea* agg. forests		*Pinus sylvestris* forests	
No. of relevés	9		9		9		9	
Mycelis muralis	.	.	11	1	78	+−1	11	1
Agrostis capillaris	.	.	.	.	78	+	22	+
Festuca rubra	.	.	.	.	67	+−1	.	.
Hieracium lachenalii	.	.	11	+	67	+	.	.
Clinopodium vulgare	.	.	.	.	67	+	.	.
Anthericum ramosum	.	.	.	.	67	+	.	.
Fragaria vesca	.	.	.	.	67	+−1	.	.
Poa compressa	.	.	.	.	67	+−m	.	.
Melica nutans	.	.	.	.	67	+−3	.	.
Silene nutans s.lat.	.	.	.	.	67	+	.	.
Campanula persicifolia	.	.	.	.	67	+	.	.
Euphorbia cyparissias	11	r	.	.	67	+	.	.
Melampyrum bohemicum	.	.	.	.	67	+−m	.	.
Poa angustifolia	11	a	.	.	67	+−1	.	.
Polygonatum odoratum	.	.	.	.	56	+	.	.
Teucrium chamaedrys	.	.	.	.	56	+	11	+
Luzula campestris	.	.	.	.	56	+−1	22	+
Anthoxanthum odoratum	.	.	.	.	56	+−1	22	+−a
Vincetoxicum hirundinaria	.	.	.	.	44	+	.	.
Platanthera bifolia	.	.	.	.	44	r	.	.
Achillea millefolium	11	+	.	.	44	+	.	.
Rubus fruticosus agg.	.	.	.	.	44	+−a	.	.
Carex caryophyllea	.	.	.	.	44	1−m	.	.
Cerastium arvense	.	.	.	.	44	+	.	.
Dactylis polygama	.	.	11	+	44	+	.	.
Trifolium alpestre	.	.	.	.	44	+	.	.
Steris viscaria	.	.	.	.	44	+	.	.
Veronica officinalis	.	.	.	.	44	+	11	+
Festuca vaginata ssp. *dominii*	.	.	.	.	.	.	67	r−a
Pinus sylvestris	11	+	.	.	11	r	67	+−a
Pleurozium schreberi	.	.	.	.	.	.	56	+−5
Dicranum polysetum	.	.	.	.	.	.	56	a−3
Dicranum scoparium	.	.	.	.	.	.	56	+−5
Cladonia arbuscula	.	.	.	.	.	.	44	+−b
Thymus serpyllum	.	.	.	.	.	.	44	+−1
Cladonia gracilis	.	.	.	.	.	.	44	+−1
Viscum album ssp. *laxum*	.	.	.	.	.	.	44	+
Cladonia rangiferina	.	.	.	.	.	.	44	a−3
Avenella flexuosa	.	.	.	.	.	.	44	r−+
Rumex acetosella s.lat.	11	+	.	.	.	.	44	+−1
Cladonia rangiformis	.	.	.	.	.	.	44	+−b
Stellaria media	89	+−3	78	+−3	22	+	.	.
Galium aparine	67	+−4	100	+−b	.	.	.	.
Brachypodium sylvaticum	.	.	89	+−1	56	+	.	.
Fallopia convolvulus	22	+	67	+−1	67	+−1	.	.
Moehringia trinervia	.	.	44	+−b	78	+−1	11	1
Quercus petraea	11	r	11	+	89	+−1	89	+−4
Festuca ovina	.	.	.	.	89	+−a	44	1−b
Frangula alnus	.	.	.	.	78	r−a	67	r−a
Hypericum perforatum	11	+	11	r	67	+	44	+−1
Pinus sylvestris	.	.	.	.	44	1−a	100	3−4
Campanula rotundifolia	.	.	.	.	44	+	44	+−1
Hypnum cupressiforme	.	.	.	.	44	+−a	44	+−1
Calamagrostis epigejos	56	+−a	.	.	67	+−m	44	+−1
Number of other species with frequency <40%	74		80		58		56	

coverage of non-native species (also neophytes and archaeophytes) in comparison to other native forest groups. Just as in the case of the obligate apophytes – those synanthropic species prefer especially synanthropic habitats and minimally growing in forests. The highest percentage number and cover of facultative apophytes – those synanthropic species, that have a focus of occurrence in natural habitats but penetrate synanthropic ones as well, were recorded in hardwood floodplain forests. The highest Shannon diversity index was recorded in hardwood floodplain forests followed by an oak forest (*Quercus*), Canadian poplar stands, and *Pinus* forests. The equitability index was more or less the same in all groups (Fig. 3).

