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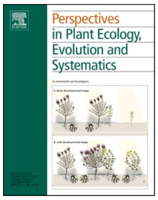

Plant-soil interactions in the communities dominated by alien and native plants

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ABSTRACT

It has been established by research on plant invasions that soil biota and availability of nutrients affect the processes of alien species establishment and spread. So far, attention was mainly on alien invaders, although some native species (expansive), vigorously spread in human-influenced landscapes and also transform the habitats they colonize. Based on indirect gradient ordination analysis of vegetation relevés dominated by five native (*Calamagrostis epigejos, Filipendula ulmaria, Phalaris arundinacea, Rubus idaeus, Urtica dioica*) and five alien taxa (*Impatiens glandulifera, Lupinus polyphyllus, Telekia speciosa, Reynoutria* sp., *Solidago canadensis* agg.) in the Czech Republic, Central Europe, we identified pairs of species differing by origin (native vs alien) and growing in similar habitats. In the resulting 10 pairs, we tested the net effect of species origin on the following soil characteristics: (i) physical properties, (ii) nutrient availability, and (iii) biological activity. We found that the impact of alien invasive and native expansive species on soil cannot be explained simply by species' origin as a factor. Regardless of the origin, a statistically significant effect was recorded only for factors expressing nitrogen supply at the peak of the vegetation season and soil biological activity. Differences in impacts attributable to origin were only verified for individual pairs, being most pronounced between the alien *Lupinus* and its native counterparts *Calamagrostis* and *Filipendula*, and least between *Solidago* vs *Calamagrostis,* and *Telekia* vs *Rubus*. Both invasive alien and expansive native dominant plants can alter the rate of decomposition by changing the litter quality and availability of nutrients, mainly inorganic nitrogen. Therefore, management actions to preserve or restore diversity and mitigate the negative impacts of dominant species should be focused both on native and alien species.

1. Introduction

Invasive alien species are recognized as a key component of global environmental change (MEA, 2005; van Kleunen et al., 2015; Kettunen et al., 2009; Pyšek et al., 2020c, 2017). They have significant negative impact on biodiversity, ecosystem functioning and economy, as well as human health (Vilà et al., 2010, 2015; Scalera et al., 2012). While the attention of policymakers, researchers, and nature conservation bodies is mainly focused on alien invaders (IAS), native species are generally considered harmless. However, even some natives vigorously spread in

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human-transformed landscapes (termed 'native expansive species' – NES; Prach and Wade, 1992; Richardson et al., 2000; Essl et al., 2019; Hejda et al., 2021) and further degrade the colonized habitats and recipient vegetation (Pivello et al., 2017). In many ecosystems, human activities and resulting land-use change, such as increasing intensification of agriculture and urbanization, or abandonment of industrial areas, can promote not only the emergence of newly introduced species but also colonization by native species. Nevertheless, rigorous data on the ecological and economic impacts of NES are only starting to appear (Hejda et al., 2021), and researchers so far have not adequately addressed this group in their studies. The issue is now debated among researchers and policymakers, with some arguing that the origin of the species should be discarded as a criterion for management action (Valéry et al., 2009; Davis et al., 2011; Majewska et al., 2018), a view opposed by other workers in the field (Simberloff et al., 2011, 2013). Yet, this debate cannot be resolved without rigorous data.

Here we argue that research on the impacts of IAS needs to be complemented with analogous studies on NES. The so-far scarce available evidence from the US suggests that although both groups of species include environmental and economic weeds, the impact of introduced species was about 40 times higher than that of native weeds (Simberloff et al., 2012). On the other hand, alien and native species alike affect the flow of energy and chemical substances, functioning as ecosystem engineers (transformers) and thus affecting other species in the community (Fiala et al., 2003). This assumption accords with the results of a recent study, showing that both expanding native and invasive dominants reduce the diversity of vegetation, and the differences among the two groups defined by origin are inconsistent – some IAS had stronger effects than corresponding NES growing in the same habitat, and vice versa (Hejda et al., 2021).

Studies that tested the impact of alien plants on plant community diversity led to an agreement that sites invaded by aliens harbour fewer species than non-invaded sites (Hejda et al., 2009; Vilà et al., 2011; but see, e.g. Čuda et al., 2017). However, the magnitude and direction of impacts depend on the ecosystem invaded, environmental conditions, and time since the invasion. The suppression of native plants results from the dominance of invasive species, and the impact differs among individual invaders and habitats (Hejda et al., 2009). The effects of invading alien species should be, therefore, measured over a range of environments, the most common approach being a comparison of invaded with ecologically corresponding but non-invaded plots in various habitats.

The poor understanding of IAS and NES interactions with invaded ecosystems, and the role they play in the spread of dominant species, is partly because even for IAS, where significant progress in categorizing impacts has been made in the past decades (Pyšek et al., 2012b; Barney et al., 2013; Blackburn et al., 2014; Kumschick et al., 2015), the knowledge is biased towards negative impacts of a few species (Pyšek et al., 2008). Impacts are usually measured in a simple way, based on static characteristics, stocks rather than flows. Additionally, the number of thoroughly studied species is low, and impacts on plants, soil and other trophic levels are usually studied separately (Hulme et al., 2013; Barney et al., 2015).

Soil biota and availability of nutrients affect the naturalization and invasion process, as feedback among plant species and the soil environment influences the biological activity of soil organisms (Lavelle et al., 1997; Wardle et al., 2004; Liao et al., 2013; Majewska et al., 2018). Yet, plant-soil interactions are an essential part of ecosystem changes following the invasion, as well as the invasibility of habitats. For example, the aboveground invasive species are known to affect the soil environment and nutrient availability (Vanderhoeven et al., 2005; Koutika et al., 2007; Woch et al., 2021). The processes are bidirectional, as shown in many studies focusing on the effects on other species through the plant-soil feedback. The changes in plant-soil feedback, manifest as the differences in soil prior and after the invasion, can presumably play an important role in the process of plant invasion (Fiala et al., 2003; van der Putten et al., 2013; Dostálek et al., 2016; Ye et al., 2019).

There are several approaches to study impacts on invaded communities (Kumschick et al., 2015), and it is commonly agreed that the comparison of similar habitats is suitable as the time series are rarely available, and there can be additional factors affecting the outcome of invasion (Hejda et al., 2009; Řehounková et al., 2018; Vítovcová et al., 2021).

2. Aims

To compare the impacts of the two species groups differing by origin, we sampled the above-ground vegetation dominated by five native and five alien taxa, and related this data to the following soil characteristics: (i) physical properties, (ii) seasonal changes in nutrient availability, and (iii) biological activity. Focus on a large amount of studied factors targeting different soil characteristics allows us to cover many processes of soil ecosystem and its functions. We also aimed at covering the changes under the dominant species over the entire growing season to identify the temporal patterns, and analyse both flows and stock. Both issues are, to our knowledge, rarely tested together (Hulme et al., 2013) and there are no data on the impact of alien and native species collected by the comparable methods.

