



Long-term impact of *Heracleum mantegazzianum* invasion on soil chemical and biological characteristics



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ABSTRACT

Exotic plant invasions often change ecosystem properties with subsequent impacts on the structure of invaded communities. Despite an increasing knowledge of post-invasion ecosystem changes, these modifications are only rarely studied within the temporal context of ongoing invasions. In this study we investigated 19 soil chemical and biological characteristics, as well as light conditions, in uninvaded grassland sites and compared them with those from sites invaded by giant hogweed (*Heracleum mantegazzianum*) for different times (from 11 to 48 years). We further related variation in these soil and light characteristics to richness and productivity of native plant species and hogweed cover measured in the field, and to common-garden performance of hogweed grown in soil inocula from the same sites.

Hogweed presence significantly reduced red/far-red light ratios but increased soil pH. Longer invasion history was associated with increasing soil conductivity and content of extractable phosphorus. There were also parameters that displayed opposite trends in different periods of invasion such as fungal/bacterial ratios or relative amount of photosynthetically active radiation (Δ PAR). These parameters initially increased (fungal/bacterial ratio) or decreased (Δ PAR), but after reaching a certain breakpoint they tended to return to pre-invasion conditions.

Differences in native species richness were best correlated with light availability and soil pH, and productivity with composition of soil microbial communities. Differences in hogweed cover were associated with soil pH and conductivity. The variation in hogweed performance in a common garden was related to the composition of soil microbial communities, soil conductivity and light availability of sites from which soil inocula were collected.

This study documents that ecosystem properties can be altered not only by an invasion event but are further modified as the invasion proceeds. These ecosystem changes likely underlie long-term impacts of invasive plants on native communities.

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1. Introduction

Impacts of invasive plants on ecosystem processes and properties are often coupled with those on the structure and composition of resident plant communities (Levine et al., 2003; Wolfe and Klironomos, 2005; Hejda et al., 2009; Ehrenfeld, 2010; Pyšek

et al., 2012). Multiple mechanisms, including post-invasion changes in resource availability, composition of soil microbial communities or fire regimes, have been documented to reduce native species richness and modify the composition of plant communities (Levine et al., 2003). For example, species richness and abundance of native forest seedlings decreased in dense cover of *Tradescantia fluminensis*, an invasive weed in New Zealand podocarp forests, due to marked reduction of light availability (Standish et al., 2001). Two other exotic plants, *Alliaria petiolata* and *Chromolaena odorata*, were shown to suppress native plant growth by disrupting their mutualistic associations with arbuscular mycorrhizal fungi or by promoting the accumulation of soil fungal

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pathogens, respectively (Stinson et al., 2006; Mangla et al. 2007). Native shrubs in the western USA declined in communities invaded by exotic annual grasses due to an unprecedented increase of fire frequency (Mack, 1989; D'Antonio and Vitousek, 1992).

The above examples document that plant invasions can initiate ecosystem changes with significant effects on invaded communities. Invasion-altered communities may feed back (Ehrenfeld et al., 2005; Seastedt and Pyšek, 2011; Yelenik and Levine, 2011) to further modify ecosystem characteristics and thus the performance of native but also of exotic populations. These feedbacks then determine long-term dynamics within invaded communities (Bever et al., 1997; Cuddington and Hastings, 2004). For example, positive feedbacks play a role in the success of the above-mentioned example of annual grass *Bromus tectorum* (D'Antonio and Vitousek, 1992). Although it originally invaded interstices of shrubs (approximately a century ago), increased fire frequency promoted its dominance that in turn led to more fires, at the expense of native shrubland (reviewed by D'Antonio and Vitousek, 1992). In contrast, invasion-triggered ecosystem changes can promote the dominance of invaders over a short-term period, but further modification of biotic or abiotic conditions can be less favorable for the invaders than for the resident species, making co-existence of the exotics and natives possible over the long-term course (Yelenik and Levine, 2011; Tang et al., 2012).

Surprisingly, although there is a large body of evidence revealing ecosystem and community impacts of invasive plants (e.g. Simberloff, 2011; Vilà et al., 2011), for most of these systems information on the temporal scale of the changes is missing (discussed by Wolfe and Klironomos, 2005; Ehrenfeld, 2010). There are few studies that document an invader's and native population dynamics, together with changes in ecosystem properties during different time points of invasion. For example, in the Great Lakes region, Mitchell et al. (2011) surveyed wetlands invaded by exotic cattails (*Typha* sp.) for different lengths of time. They found that cattail dominance (stem density) increased linearly from the beginning of the invasion, but there was a delay of 10 years before native diversity started to decline, likely due to litter accumulation.