All four forest groups were divided according to the differential species. Canadian poplar coppices (Group No. 1) consisted mostly from neophytes, archaeophytes and obligate apophytes in comparison with other types of forests, where these species hardly occur. A lot of ruderal and nitrophilous species occurred in this group. Differential species are as follows: *Cirsium arvense, Setaria pumila, Taraxacum* sect. *Ruderalia, Erigeron canadensis, Ambrosia artemisiifolia, Populus* x *canadensis, Solidago gigantea*, etc. (Table 1). Differential species for hardwood floodplain forests (Group No. 2) are as follows: *Acer campestre, Ranunculus ficaria* ssp. *bulbifera, Viola reichenbachiana, Geum urbanum, Alliaria petiolata, Geranium robertianum, Fraxinus angustifolia, Veronica sublobata, Impatiens parviflora,*

Chaerophyllum temulum, Crataegus monogyna, and *Euonymus europaeus* (Table 1).

Another group with *Quercus petraea* agg. (Group No. 3) consists of the following differential species: *Hieracium murorum, Sorbus aucuparia, Quercus petraea, Mycelis muralis, Agrostis capillaris, Festuca rubra,* etc. (Table 1). In the *Pinus sylvestris* forests (Group No. 4) were recorded the fewest plant species taxa among the compared forest groups/types. Differential species here were recorded as follows: *Festuca vaginata* ssp. *dominii, Pinus sylvestris, Pleurozium schreberi, Dicranum polysetum, Dicranum scoparium,* etc. (Table 1). Higher number of bryophytes occurred in the *Pinus* group compared to other groups, where bryophytes were not found at all or only minimally.

There were several species recorded in two or more groups of forest in higher frequencies. One group are mesophilous species such as *Stellaria media, Galium aparine,* with higher frequencies in Canadian poplar coppices and floodplain forest. *Brachypodium sylvaticum, Fallopia convonvulus, Moehringia trinervia* are recorded with high frequencies mostly in floodplain forest or *Quercus* stands. Second group are termophilous species with *Quercus petraea, Festuca ovina, Hypericum perforatum, Pinus sylvestris, Campanula rotundifolia* and *Hypnum cuppresiforme* in high frequencies in *Quercus* and *Pinus* forests. *Calamagrostis epigejos* was recorded with high frequency in each forest group except the floodplain forest.

Pinus forests are similarly species poor as the Canadian poplar coppices.

Soil fauna

Sequencing of the DNA yielded in ~4.9M sequences after filtering the raw data, which were combined into 73783 barcoding marker sequences. Totally 346 putative species were identified based on the standard interspecific genetic distance (3%). The species detected in the repetitions within the localities were combined into the resulting species lists for individual localities (Table S2). Some of recorded species were not determined to species level due to problematic morphological identification and the related absence of reference data in DNA barcode databases (Fig. 4).

After filtering out species irrelevant to soil fauna (apparently, only allochthonous DNA remained present in the soil), 147 species were identified. In total, 29–88 taxa were captured at respective sites (Table 2).

Invertebrates comprised the most significant group of soil fauna in the studied localities, of which the most species-rich were annelids (Annelida), arachnids (Arachnoidea), springtails (Collembola), insects (Insecta) and myriapods (Myriapoda) (Fig. 4, Table 2). The annelids were mainly represented by
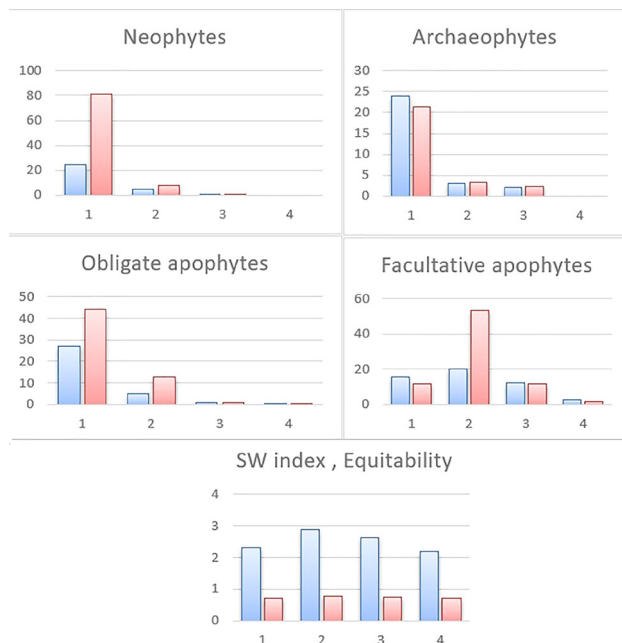