Two points need to be highlighted. All effects were tested on values corrected by those recorded in control plots; therefore, we were able to identify the negative or positive sign of the observed change compared to the vegetation without the given dominant species. Yet, any increase or decrease in relation to ecosystem processes needs to be interpreted with caution and within the context of other factors. To account for the context-dependence of invasion processes (Pyšek et al., 2020b), we compared the impacts of alien and native species of similar growth forms and occurring in the same habitats (Hejda et al., 2021), rather than aiming at a general comparison of all alien and native species that would require many more species in the dataset.

3. Methods

The study was conducted in the Czech Republic, Central Europe, a country located in the temperate broad-leaved deciduous forest zone (Chytrý et al., 2005; Divíšek et al., 2014), with mean annual temperatures of 5.0–9.5 °C and annual precipitations of 320–1450 mm (Tolasz et al., 2007).

To minimize the bias due to rapid changes in the community structure that occur shortly after disturbance at the early stages of succession, only habitats that are structured by competition and not by disturbance were selected for sampling (as in Hejda et al., 2021), i.e. non-forested habitats including riparian habitats and mesic grasslands (Appendix A). The impact of each species was studied in eight study plots 4 × 4 m in size with a minimum distance of 1 km between them. In some cases, one study site hosted more than one study plot, with different dominant species sharing the same control plot. The target species dominated on the study plots with a cover exceeding 80%. The criterion for control plots was to harbour vegetation with no dominant species; the cover of each present species did not exceed 25%.

3.1. Species selection

Five neophytes (taxa introduced to the Czech Republic after the year 1500; Pyšek et al., 2004 – *Impatiens glandulifera*; *Lupinus polyphyllus*; *Telekia speciosa*; *Reynoutria* ×*bohemica* and *R. japonica*; *Solidago canadensis* and *S. gigantea*) and five native species (*Calamagrostis epigejos*; *Filipendula ulmaria*; *Phalaris arundinacea*; *Rubus idaeus*; *Urtica dioica*) were selected for studying their impacts on soil characteristics. The species included annual herbs, rhizomatous herbs and grasses, and semi-shrubs (Table 1) and were representative of dominants commonly occurring in Central Europe (Pyšek et al., 2012a; Kaplan et al., 2020). In

Table 1

Studied species, their abbreviations, and status in the Czech Republic (taken from Pyšek et al., 2012a). Information on taxonomy, life form, and ecological requirements is provided. The water regime of the habitat ranges from moist to dry; trophic demands link to nutrients in the soil, and habitat describes the prevailing combination of land-use and habitat category. Names of the taxa follow Danihelka et al. (2012).

Species	Abbreviation	Status	Taxonomy	Life form	Water regime of the habitat	Trophic demands	Habitats
Impatiens glandulifera	Imp	alien	dicot, Balsaminaceae	non-clonal annual	mesic, moist	high	Riverine
Lupinus polyphyllus	Lup	alien	dicot, Fabaceae	non-clonal perennial	dry, mesic	low	Post-meadow
Reynoutria sp. div.	Fal	alien	dicot, Polygonaceae	clonal perennial	mesic, moist	high	Urban, post-meadow, riverine
Solidago canadensis agg.	Sol	alien	dicot, Asteraceae	clonal perennial	dry, mesic	medium	Urban, post-meadow
Telekia speciosa	Tel	alien	dicot, Asteraceae	clonal perennial	mesic, moist	medium	Post-meadow, riverine
Calamagrostis epigejos	Cal	native	monocot, Poaceae	clonal perennial	dry, mesic	low	Urban, post-meadow
Filipendula ulmaria	Fil	native	dicot, Rosaceae	clonal perennial	moist, waterlogged	high	Post-meadow
Phalaris arundinacea	Pha	native	monocot, Poaceae	clonal perennial	moist, waterlogged	high	Post-meadow, riverine
Rubus idaeus	Rub	native	dicot, Rosaceae	clonal semi-shrub	mesic	medium	Post-meadow
Urtica dioica	Urt	native	dicot, Urticaceae	clonal perennial	mesic, moist	high	Urban, post-meadow, riverine

the paper, the species are referred by their genus names. We did not include the phylogenetic correction as the species were selected to cover many different families and growth forms.

3.2. Paired comparisons

As the invasions are highly context-dependent, we focused on comparisons of pairs of similar alien vs native dominant species growing in comparable habitats and having similar life forms. The selection of the pairs was based on field observations and analysis of vegetation data (Hejda et al., 2021). Each alien species was paired with the two most similar natives, and vice versa – each native created a pair with the two most similar aliens (see Table 2 for species forming individual pairs). The selection of pairs was based on indirect gradient ordination analysis (Detrended Correspondence Analysis, DCA; Šmilauer and Lepš, 2014) and the distances between the centroids of individual native and invasive dominant species, where the vegetation composition of plots with less than 25% dominant species' cover was used (Hejda et al., 2021).

Table 2

Pairs of studied alien and native dominants with description of their characteristics.

Alien	Native	Description of growth form, soil and habitat
Impatiens	*Filipendula*	Tall dicots. Wet soils. Open brook wetlands.
Impatiens	*Phalaris*	Wet and nutrient-rich soils. Rapid colonization of disturbed sites. Open wetlands and wet forests in river floodplains. Resistant to floods.
Lupinus	*Calamagrostis*	Semi-dry, nutrient-poor soils. Rapid colonization of disturbed sites. Grasslands, forest clearings, ruderal habitats.
Lupinus	*Filipendula*	Mesic, nutrient-poor soils. Disturbed grasslands, herbaceous fringes.
Reynoutria	*Rubus*	Tall, robust dicots, dense rhizomes, large clonal stands, long marcescence of stems. Mesic to wet forest and their clearings.
Reynoutria	*Urtica*	Tall robust dicots, dense rhizomes, large and permanent clonal stands. Mesic to wet soils, very rich in nutrients. Open loamy wetlands, wet shrubs and forests, ruderal habitats.
Solidago	*Calamagrostis*	Dense net of thin rhizomes. Dry to semi-wet soils. Grasslands and ruderal habitats.
Solidago	*Urtica*	Tall dicots, dense net of thin rhizomes. Ruderal habitats.
Telekia	*Phalaris*	Nutrient-rich wet soils. Open brook wetlands and wet forest fringes.
Telekia	*Rubus*	Tall dicots. Acido-nitrophilous conditions after soil disturbance. Mesic forest clearings.