It also remains underexplored whether the mechanisms promoting the dominance of invaders are identical with the mechanisms causing the native species to decline. Allison and Vitousek (2004) found faster decomposition and nutrient release from invasive than native litter in Hawaii. The authors hypothesize that novel soil nutrient conditions should favor exotics at the expense of natives that are less nutrient-limited. Levine et al. (2003) pointed out, however, that the decline of native species in Hawaiian ecosystem is not necessarily due to new dynamics of nitrogen cycling, but rather due to increased levels of shading in the presence of invaders. Usually many environmental factors change simultaneously during invasion and their relative contributions to community change should be distinguished; yet they are rarely examined in concert (Hulme et al., 2013).

In this study, we examined soil biological and chemical characteristics together with light availability at five uninvaded grassland sites that served as controls for 19 sites invaded by giant hogweed (*Heracleum mantegazzianum*) for different time periods ranging from 11 to 48 years in the Slavkovský les, the Czech Republic. In these same communities, native plant richness and native productivity was reduced by hogweed invasion and this negative impact peaked in grasslands invaded for ca. 30 years. At sites with a longer invasion history both parameters tended to recover whereas hogweed cover declined linearly over the whole period assessed. Interestingly, hogweed performance in a complementary common garden experiment declined in non-sterile inocula collected at sites with a longer invasion history (Dostál et al., 2013).

Here we analyzed the effect of hogweed invasion (i.e., presence/absence) and its invasion history (i.e., time since invasion) on 19 soil and light parameters: pH (water), pH (KCl), conductivity, extractable phosphorus, carbon, nitrogen, carbon/nitrogen ratio, relative amount of photosynthetically active radiation, red/far-red light ratio, arbuscular mycorrhizal neutral lipid fatty acids (NLFA), fungal phospholipid fatty acids (PLFA), bacterial PLFAs, actinobacterial PLFAs, G+ bacteria, G- bacteria, total microbial biomass, fungal/bacterial ratio, G-/G+ ratio and ergosterol concentration. We also analyzed the effect of the invasion and of its history on the composition of soil microbial communities based on 19 PLFAs and NLFA detected at each site. We expected a post-invasion increase in available nutrients coupled with changes in soil microbial communities, but decrease in light availability.

In the second part of the study we used a subset of eight parameters, uncorrelated to each other, selected from the above characteristics, to investigate how they predict variation in native species richness and productivity, and hogweed performance that were studied by Dostál et al. (2013). We hypothesized that variation in native species richness and productivity would be related to changes in nutrient and light availabilities, whereas variation in hogweed performance would be related to differences in composition of soil microbial communities, indicating the presence of possible soil pathogen(s) of hogweed.

2. Methods

2.1. Study species

The giant hogweed (*Heracleum mantegazzianum*) is a monocarpic perennial umbellifer native to the Western Greater Caucasus (Russia, Georgia). It has spread in a number of European countries (Tiley et al., 1996; Pyšek et al., 2007b, 2008), Canada (Page et al., 2006) and the USA (Kartesz and Meacham, 1999). It may form extensive, almost monospecific stands with negative effects on biodiversity (Pyšek and Pyšek, 1995; Pergl et al., 2006; Thiele and Otte, 2007; Hejda et al., 2009). The species is rich in secondary metabolites and especially known for linear fouranocoumarins that defend the plant against herbivory (Berenbaum, 1981; Hattendorf et al., 2007) and for angular fouranocoumarins that serve as a defence mechanism against microbial infection (Ivrie, 1978; Fischer et al., 1978). Hogweed invasiveness is also attributed to allelopathic effects (Myras and Junttila, 1981) but allelopathy is probably of minor importance for its dominance (Wille et al., 2013).

2.2. Study region

We performed our research in the Slavkovský les Protected Landscape Area, located in the western part of the Czech Republic, where the giant hogweed was introduced as a garden ornamental plant in the 19th century. The species started to spread after World War II, probably due to a lack of appropriate landscape management caused by displacement of German inhabitants and establishment of a military zone (Müllerová et al., 2005; Pyšek et al., 2007c).