Fig. 3. Average values of percentage number (blue) and coverage (red) of neophytes, archaeophytes, obligate and facultative apophytes together with Shannon-Wiener diversity index (blue) and equitability (red) across four studied groups (1 – Canadian poplar plantation, 2 – hardwood floodplain forest, 3 – *Quercus petraea* agg., 4 – *Pinus sylvestris*)

Clitellata families Lumbricidae and Enchytreidae. The myriapods were mainly represented by centipedes (Chilopoda) and millipedes (Diplopoda). Arachnids were mainly represented by mites, while insects were dominated by flies (Diptera) and beetles (Coleoptera), both very likely represented by preimaginal stages (eggs, larvae, pupae) in the soil samples. Other groups of invertebrates (crustaceans, molluscs, helminths, flatworms, rotifers, and slugs) were represented by a significantly lower number of species The species diversity of the dominant invertebrate soil taxa was comparable between coppice and reference sites (Fig. 4). However, the species composition differed distinctly, according to nMDS analysis (Fig. 5).
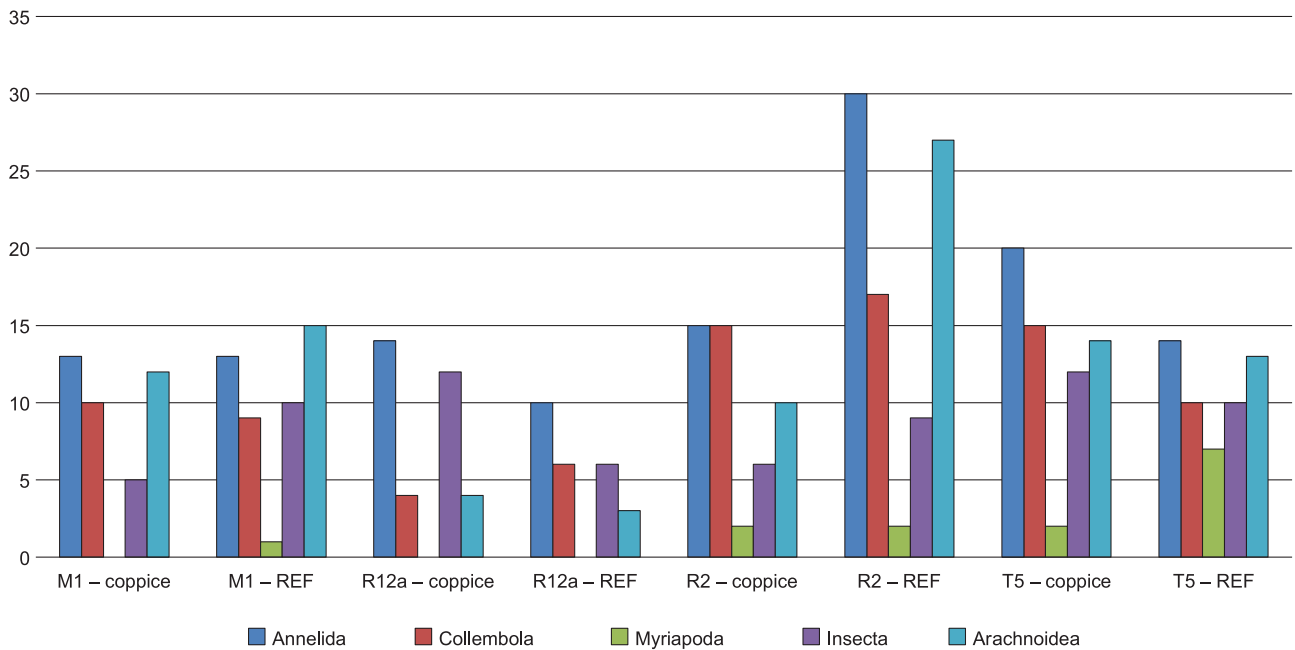
Fig. 4. Representation of the most important taxonomic groups of soil fauna in the studied localities

Table 2. The number of species of more important taxonomic groups captured at individual locations