3.3. Measuring soil attributes

In total, we measured 80 soil variables (Appendix B). Some specific soil characteristics, such as physical properties, seasonal variation of nutrient availability, and biological activity were selected to measure the interaction with the above-ground impacts to cover a range of important aspects of soil physico-biogeochemical parameters (Barney et al., 2015). The sampling at permanent plots was done in three periods to capture spring (April–May), early summer (June–July), and late summer (August–September) aspects of the vegetation season. The soil was sampled at the same depth in the rhizosphere of plants, as it is common in studies comparing nutrient supply in the soil of different plant communities and life forms using Plant Root Simulator™ (PRS) probes (described below), e.g. Blumenthal (2009), Metcalfe et al. (2011), Sorenson et al. (2017), and Sarneel et al. (2020). To minimize the spatial variability and achieve homogeneity of samples, two subplots of 1 × 1 m were permanently marked in each study plot for soil sampling. (i) One mixed sample consisting of five subsamples was taken along the perimeter of each subplot for the actual physicochemical properties in the top vegetation season (June 2018). (ii) Four (two cations and two anions) (PRS)™ probes (Kusbach and Van Miegroet, 2013) were buried vertically in the centre of each subplot (i.e. eight probes for each study plot) for measuring seasonal nutrient availability during vegetation season (April–September 2018). The probes consisted of a plastic casing containing a 55 mm × 16 mm ion exchange resin membrane (two-sided area of 176 cm^2), which was intended to simulate the action of a plant root until membrane saturation. To reduce the damage by wild boars, the probes were protected by cages 25 × 25 × 12 cm. (iii) Next to the (PRS)™ probes, actual soil moisture was measured by the HH2 Moisture Meter device, and soil reaction and soil temperature using pH meter HI 99121 (Hanna Instruments). One undisturbed soil sample was taken from each subplot using Kopecký cylinders to analyse the water capacity of the soil. (iv) Both subplots were separated by a strip where litter bags filled with pure cellulose (filter papers) were installed to measure the cellulose decomposition rate in the soil (Fig. 1).

3.4. Actual physical and chemical properties

Conductivity, total carbon (TC), total nitrogen (TN), and organic matter (OM) were detected in June 2018, using standardized methods

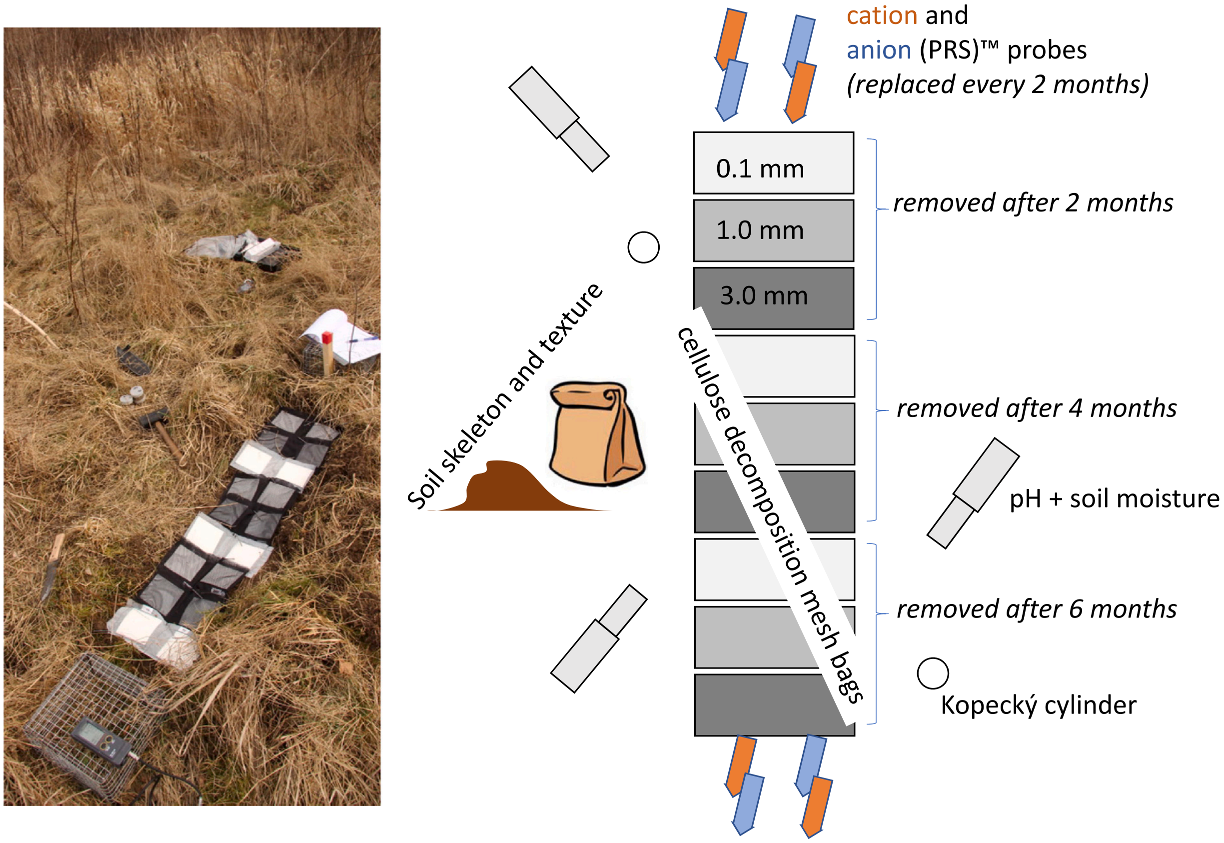

Fig. 1. Design of field sampling. Ion probes were replaced every two months, mesh bags (grey rectangles) were of three mesh sizes, and were being removed successively. Soil samples for skeleton and texture were sampled once in the season (see sampling details in the method section).

suggested for measuring the ecological impacts of invasive plants (Barney et al., 2015). Soil skeleton and texture were determined following standard soil analyses and ISO standards (ISO 14238, 1997). Volumetric soil moisture, dry matter, soil bulk density, and available water capacity were measured in April and June 2018 using undisturbed soil samples in the Kopecký cylinders (e.g. Klute, 1986). Laboratory analyses were processed in the Analytic Laboratory of the Institute of Botany of the Czech Academy of Sciences.

3.5. *Seasonal nutrient availability*

The supply of 15 soil nutrients/elements (NO_3^--N, NH_4^+-N, P, K, S, Ca, Mg, Mn, Al, Fe, Cu, Zn, B, Pb, Cd) was measured by anion and cation exchange (PRS™) probes (Kusbach and Van Miegroet, 2013). Four paired probes were buried to a depth of 5–10 cm in the primary rooting zone of each plot three times during the vegetation season of 2018. Because of the limited adsorption capacity of the ion-exchange membrane in the probes, the burial period was divided into three two-month phases when the probes were replaced and analysed in the laboratory. The burial length was tested a year before (2017) on nitrate-rich plots to obtain an estimate of the maximum period before the membrane becomes saturated for NO_3^--N in comparison with blank PRS™ probes placed in pure sand. PRS™ probes were analysed in laboratories of Western Ag Innovations, Canada.