Müllerová et al. (2005, 2013) reconstructed the hogweed invasion dynamics in this region using a series of aerial photographs and identified sites invaded (i) in 1962 or earlier, (ii) between 1963 and 1973, (iii) between 1974 and 1991, (iv) between 1992 and 2006, together with (v) uninvaded sites. Using this information we carried out field surveys in 2010 and included 24 sites from 5 areas differing in invasion history in this study (each community type was thus represented by 5(4) replicates; see Appendix 1). We estimated mean age of the hogweed stands at each site, yielding a chronosequence of invasive populations of a differing age, i.e. (i) a

minimum of 48 years, (ii) 42 years, (iii) 28 years, (iv) 11 years and (v) 0 years (indicating hogweed-free sites).

2.3. Soil chemical characteristics

At each of 24 sites, we set up 3 transects (separated by 7 m) with three 2 × 2 m plots per transect in June 2011. At several sites we were only able to install two transects due to the linear shape of the hogweed populations growing, e.g., along road edges. The sampling was thus done in 9 or 6 plots per site. These plots served to estimate native species richness and productivity, and hogweed cover (in %) at invaded sites (see Appendix 1). During the vegetation surveys soil samples of 100 cm³ were collected from 0 to 10 cm soil profiles in the same plots; they were further pooled to obtain one composite sample per site, air-dried, sieved on 2 mm mesh and subjected to following analyses.

The pH was measured according to ISO 10390:2005 in a 1:5 (volume to volume) suspension of soil in water and soil in 0.1 M KCl using a glass electrode. The specific electrical conductivity was measured according to ISO 11265:1994 in 1:5 (weight to volume) aqueous extracts. Mehlich 3-extractable phosphorus was determined spectrophotometrically by the ammonium-molybdate ascorbic acid method at 750 nm (Genesys 10, Thermo Scientific, USA). Contents of total carbon and nitrogen were measured with a CHN elemental analyser (Carlo Erba NC2500, Italy). As the soil samples have been proved to be carbonate free by the carbonate qualitative test (known as the “fizz” test), the total carbon stands for the organic carbon fraction (Peveřill et al., 1999).

2.4. Soil microbial community

To assess the composition of soil microbial communities, soil samples of the same localities except “Lazy” area were analyzed ($n = 20$ sites; see Appendix 1). In August 2012, we set up two transects per site 14 m apart with three 2 × 2 m plots per transect separated by 10 m. In each plot we took a soil sample of 100 cm³ from 0 to 10 cm soil profiles. Samples were then pooled to obtain one composite sample per site and frozen immediately after sampling. When brought to the laboratory (1–2 days after sampling), the frozen samples were freeze-dried and sieved on 2 mm mesh prior to analyses. All analyses were performed in triplicate and mean values were used for statistical analyses.

Phospholipid (PLFA) and neutral lipid (NLFA) fatty acids were determined as biomarkers of composition of soil microbial communities. The soil was extracted by a mixture of chloroform–methanol–phosphate buffer (1:2:0.8) according to Blich and Dyer (1959). Lipids were separated into neutral lipids, glycolipids and phospholipids using silicic-acid solid-phase extraction cartridges (LiChrolut Si 60, Merck). Neutral and phospholipid fractions were collected and transesterified with mild alkaline to obtain methyl esters of respective fatty acids and these were analyzed by gas chromatography–mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA) following the method previously published in Šnajdr et al. (2008a). Methylated fatty acids were identified according to their mass spectra and quantified using a mixture of authentic chemical standards obtained from Sigma. When referring to different fatty acids, rules described in Frostegard et al. (1993) were followed.

In spite of concerns regarding the specificity of categorization by particular fatty acids, discussed for example in Frostegard et al. (2011), here we have indicated different microbial groups following subsequent criteria. These PLFAs were summed up to estimate bacterial biomass: i14:0, i15:0, a15:0, 15:0, i16:0, 16:1 ω 9, 16:1 ω 7, 16:1 ω 5, 10Me-16:0, i17:0, a17:0, cy17:0, 17:0, 10Me-17:0, 18:1 ω 7, 10Me-18:0 and cy19:0 (Frostegard and Baath, 1996; Baath