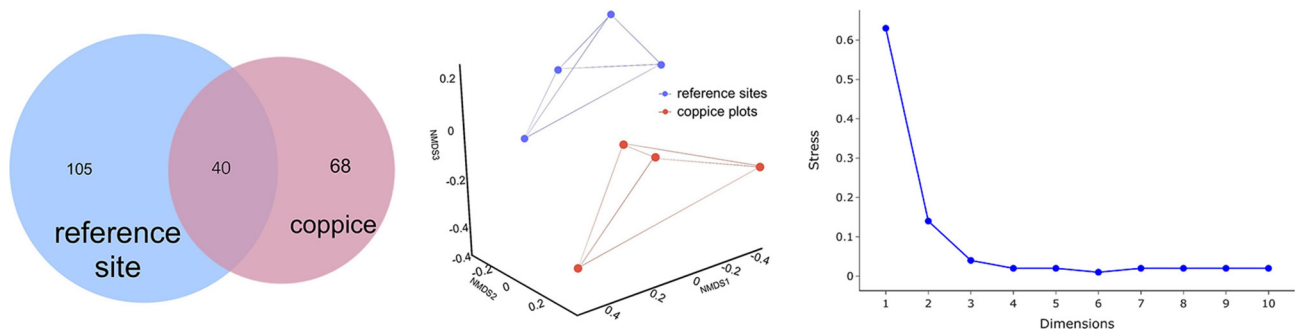|	Annelida	Collembola	Myriapoda	Insecta	Arachnida
M1 – coppice	13	10	0	5	12
M1 – REF	13	9	1	10	15
R12a – coppice	14	4	0	12	4
R12a – REF	10	6	0	6	3
R2 – coppice	15	15	2	6	10
R2 – REF	30	17	2	9	27
T5 – coppice	20	15	2	12	14
T5 – REF	14	10	7	10	13

Fig. 5. Number of unique and shared soil fauna taxa detected (left) and NMDS analysis comparing soil fauna communities and its stress values for NMDS

Discussion

Certain forest habitats, such as riverine *Salix* woodlands, as well as *Populus* and *Robinia* plantations, are so heavily invaded that it is important from a syntaxonomical point of view. The non-native species serve as the diagnostic species that differentiate these forests from other forest communities. In particular, neophytes associated with riparian habitats, such as *Aster novi-belgii* agg., *Fraxinus pennsylvanica*, *Impatiens glandulifera*, *Acer negundo*, or *Solidago gigantea* are found there with rather high frequency (Schnitzler et al., 2007). Similarly, our results showed that neophyte species are one of the most abundant species groups in short coppice plantations. Comparable numbers of aliens, both archaeophytes and neophytes, are found on arable land and waste deposits, anthropogenic tall-forb stands, and trampled habitats. In the broadleaved forestry plantations of *Robinia pseudoacacia* or *P.* ×*canadensis* neophytes also prevail (Chytrý et al., 2005; Medvecká et al., 2018).

Such plantations are widely planted along the rivers of Europe, destroying the native riparian communities (Botková et al., 2016) and also on agricultural land. The mean number of species per plot (30 m²) in short rotation coppice of *P.* ×*canadensis* was 17.5, according to the study by Pöltl & Berg (2016), compared to an average of 26 species per plot (400 m²) in our study. The effect on fungal diversity was negatively correlated to coppice rotation length, due to a higher nutrient demand after coppicing. Short rotation coppice provides higher biodiversity than agricultural monocultures, but still lower than that of mixed deciduous forests. These changes in the plant community influence animal diversity. Arthropods and small mammals use the short rotation coppice to fulfill all of their habitat needs, while birds and large mammals only use the plantation for a limited number of resources (Vanbeveren & Ceulemans, 2019).

Mixed and unmanaged plantation forests with native species are capable to sustain more biodiversity than monoculture and managed plantation forests with non-native species (Wang et al., 2022). The ensuing biodiversity is influenced by the choice of plant species and original land use (Bremer & Farley, 2010; Felton et al., 2020; Pandey & Luitel, 2020). It is a frequent practice to choose generalist (with wide habitat adaptability) or fast-growing species for the plantation forests for economic reasons (Rédei et al., 2020). Due to this expectation, these alien species-biased forests could never match the biodiversity level of a natural forest located in its buffer (Calviño-Cancela et al., 2012).