3.6. *Soil microbial activity*

To compare the overall biological activity of soil at different ecosystems and soil depths, we measured the rate of cellulose decomposition (e.g. Frouz et al., 2009; Sotiriou and Arianoutsou, 2009). Three dried and weighed sheets of filter paper (ash content below 0.5%, weight 80 g/m^2) of 10 × 10 cm in size were placed into 14 × 14 cm mesh bags (Barney et al., 2015). Bags with three mesh sizes were used to assess different soil faunas: 0.1 mm (permeable to bacteria, fungi, and protozoa), 1 mm (permeable to microflora, microarthropods, and mesoarthropods), and 4 mm (freely permeable to soil fauna; Swift et al., 1979). Six replicates of each type of litterbags (18 bags at each plot) were buried between the litter layer and the soil surface (between O and A soil horizons) in the first half of April 2018. One set of litterbags (two replicates for each mesh size) was collected after two months in the field (at the same time as PRS™ probes). The litterbags were dried, and the remaining filter paper was carefully removed, weighted, and ashed at 550 °C for five hours to remove contamination with soil. The cellulose decomposition rate was counted as the weight loss of a filter paper during incubation in the field.

3.7. *Statistical analysis*

To account for the variation among plots, each study plot was standardized by the corresponding control plot as $x_{\text{species plot}}/x_{\text{control}}{}^{*}\ 100$, expressing an increase or decrease in a given characteristic due to the presence of the dominant species (net effect) compared to the control. This approach ensured that the different scales for various soil measurements were in the same range and that the values comparable to control plots approached 100%.

To analyse the effect of individual studied factors within the native and alien dominant pairs, we used GLS models with the VarIdent parameter to cope with the different levels of variance among plots (Zuur et al., 2009). The less conservative testing (i.e. $p < 0.1$) was chosen due to the presumed high variability in the soil environment and it would not be possible to detect even strong patterns with conservative testing. Deciding what is acceptable is a balance of the costs of type II (power) vs. type I errors, and weighting depends on the noise and costs (design, replicates). The identity of the species was used as an explanatory variable. A separate model was developed for each pair and studied factor. No method of correction against the type I error inflation (i.e. Bonferroni) was used as it would lead to very weak tests, given the high number of analysed factors. A serious problem associated with using the standard Bonferroni procedure is a substantial reduction in the statistical power of rejecting an incorrect null hypothesis in each test (Moran, 2003; Nakagawa, 2004).

To reveal the patterns in effects of individual species we used multiple comparisons based on linear models (SNK method; Underwood, 2005; if needed data were transformed by natural log). There were separate models for the factors where explanatory variable was identity of species.

To facilitate the interpretation of the measured characteristics, we grouped the soil attributes to structural, functional and seasonal characteristics (Appendix B). The data were visualized by CANOCO (CCA method; Šmilauer and Lepš, 2014) and analysed by the contingency-table analysis that was followed, by summing up the significant differences analysed by chi-square test (Crawley, 2007). The over- or under-representation of the number of significant differences was then compared by G-tests against a random sample (Řehák and Řeháková, 1986).

4. Results

4.1. Relationships between the occurrence of the dominant species and soil characteristics

The clustering of species in the ordination space indicates that native and alien dominants did not exert different impacts on soil characteristics (as measured by net effects with controlling for the local soil variation; Fig. 2). The first ordination axis represented factors such as physical soil properties, namely soil texture and ability to keep water in the soil. Fine soils with predominant particles up to 10 μm in size (clay and silty clay) and a high water capacity (AWC – available water capacity and VSM – volumetric soil moisture) were located on the left in the ordination space. Such soils were associated with both native species (*Filipendula*, *Rubus* and *Urtica*) and aliens (*Lupinus* and *Solidago*). Coarse soils displayed on the right side had most soil particles bigger than 50 μm and a low available water capacity. Such factors were positively correlated with the occurrence of the alien *Impatiens* growing in riverine habitats with a high groundwater level, compensating for the low ability of the soils to retain water. Soil nitrates and mineral nitrogen were positively correlated with the second ordination axis and the occurrence of alien *Solidago*, while ammonium nitrogen is displayed on the opposite side and correlated with native *Urtica* and the aliens *Lupinus* and *Reynoutria*.

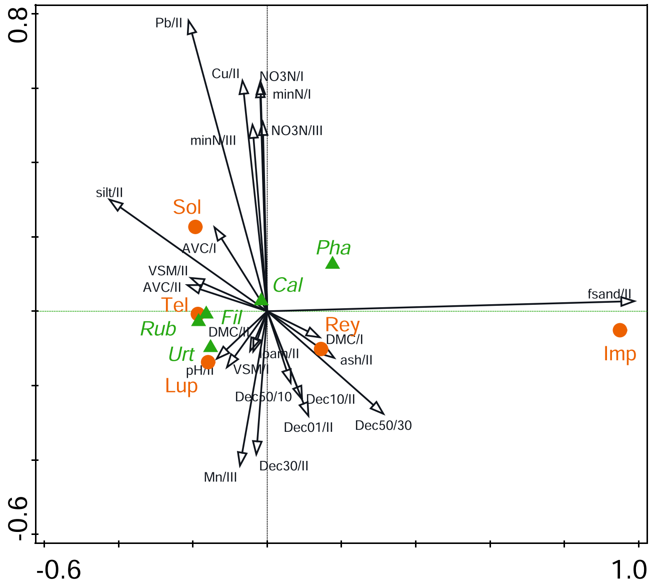

Fig. 2. - Unconstrained ordination diagram (PCA) showing variables with > 20 % fit. The figure with all variables is then shown in elecronic Appendix D. Alien dominants are shown as orange circles, native dominants as green triangles with italicised captions. Dominant species are projected onto the diagram ex post as passive variables. Species abbreviations follow Table 1 and codes of soil characteristics are explained in Appendix B.

The differences among species (Fig. 3) were statistically significant only for factors expressing nitrogen supply (NO_3N/II, mineralN/II, and N/II) in the top vegetation season (June–July) and decomposition rate (Dec50/01, Dec50/10, Dec01/III, Dec10/III Dec30/II). Other physico-chemical soil properties did not reveal statistical differences among species. The lowest contents of nitrates (NO_3N/II) and mineral nitrogen (NO_3NH_4N/II) were detected in soils with dominant *Impatiens*, followed by *Urtica* and *Lupinus*, whereas the highest concentrations were found in *Solidago* and *Telekia*. Actual total soil nitrogen measured at the beginning of June reached the lowest value in *Calamagrostis* and the highest in *Reynoutria*.