On the other hand, previous literature has suggested that plantation forests provision basic ecosystem services such as erosion alleviation, water and nutrient retention, and habitat creation to nurture healthy biodiversity (Cawsey & Freudenberger, 2008) and there is always a need to look at these issues in a specific context (Brockerhoff et al., 2008). Bremer and Farley (2010) opined that the biodiversity values of plantation forests rely on what was the original land use – intensive agricultural land, grassland, shrubland, primary forest, secondary forest, degraded, or exotic pasture. Not only biodiversity but also the suitability of a tree-based plantation forest is affected by the original land use. Short-coppice plantations were established on agricultural land, so the species pool of typical floodplain forests is missing, and even environmental conditions are different and usually not situated in river alluvia. Invasive species typical for floodplain forests usually spread along the rivers (Schnitzler et al., 2007; Zając et al., 2011), so their penetration to short coppice plantations may be more difficult. The community assembly of undergrowth under short coppice poplar woodlands remains unclear, as well as the species composition of fauna within these plantations.

Comparison of the obtained data with published faunistic data is problematic. Most of the works focused on the soil fauna of the area in question are specialized for a specific taxonomic group, or there are data on the fauna of specific biotopes (e.g., Fena & Cicáková, 2005; Mock et al., 2015; Topp et al., 2006). Soil fauna contributes significantly to the functioning of ecosystems and forms an essential part of the biodiversity of the area. Intensive management with short rotation and frequent soil disturbance can have a major impact on it, but critically little is known about the composition of the soil fauna or changes concerning forest management and wood production. DNA metabarcoding has the potential to greatly advance understanding of soil biodiversity, but the application of this approach is still limited (Schulz et al., 2009; Young & Hebert, 2022). Regarding the use of DNA metabarcoding in analyses of short rotation coppice (SRC) soil fauna, this is likely the first study of its kind. In general, the soil fauna of SRC has not received much attention. According to available published information, its composition and abundance are mostly influenced by the tree species grown, soil moisture, amount of dead organic matter, or addition of fertilizers (Baum et at., 2009; Faly et al., 2017; Li et al., 2018; Wang et al., 2016). Our results, although obtained only from a limited number of sites, suggest that SRCs have a visible impact on the soil fauna. Although the level of diversity remained comparable between SRCs and reference sites, its composition changed, as suggested by Gallé et al. (2017). Cultivation of SRCs can lead to a slight increase in biodiversity in cleared agricultural landscapes, but can have adverse effects in landscapes with higher conservation value. As our sites represent more of the latter type, likely, their impact on the original

fauna will not be positive. Obviously, to characterize in more detail the changes and composition of soil fauna in the studied conditions will require analysis of data from multiple sites, focusing also to individual taxonomic groups that may respond differently to the cultivation of SRCs. An important result is that different groups of organisms react differently to Canadian poplar short rotation coppice.

Conclusion

It appears that plantation forests possess unique biodiversity, distinct from original forests as well as from previous agricultural land, and economic benefits that are closely tied to their local contexts due to various environmental and social factors. Therefore, these forests should not replace native habitats or undisturbed ecosystems, rather, they should serve as essential habitat remnants to sustain native species and benefit local populations in the most comprehensive manner possible. In comparison to native forests short rotation plantations and comprehensive soil treatment have a negative effect on species diversity. On the other hand, in comparison with agricultural land, they have the potential to enhance homogeneous landscapes and biodiversity.

Acknowledgements

References

Bagella S (2014) Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. Comptes Rendus Biologies 337: 276–282. doi:10.1016/j.crvi.2014.01.003.

Barkman JJ, Doing H & Segal S (1964) Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. Acta Botanica Neerlandica 13: 394–419. doi:10.1111/j.1438-8677.1964.tb00164.x.

Baum C, Leinweber P, Weih M, Lamersdorf N & Dimitriou I (2009) Effects of short rotation coppice with willows and poplar on soil ecology. Agriculture and Forestry Research 3: 183–196.

Botková K, Bazalová D, Jarolímek I, Zedníček Ľ & Petrášová M (2016) Canadian poplar plantations–threat to softwood floodplain forests: Book of abstracts, Posters, 25th meeting of the European Vegetation Survey (ed. by E Agrillo, FAttorre, F Spada & L Casella) Rome, Italy.

Braun-Blanquet J (1964) Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verlag, Wien.

Bremer LL & Farley KA (2010) Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodiversity and Conservation 19: 3893–3915. doi:10.1007/s10531-010-9936-4.

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP & Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17: 925–951. doi:10.1007/s10531-008-9380-x.