The trends in the decomposition rates were similar regardless of litter-bag mesh sizes. The fastest paper loss indicating the highest activity of soil biota was recorded in *Lupinus*, followed by *Telekia*. On the contrary, the lowest activity was detected in *Solidago* and *Calamagrostis*. The differences among other species were negligible. Statistically significant relationships were detected only for the seasonal peak (June–July) of vegetation development (for the mesh size 4 mm) and at the late vegetation season (mesh sizes 0.1 mm and 1.0 mm). The reason for different timing is probably a faster decomposition in litter bags freely permeable to soil fauna (4 mm) which caused a complete loss of filter paper in 37% of litter bags at the end of the experiment (after six months from burying), and the other 24 % were containing less than 10 % of the paper.

The decomposition time, calculated as the 50% filter-paper loss, is displayed in Fig. 3. The differences among study species were the same as for the decomposition rates and were significant only for mesh sizes of 0.1 and 1.0 mm.

4.2. Comparison of soil characteristics between pairs of native and alien dominant species

Comparing the net effects of native and alien dominants revealed statistically significant differences in 60 soil variables (out of the 80 measured). The most frequent were the differences in Dec01/III, NH_4N/I, NO_3N/II, and mineral N/II, which were recorded for three of the 10 pairs of species (Appendix C). Ammonium ions were always higher for native dominants, but other parameters differed also according to the dominant's status. Thirteen variables were significantly different in two species pairs, and 22 variables in one pair.

With regard to physical soil properties, no significant differences were found in soil texture and available water capacity. Volumetric soil moisture was significantly higher in native *Filipendula* than in alien *Impatiens*. The soil under invasive *Lupinus* was significantly more compacted (higher oven bulk density; OBD) than under both of its native counterparts, *Calamagrostis* and *Filipendula*.

During the early period of vegetation development, we found significantly higher concentrations of NH_4-N in soil under the native counterparts of the *Phalaris* vs *Impatiens* and *Urtica*, and *Rubus* vs *Reynoutria* pairs, whereas no significant differences were detected between native and alien dominants in nitrates (NO_3N/I). The early period was characterized by a profound temperature reversal in early April, where frost days were rapidly followed by temperatures around 20 °C. The rapid growth of plants observed in all study plots was associated with the intense depleting of nitrates from the soil. The accumulation of ammonium providing a stock of mineral nitrogen for further nitrification was not significantly different between native and alien dominants'

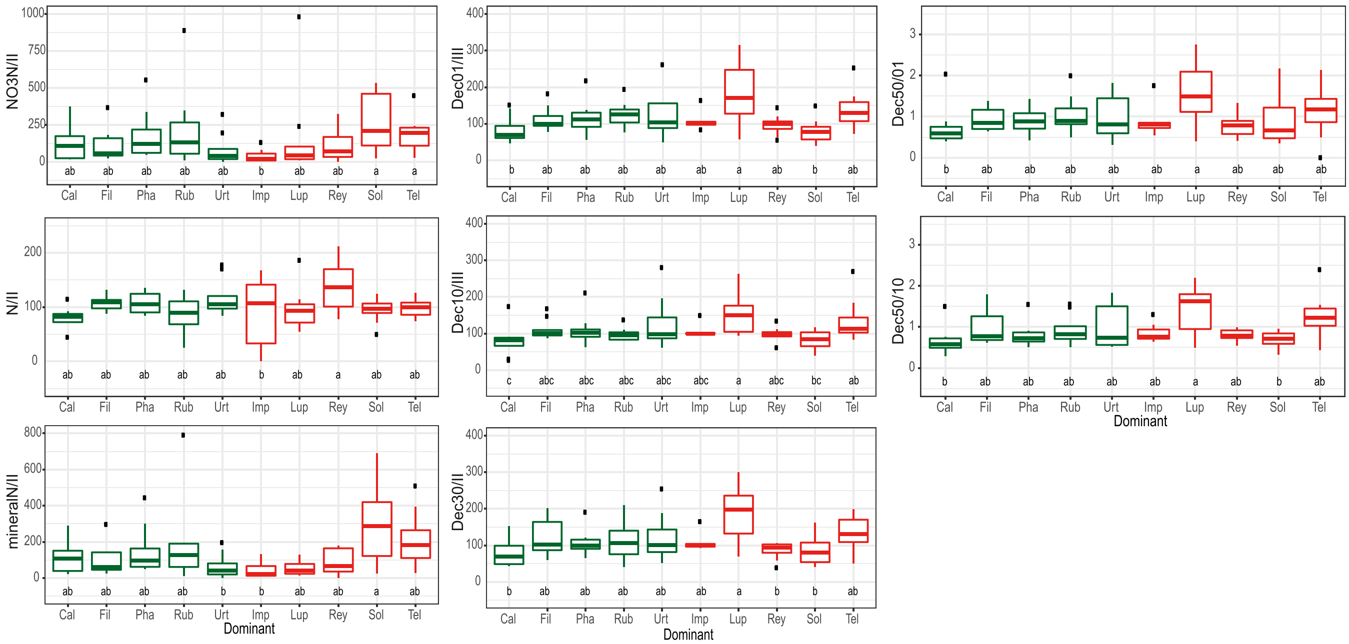

Fig. 3. The significant factors studied (net impact, standardized by control, %) with an indication of multiple comparisons among dominant species. Native dominants are on the left (green), alien dominants on the right (red) side of the panels. Boxplot shows the median, quartiles, and minimum and maximum. Outliers are shown as points. The results of multiple comparisons (SNK test) are indicated at the level of $p < 0.05$ by letters.

soils during the later vegetation period. On the other hand, nitrates (NO_3-N) and associated mineral nitrogen (NO_3NH_4-N mineralN/II) were higher in alien *Solidago* than in its native counterparts *Urtica* and *Calamagrostis* at the top of vegetation season (June–July). By contrast, these factors were significantly lower in alien *Impatiens* than in its native counterparts *Filipendula* and *Phalaris*. Other soil macronutrients (P, Ca, Mg, K, and S) played a minor role in differentiating between paired aliens and natives.

The concentrations of micronutrients (Mn, Fe, B) and Al were significantly higher in soils with native dominants than under corresponding aliens, but repeatedly so only in *Phalaris* vs *Telekia*, *Calamagrostis* and *Urtica* vs *Solidago*, and *Urtica* vs *Reynoutria* (Appendix C). In general, the higher solubility of these elements corresponded with acid soils. Nevertheless, our results did not confirm such a relationship. Zn and Cu did not differ in any pairs of alien and native dominants.

Consistently with our findings reported in Chapter 4.1, *Lupinus* and *Telekia* had significantly higher activity of soil biota than their native counterparts. Among natives, only *Urtica* had significantly higher activity of bacteria, fungi, and protozoa (0.1 mm mesh size) than alien *Solidago* after six months since burial.

Summarized by species, *Lupinus* was an alien that most frequently differed from its native counterparts, i.e. *Calamagrostis* in semi-dry habitats (12 significant differences in soil characteristics) and *Filipendula* in moist habitats (nine differences) (Appendix C, Fig. 2). For both pairs, the soil under *Lupinus* had significantly higher oven bulk density, reflecting more compact soil and accumulation of less organic matter. Together with higher Ca^{2+} (Ca/II) in peak vegetation season (significant only in the pair with *Calamagrostis*) and the ability of *Lupinus* to fix air nitrogen, there are favourable conditions for soil biota and faster decomposition in comparison with native counterparts *Calamagrostis* and *Filipendula*. Nine differences were found also in the pair of alien *Reynoutria* vs native *Rubus*, followed by *Telekia* vs *Phalaris* and *Solidago* vs *Urtica*, both six differences each (Appendix C). On the other hand, the most similar net effects were detected between *Solidago* vs *Calamagrostis* and *Telekia* vs *Rubus* with only two significant differences.

4.3. Impact of structurally, functionally and temporally grouped soil properties

Synergistic effects of soil properties grouped according to their relevance for soil structure, function and dynamics over the season are shown in Fig. 4a-c. The classification of the soil properties is shown in Appendix B. The temporal pattern was analysed by using only soil properties which were measured throughout the whole vegetation season. The model did not reveal a significant effect of the sampling period and the pairs of native and alien species (chi-square test; dev 21.5, DF=18, NS; Fig. 4c).

4.3.1. Clustering according to the structure

There were significant differences among the studied native and alien species in the counts of significantly different soil variables related to soil structure (chi-square test; dev 69.64, DF $= 36$, $p < 0.001$). For some species pairs, we found over-representation of the significant differences in macronutrients (*Phalaris* vs *Impatiens*), physical properties (*Urtica* vs *Reynoutria*) and activity of soil biota (*Calamagrostis* vs *Lupinus*). Less significant differences than expected by chance were found for cluster soil biota in pairs *Phalaris* vs *Impatiens* and *Urtica* vs *Reynoutria*, and macronutrients in *Rubus* vs *Solidago* and *Phalaris* vs *Telekia*. The distribution among the studied pairs is shown in Fig. 4a.

4.3.2. Clustering according to the functional role

There were significant differences among the studied native and alien species in the counts of significantly different soil variables related to their functional role (chi-square test; dev 58.4, DF $= 27$, $p < 0.001$). The G-tests revealed over-representation of the significant differences in impact on decomposition in the *Calamagrostis* vs *Lupinus* pair, and mineralization in *Phalaris* vs *Impatiens*. Differences less frequent than expected by chance were represented in decomposition (*Phalaris* vs *Impatiens*, *Urtica* vs *Reynoutria*), mineralization (*Phalaris* vs *Telekia*), and microelements (*Calamagrostis* vs *Lupinus*). The distribution among the studied pairs is shown in Fig. 4b.

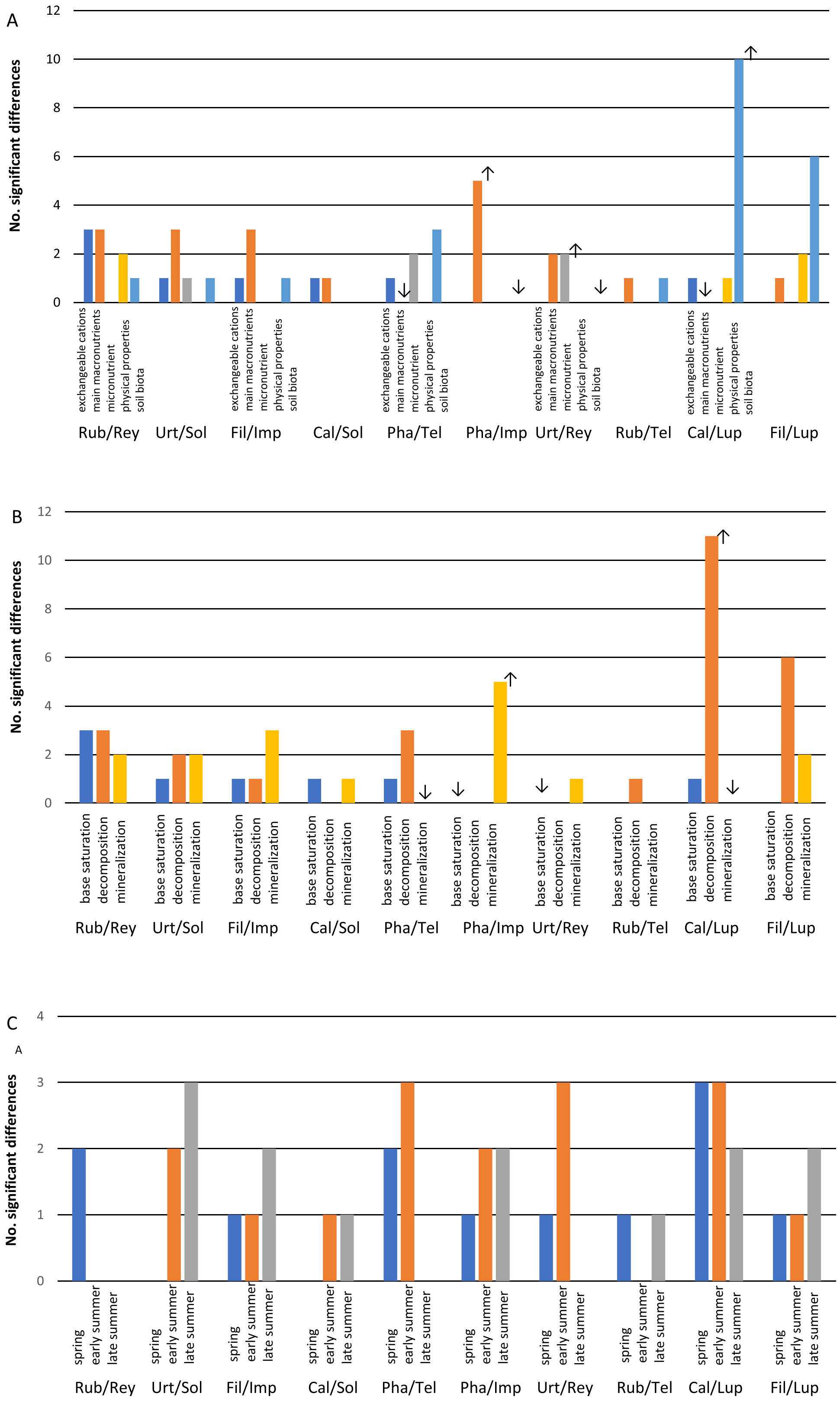

Fig. 4. Cumulative numbers of significant differences for the tested pairs of native and alien dominants grouped according to their relevance for soil structure (A), function (B) and seasonal dynamics (C). Arrows indicate whether the observed counts are above or below the counts expected by chance (G-test). Factors assigned to individual groups follow Appendix B.