Broeck AV, Villar M, Van Bockstaele E & VanSlycken J (2005) Natural hybridization between cultivated poplars and their wild relatives: evidence and consequences for native poplar populations. Annals of Forest Science 62: 601–613. doi:10.1051/forest:2005072.

Burrascano S, Sabatini F & Blasi C (2011) Testing indicators of sustainable forest management on understorey composition and diversity in southern Italy through variation partitioning. Plant Ecology 212: 829–841.

Burrascano S & Trentanovi G (2022) Handbook of field sampling for multi-taxon biodiversity studies in European forests. Handbook of field sampling for multi-taxon biodiversity studies in european forests.

Cawsey EM & Freudenberger D (2008) Assessing the biodiversity benefits of plantations: the plantation biodiversity benefits score. Ecological Management & Restoration 9: 42–52. doi:10.1111/j.1442-8903.2008.00386.x.

Chytrý M, Pyšek P, Tichý L, Knollová I & Danihelka J (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. Preslia 77: 339–354.

Chytrý M, Wild J, Pyšek P, Tichý L, Danihelka J & Knollová I (2009) Maps of the level of invasion of the Czech Republic by alien plants. Preslia 81: 187–207.

Du S, Hu X, Yang Y & Wang Z (2022) Molecular phylogeny of *Populus* (Salicaceae, Salicales) with focus on inter-and intrasectional relationships. Dendrobiology 88: 56–69. doi:10.12657/denbio.088.004.

Euro+Med (2006) Euro+Med PlantBase – the information reource for Euro-Mediterranean plant diversity. Available at: http:/ww2.bgbm.org/EuroPlusMed.

Faly LI, Kolombar TM, Prokopenko EV, Pakhomov OY & Brygadyrenko VV (2017) Structure of litter macrofauna communities in poplar plantations in an urban ecosystem in Ukraine. Biosystems Diversity 25: 29–38. doi:10.15421/011705.

Felton A, Löfroth T, Angelstam P, Gustafsson L, Hjältén J, Felton AM, Simonsson P, Dahlberg A,

Lindbladh M, Svensson J, Nilsson U, Lodin I, Hedwall PO, Sténs A, Lämås T, Brunet J, Kalén C, Kriström B, Gemmel P & Ranius T (2020) Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. Ambio 49: 1050–1064. doi:10.1007/s13280-019-01248-0.

Fenda P & Ciceková J (2005) Soil mites (Acari, Mesostigmata) of oak forests in the Malé Karpaty Mts (W Slovakia). Ekológia (Bratislava) 24: 102–112.

Fonseca BM, de Mendonça-Galvão L, Sousa FDR, Elmoor-Loureiro LMA, Gomes-e-Souza MB, Pinto RL, Petracco P, de Oliveira RC & de Jesus Lima E (2018) Biodiversity in pristine wetlands of central Brazil: a multi-taxonomic approach. Wetlands 38: 145–156. doi:10.1007/s13157-017-0964-7.

Gadow Kv, Zhang CY, Wehenkel C, Pommerening A, Corral-Rivas J, Korol M, Myklush S, Hui GY, Kiviste A & Zhao XH (2012) Forest structure and diversity: Continuous cover forestry. Managing Forest Ecosystems 23: 29–83. doi:10.1007/978-94-007-2202-6_2.

Gallé R, Gallé-Szpisjak N & Torma A (2017) Habitat structure influences the spider fauna of short- rotation poplar plantations more than forest age. European Journal of Forest Research 136: 51–58. doi:10.1007/s10342-016-1008-1.

Gelatičová K (2021) Porovnanie lužných lesov a monokultúr hybridných topoľov (Populus x canadensis) z hľadiska mikroenvironmentálnych podmienok a diverzity podrastu. Vol. master: Enviromentálna ekológia, Univerzita Komenského v Bratislave.

Genova B, Jarolímek I, Gelatičová K, Klačanová S, Nazarov M, Slabejová D, Slezák Ml, Vassilev K, Šibík J & Šibíková M (2022) The effect of Poplar plantations on undergrowth diversity and neophyte distribution. 30th Conference of the European Vegetation Survey: Plant communities in changing environment. May 9–13, 2022, Slovakia. Plant Science and Biodiversity Center SAS, Bratislava.

Haeussler S, Bartemucci P & Bedford L (2004) Succession and resilience in boreal mixedwood plant communities 15–16 years after silvicultural site preparation. Forest Ecology and Management 199: 349–370. doi:10.1016/j.foreco.2004.05.052.

Hennekens SM & Schaminée JH (2001) TURBOVEG, a comprehensive data base management system for vegetation data. Journal of Vegetation Science 12: 589–591. doi:10.2307/3237010.

Hofmeister J, Hošek J, Baltaziuk K, Tenčík A, Iarema V, Brabec M & Pettit J (2022) Species-rich plant communities in interior habitats of small forest fragments: The role of seed dispersal and edge effect. Journal of Vegetation Science 33: e13152. doi:10.1111/jvs.13152.

Li Y, Chen Y, Xu C, Xu H, Zou X, Chen HY & Ruan H (2018) The abundance and community structure of soil arthropods in reclaimed coastal saline soil of managed poplar plantations. Geoderma 327: 130–137. doi:10.1016/j.geoderma.2018.05.004.

Macher TH, Beermann AJ & Leese F (2021) TaxonTableTools: A comprehensive, platform-independent graphical user interface software to explore and visualise DNA metabarcoding data. Molecular Ecology Resources 21: 1705–1714. doi:10.1111/1755-0998.13358.

Medvecká J, Jarolímek I, Hegedüšová K, Škodová I, Bazalová D, Botková K & Šibíková M (2018) Forest habitat invasions – Who with whom, where and why. Forest Ecology and Management 409: 468–478. doi:10.1016/j.foreco.2017.08.038.

Medvecká J, Jarolímek I, Senko D & Svitok M (2014) Fifty years of plant invasion dynamics in Slovakia along a 2,500 m altitudinal gradient. Biological Invasions 16: 1627–1638. doi:10.1007/s10530-013-0596-7.

Medvecká J, Kliment J, Majekova J, Halada L, Zaliberova M, Gojdičová E, Ferakova V & Jarolimek I (2012) Inventory of the alien flora of Slovakia. Preslia 84: 257–309.

Michalko J (1987) Geobotanical map of CSSR: slovak Socialist Republic text part. VEDA, Publishing House of the Slovak Academy of Sciences.

Mock A, Šašková T, Raschmanová N, Jászay T, Ľuptáčik P, Rendoš M, Tajovský K & Jászayová A (2015) An introductory study of subterranean communities of invertebrates in forested talus habitats in southern Slovakia. Acta Societatis Zoologicae Bohemicae 79: 243–256.

Mottl J & Špalek V (1961) Pěstujeme topoly. SZN.

Nageleisen L-M & Bouget C (2009) Forest insect studies: methods and techniques, key considerations for standardisation. An overview of the reflections of the Entomological Forest Inventories working group (Inv. Ent. For.). Office National des Forêts.

Pandey HP & Luitel DR (2020) Diversity and species selection in urban forestry: reflection from Maitighar to Tinkune Road of Kathmandu Valley, Nepal. Journal of Environment Sciences 6: 19–26.

Pharo EJ, Beattie AJ & Pressey RL (2000) Effectiveness of using vascular plants to select reserves for bryophytes and lichens. Biological Conservation 96: 371–378.

Pöltl M & Berg C (2016) Vegetationskundliche Untersuchung von Kurzumtriebsplantagen (KUP) bestockt mit *Populus ×canadensis* im südoststeirischen Alpenvorland. Mitt. Nat. Ver. Steiermark 146: 5–18.

Pospíšková M & Šálková I (2006) Population structure and parentage analysis of black poplar along

the Morava River. Canadian Journal of Forest Research 36: 1067–1076. doi:10.1139/x06-003.

R Core Team (2023) R: A language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria.

Rédei T, Csecserits A, Lhotsky B, Barabás S, Kröel-Dulay G, Ónodi G & Botta-Dukát Z (2020) Plantation forests cannot support the richness of forest specialist plants in the forest-steppe zone. Forest Ecology and Management 461: 117964. doi:10.1016/j.foreco.2020.117964.

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E & Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. Annual Review of Entomology 55: 421–438. doi:10.1146/annurev-ento-112408-085432.

Schnitzler A, Hale BW & Alsum EM (2007) Examining native and exotic species diversity in European riparian forests. Biological Conservation 138: 146–156. doi:10.1016/j.biocon.2007.04.010.

Schultz U, Brauner O & Gruß H (2009) Animal diversity on short-rotation coppice. A review. Landbauforschung Volkenrode 59: 171–182.

Slabejová D, Čejka T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Šustek Z & Jarolímek I (2023) Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. Forest Ecology and Management 548: 121413. doi:10.1016/j.foreco.2023.121413.