5. Discussion

Our study is the first comparing in situ impacts of several alien invasive and native expansive dominant plant species on the soil environment. We are aware that the studies of impact should be in the optimal conditions based on temporal data studying the ecosystem change before and after the invasion. However, such data are rarely available (Pergl et al., 2020). Therefore, we use the space for time substitution approach with correction at affected plots by control plots. Overall, there are not many studies comparing native species with aliens (but see, e.g. Thompson et al., 1995; Májeková and Zaliberová, 2008; Sabat-Tomala et al., 2020), and regarding the impact on soil environment, such comparisons are missing completely. The only exception we are aware of is a study by Majewska et al. (2018), in which the authors analysed the direct impact of native and alien species on arbuscular mycorrhizal fungi under experimental conditions.

Furthermore, it has been shown that impacts are studied in most cases separately, and there is a lack of complex view on the measured characteristics (Hulme et al., 2013). The soil environment contains a large number of complex layers and trophic structures ranging from the physical structure to macrofauna involved in litter decomposition. Such complexity needs to be accounted for because focusing on a single parameter or on short periods during the growing season may hinder understanding of the ecosystem processes associated with invasion. To reflect these research needs, in our study we covered five native and five alien taxa, with eight localities for each, and measured over 80 soil characteristics with the same methodology. In addition, soil analyses are usually based on few snapshots over the season. To overcome this limitation, we used continuous measurements of nutrient availability and activity of soil biota. Analysis of such a number of various factors brings an interpretation problem, as many of them are not acting in the same directions (e.g. high C/N vs low pH, base saturation or decomposition rate; Manzoni et al., 2010; Vítková et al., 2015) or their effects are not happening in sequence (Zhang et al., 2009; Stefanowicz et al., 2017). On the other hand, in a study covering such a wide range of parameters, it is challenging to select and interpret the most important ones. As invasions are context-dependent and the importance of individual impacts can differ in various habitats (Bartz and Kowarik, 2019), we interpret our findings by comparing the pairs of native and invasive species growing in the same habitats (see Hejda et al., 2021). It is important to bear in mind that data used in this paper come from a highly heterogeneous soil environment sampled in the field which made us accept a higher statistical probability of confirming non-existing relationships compared to standard procedures used in the laboratory and common garden studies. We decided to accept this risk and present all results from the analyses, including non-significant, to reduce the publication bias that can hinder the advance of the field when articles mostly publish only the significant results.

It is well documented that invasive alien species can modify the physicochemical and microbiological soil properties in ways that differ from resident natives (e.g. Dassonville et al., 2008; Liao et al., 2008; Weidenhamer and Callaway, 2010; Vilà et al., 2011; Steinlein, 2013; Stefanowicz et al., 2016, 2017; Majewska et al., 2018). Most published studies report increased soil nutrient stock and its availability under invasive plant species compared to uninvaded ecosystems (Myrold and Huss-Danell, 2003; Dassonville et al., 2007; Liao et al., 2008; Castro-Díez et al., 2014), but other studies show the opposite pattern (Christian and Wilson, 1999; Ehrenfeld, 2003; Lavoie, 2017). Moreover, the same species may have different impacts depending on seasonal variability (Tharayil et al., 2013) or local conditions, suggesting that the resident community and environmental factors can determine the direction and magnitude of plant invasions (Meyerson et al., 2000; Belnap and Phillips, 2001; Ehrenfeld, 2003; Vítková et al., 2015; Power and Vilas, 2020). This complexity shows that the alteration of one process does not necessarily result in changes in related processes; similarly, differences in one component of a cycle do not necessarily imply differences in linked factors (Ehrenfeld, 2003).

On the other hand, the impact of native species on soil and vegetation is also a neglected research topic, and available papers dealing with their impact on soil concern a few prominent species, such as *Calamagrostis epigejos* (e.g. Rebele, 2000; Fiala et al., 2003; Holub et al., 2012), or *Phragmites australis* (e.g. Pyšek et al., 2019, 2020a).

5.1. Impact of individual species on soil

Similarly to Hejda et al. (2021), alien invasive and native expansive species did not differ in their impacts as groups defined by origin; the differences in our study manifest rather at the level of individual species. If the studied species were pooled regardless of the origin, the factors that statistically differed among species were associated with the decomposition rate, nitrogen supply, and ability to retain water in soil (Figs. 2, 3). It needs to be borne in mind that the naturalization-invasion potential of an alien species is affected by many more traits than the change in soil properties (Aldorfová et al., 2020; Ehrenfeld, 2003), such as those related to morphology, life history, growth form and reproduction (Pyšek and Richardson, 2007; van Kleunen et al., 2010). However, the litter quality and its decomposition rate are crucial as they affect the growth conditions in a given site. Liao et al. (2008) found that invasive species had, in general, higher plant and litter N concentrations and lower litter C:N and lignin:N ratios than native species, which primarily accounted for the higher decomposition rate in invaded ecosystems. However, there are examples of invasive and expansive grasses, such as *Miscanthus ×giganteus*, *Calamagrostis epigejos*, and *Phragmites australis*, that have an opposite effect (decreasing the decomposition rate) due to a high lignin content in their tissues (e.g. Windham and Ehrenfeld, 2003; Frouz et al., 2011; Amougou et al., 2012; Waliszewska et al., 2021). In our study, individual species, be it native expansive (NES) or alien invasive (IAS), differed from each other in many traits, suggesting that the impact on soil environment is highly dependent on plant species identity.

The quality and quantity of produced litter (Šrůtek and Teckelmann, 1998; Fiala et al., 2003; Taylor, 2009; Mincheva et al., 2014; Stefanowicz et al., 2017) together with root exudates influence the activity of soil microbial communities (Lecerf et al., 2007; Suseela et al., 2016; Majewska et al., 2018). As expected, in our system the activity of soil biota (decomposition of cellulose) was fastest in litterbags with the largest mesh size and the slowest in litterbags with the smallest mesh size. The highest activity in all categories of soil biota was recorded in soil covered by the invasive *Lupinus*, followed by invasive *Telekia*. This is consistent with a study of Halvorson et al. (1991), who recorded higher microbial biomass and activity in the root zone of *Lupinus* sp. than in the zone where no roots were present. The populations of soil microorganisms were supported by larger amounts and more available forms of C and N in litter originating from activities of N-fixing symbiotic bacteria *Bradyrhizobium* in *Lupinus* root nodules (Halvorson et al., 1991; Andrews et al., 2015; Loydi et al., 2015). Such ability to utilize nitrogen can be linked to the strong competition ability of *Lupinus* on nitrogen-limiting soils.

By contrast, the lowest activity in all categories of soil biota was detected in invasive *Solidago* and native *Calamagrostis*. *Solidago canadensis* is known to inhibit the growth of many microorganisms (e.g. *Thanatephorus cucumeris*, *Rhizoctonia solani*, *Botrytis cinerea*, *Alternaria solani*) due to the release of allelopathic compounds (Zhang et al., 2009). Similarly, the presence of the congener of *S. canadensis*, *S. gigantea* is associated with a decrease in soil bacterial and increase in soil fungal biomass (Scharfy et al., 2010). The expansion of *Calamagrostis epigejos* is associated with a decrease of the number of actinomycetes, N_2 fixators and mainly microorganisms involved in cellulose decomposition (Fiala et al., 2003). This leads to the accumulation of necromass, which together with a stable and high production of above-ground biomass of *Calamagrostis*, significantly decreases the penetration of solar radiation to the soil surface. The shading effect and low soil temperatures further limit the growth of other plant species as well as the activity of soil microorganisms (Pruchniewicz and Żołnierz, 2017).

The flow of nutrients through soil microbial biomass is the driving force for N mineralization or immobilization which govern the availability of soil nitrogen; it is often reported that soil N availability, i.e. $NH_4^+$and NO_3^- concentrations increase under canopies dominated by invasive species relative to native-dominated ecosystems, even if not considering N-fixing invaders (e.g. Ehrenfeld, 2003; Liao et al., 2008; Pyšek et al., 2012b; Castro-Díez et al., 2014). The same relationship was detected in stands of some native expansive species, such as *Calamagrostis epigejos* (Fiala et al., 2003) and *Urtica dioica* (Taylor, 2009). We found that the values of nitrates were lowest under *Impatiens, Urtica* and *Lupinus* stands, and highest in *Solidago* and *Telekia* stands during the top vegetation season, from June to July. This finding corresponds to the results of Castro-Díez et al. (2014) that the impact on N pools depended mainly on functional differences among plants. *Urtica* and *Impatiens* accumulate high levels of nitrogen in their tissues (e.g. Šrůtek and Teckelmann, 1998; Andrews et al., 2005; Taylor, 2009), which explains why nitrates were missing from the soil during the period of rapid plant growth. *Lupinus* is a N-fixing plant whose foliar nitrogen is almost totally derived from N_2 fixation (Lyytinen and Lindström, 2019). According to Hirose (1971), *Solidago* transferred nitrogen efficiently in its body, therefore the absorption from the soil to create new tissues was postponed to the later part of vegetation season. The remaining nitrates in the soil thus can be utilized by other plant species and may result in an increase of biodiversity in our studied plots. Unlike *Urtica*, a lack of soil nitrogen is solved by enhancing the growth of long rhizomes in *Solidago* and *Calamagrostis* to reach up to 2 m deep and be more successful in the competition for nutrients to outcompete other plants (Myrold and Huss-Danell, 2003; Fiala et al., 2011).

5.2. Impact of alien and native dominants growing in the same habitats

Comparing dominant species in habitat-defined pairs confirmed the results of analyses involving all species. Most differences were in the decomposition rates and concentrations of soil mineral nitrogen. The concentration of iron and manganese were significantly higher in native counterparts than in invasive aliens, while other macro- and micronutrients, as well as physical soil properties, had none or only a little effect.

Using the structural categorization of studied factors, we showed that the net effect of the same species could be considerably different depending on the paired species. For example, *Phalaris* had a larger effect on macronutrients than expected in a pair with *Impatiens*, but the lowest with *Telekia* as a counterpart. Structurally and functionally, native and alien counterparts differed in many soil properties, such as *Lupinus* vs *Calamagrostis* or *Filipendula*. On the other hand, the analysis of temporal patterns did not reveal significant differences (Fig. 4c). The first pair of species is known to have structural and functional diversification influenced in the early season, namely by N-fixation in *Lupinus* and very dense above- and belowground biomass in *Calamagrostis* and *Filipendula* (Balsberg, 1982; Fiala et al., 2003). A similar seasonal trend was observed between *Reynoutria* vs *Rubus*; these species differed only at the beginning of vegetation season when *Reynoutria* rapidly builds new stems, which is accompanied by intensive nutrient uptake. Overall, their soil environment differed significantly in nine properties related to abundant litter production, chemical composition, and deep rhizome system of *Reynoutria* (Lavoie, 2017).

On the other hand, similar net effects and their temporal dynamics were recorded for *Calamagrostis* vs *Solidago* and *Telekia* vs *Rubus.* Whereas the impact of *Telekia* on soil has not been studied yet, for *Calamagrostis* and *Solidago,* some data are available (Rebele, 2000; Dassonville et al., 2007). Although both species are tall perennials with vigorous clonal growth, often coexisting in the same locality, the native grass *Calamagrostis* was reported to exclude the alien *Solidago* under certain site conditions, and dense living biomass and necromass of *Calamagrostis* further inhibited new germination and establishment of *Solidago* (Rebele, 2000). This confirms our assumption that soil under dominant species is primarily influenced by site conditions, structural and functional traits of dominant species, relationships with coexisting species, but also by their mutual interactions.

5.3. Implication for nature conservation

The current phase of the Anthropocene is characterized by a substantial transformation of the landscape, including biota, soil and land use (Lewis and Maslin, 2015). Inappropriate management of many natural and semi-natural ecosystems leading to the emergence of new habitats with a strong dominance of some species. The traditional approach to nature conservation considers the invasive spread and dominance of alien species as a threat to biodiversity, while the same processes in the case of native species are often seen as natural. However, our results suggest differently. Both invasive and expansive species colonize a wide range of environments, strongly dominate their communities, reduce diversity, change the soil environment, and homogenize species composition. Although the topic needs further research involving more species in other biomes and among other taxonomic groups, the results from our study system suggest that there is little systematic difference between the two categories of origin and the appropriate measures to preserve or restore the diversity should be the same.

With respect to the soil, it is important to prevent the accumulation of dead biomass and the increase of available nitrogen in open habitats. A thick, continuous layer of litter not only mechanically prevents the establishment of seedlings of native species but also interferes with nutrient cycling. Higher soil nitrogen availability promotes further spread of dominants with wide ecological amplitudes, altering soil processes and thus natural habitat conditions. Native species adapted to certain habitat characteristics continue to decline. A suitable method for reducing nitrogen availability under certain conditions is presented by Blumental (2009). Biological methods have also been introduced to eradicate some species (e.g. Těšitel et al., 2017).

6. Conclusions

We found that the impact of alien invasive and native expansive species on soil cannot be explained by species origin. Changes in the soil, compared to ecosystems without the given strong dominant, depend to a large extent on species identity, be it native or alien. The homogenization of the species composition is thus accompanied by the homogenization of the soil environment, in which a high spatial variability is a common feature under natural conditions. The rate and direction of these changes depend on habitat conditions, the structural and functional characteristics of the studied variables in vegetation with dominant species, and relationships with other abundant species. The decomposition rate and soil nitrogen availability were the most important factors. Dominant species can alter the rate of decomposition by changing the quality of the litter and consequently, the soil environment. These two factors should be in the focus of conservation management of valuable sites.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2023.125721.

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