Spies TA (2004) Ecological concepts and diversity of old-growth forests. Journal of Forestry 102: 14–20. doi:10.1093/jof/102.3.14.

Stanturf J & Van Oosten C (2014) Operational poplar and willow culture: Poplars and willows: trees for society and the environment (ed. by JG Isebrands & J Richardson) CABI International, pp. 200–257.

Šenkýř M (2015) Vliv nepůvodních listnatých dřevin na diverzitu bylinného patra. Diploma thesis: Masarykova univerzita, Přírodovědecká fakulta.

Šuvada R, Bernátová D, Dítě D, Dítě Z, Dúbravková D, Eliáš jun P, Hegedüšová Vantarová K, Hrivnák R, Jarolímek I, Kliment J, Kollár J, Máliš F, Novák P, Oťaheľová H, Slezák M, Šibík J, Šibíková M, Škodová I, Uhlířová J, Ujházy K, Valachovič M & Vaško Ľ (2023) Katalóg biotopov Slovenska (druhé, rozšírené vydanie). Štátna ochrana prírody SR, Banská Bystrica.

Taberlet P, Proud'Homme SM, Campione E, Roy J, Miquel C, Shehzad W, Gielly L, Rioux D, Choler P, Clément JC, Melodelima C, Pompanon F & Coissac E (2012) Soil sampling and isolation of extracellular DNA from large amount of starting material suitable for metabarcoding studies. Molecular Ecology 21: 1816–1820. doi:10.1111/j.1365-294X.2011.05317.x.

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. doi:10.1111/j.1654-1103.2002.tb02069.x.

Topp W, Kappes H, Kulfan J & Zach P (2006) Distribution pattern of woodlice (Isopoda) and millipedes (Diplopoda) in four primeval forests of the Western Carpathians (Central Slovakia). Soil Biology and Biochemistry 38: 43–50. doi:10.1016/j.soilbio.2005.04.012.

Úradníček L & Chmelař J (1995) Dendrologie lesnická. 2. část–Listnáče I. MZaLU Brno.

Valachovič M, Kliment J & Hegedüšová VK (2021) Rastlinné spoločenstvá Slovenska 6. Vegetácia lesov a krovín: Veda, Bratislava.

Vanbeveren SP & Ceulemans R (2019) Biodiversity in short-rotation coppice. Renewable and Sustainable Energy Reviews 111: 34–43. doi:10.1016/j.rser.2019.05.012.

Wang S, Chen HY, Tan Y, Fan H & Ruan H (2016) Fertilizer regime impacts on abundance and diversity of soil fauna across a poplar plantation chronosequence in coastal Eastern China. Scientific Reports 6: 20816. doi:10.1038/srep20816.

Wang Z, Bai L, Zhang Y, Zhao K, Wu J & Fu W (2022) Spatial variation, sources identification and risk assessment of soil heavy metals in a typical Torreya grandis cv. Merrillii plantation region of southeastern China. Science of the Total Environment 849: 157832. doi:10.1016/j.scitotenv.2022.157832.

Westhoff V & van der Maarel E (1978) The Braun-Blanquet approach: Classification of plant communities (ed. by RH Whittaker) Dr W. Junk Publishers, The Hague, pp. 289–399.

Wohlgemuth T, Gossner MM, Campagnaro T, Marchante H, van Loo M, Vacchiano G, Castro-Díez P, Dobrowolska D, Gazda A, Keren S, Keserű Z, Koprowski M, La Porta N, Marozas V, Nygaard PH, Podrázský V, Puchałka R, Reisman-Berman O, Straigytė L, Ylioja T, Pötzelsberger E & Silva JS (2022) Impact of non-native tree species in Europe on soil properties and biodiversity: a review. NeoBiota 78: 45–69. doi:10.3897/neobiota.78.87022.

Young MR & Hebert PD (2022) Unearthing soil arthropod diversity through DNA metabarcoding. PeerJ 10: e12845. doi:10.7717/peerj.12845.

Zając A, Tokarska-Guzik B & Zając M (2011) The role of rivers and streams in the migration of alien plants into the Polish Carpathians. Biodiversity Research and Conservation 23: 43–56. doi:10.2478/v10119-011-0012-z.

Zedníček Ľ (2016) Vplyv výsadby nepôvodných topoľovna druhové zloženie lužných lesov Podunajskej roviny., Vol. master: Comenius University, Bratislava, Slovakia, Faculty of Natural Sciences.