and Anderson, 2003). PLFAs 10Me-16:0 and 10Me-18:0 were used to calculate the biomass of actinobacteria (Frostegard et al., 1993). 10Me-17:0 was excluded from further analyses as it occurred at three sites only. The PLFAs i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0 were used to calculate the biomass of G+ bacteria, and 16:1 ω 7, 16:1 ω 5, cy17:0, 18:1 ω 7 and cy19:0 were used to calculate the biomass of G– bacteria (Šnajdr et al., 2008b). The PLFA 18:2 ω 6,9 was used as a marker for fungal biomass (Kaiser et al., 2010). We relied on NLFA 16:1 ω 5 to indicate arbuscular mycorrhiza rather than on PLFA 16:1 ω 5, which is a good indicator of AM in roots but not in soil (Olsson et al., 1999; Hedlund, 2002). Total content of all determined PLFA molecules was used as a measure of total microbial biomass. The fungal/bacterial ratio was calculated as fungal PLFA/bacterial PLFAs.

To support the estimation of fungal abundance, another membrane-bound substance specific to fungi, ergosterol, was extracted and determined as described in Šnajdr et al. (2008b) using a Waters Alliance HPLC system (Waters, USA) with methanol as a mobile phase at a flow rate of 1 ml/min and UV detection at 282 nm. The ergosterol content was correlated to the PLFA 18:2 ω 6,9 ($R = 0.772$, $P < 0.001$).

2.5. Measurements of light conditions

In the same plots where we sampled soil for the analysis of soil microbial community ($n = 20$ sites) we also measured light conditions. In five randomly selected positions per plot, we measured red/far-red light ratio (R/FR ratio) at 5 cm above the ground and photosynthetically active radiation at 5 cm above the ground and 20 cm above the vegetation. In further analyses, we used measured R/FR ratio, and relative amount of photosynthetically active radiation (Δ PAR) obtained by dividing light quantity above the ground by light quantity above the vegetation. Smaller values of R/FR ratio and of Δ PAR indicate the presence and proximity of neighbors competing for light (Franklin, 2008). We did light measurements using a SPh 2020 Photometer (Optické dílny ASCR, Turnov, the Czech Republic).

2.6. Statistical analyses

We performed two types of statistical analyses. First, we analyzed the effect of hogweed invasion (hogweed presence or absence) and of hogweed invasion history on soil chemical properties (pH (water), pH (KCl), conductivity, extractable phosphorus, carbon, nitrogen, carbon/nitrogen ratio), light conditions (Δ PAR, R/FR ratio) and the soil microbial community (arbuscular mycorrhizal NLFA, fungal PLFA, bacterial PLFAs, actinobacterial PLFAs, G+ bacteria, G– bacteria, total microbial biomass, fungal/bacterial ratio, G–/G+ ratio and ergosterol concentration). To explore invasion history, we used hogweed residence time, which was entered as linear or as linear and quadratic terms. Numerous studies indicate the existence of a threshold or breakpoint where natural systems respond rapidly to a relatively small change in a driver (Dodds et al., 2010; Elgersma and Ehrenfeld, 2011). Therefore we also searched for a possible threshold effect due to hogweed presence or due to hogweed invasion history. Based on visual inspection of the data, for pH (water), pH (KCl), extractable phosphorus, R/FR ratio, Δ PAR and fungal/bacterial ratio we ran an additional model with a threshold identified by an iterative search procedure (Crawley, 2007).

For each environmental variable we ran 4 or 5 linear models, including models with intercept only. The model with the best fit was identified based on AICc, Akaike Information Criterion corrected for small sample size. Each site was represented by the mean value of respective soil chemical, biological or light characteristics.

Hogweed management was initiated at six sites in 2011 leading to bias in light measurements. For these sites we therefore used values of Δ PAR and R/FR ratio obtained by regression of the two variables against estimated mean age of the hogweed stands. Prior to analyses, all environmental variables were inspected and, if necessary, square-root- or log-transformed to meet the assumptions of homoscedasticity and normality of residuals.

In addition, we performed principle component analysis (PCA) to see if the sites could be grouped based on the composition of their soil microbial communities. For that we used concentrations of all 19 phospholipid and neutral lipid fatty acids detected at each site. Further we conducted redundancy analysis (RDA) testing the effects of hogweed invasion and its history on composition of soil microbial communities. A Monte–Carlo permutation test (with 999 permutations within blocks defined by areas) was used to assess the significance of hogweed presence and of its invasion history. In both PCA and RDA analyses we used relative amounts of fatty acids within samples obtained by data centering and standardization by samples (*sensu* Lepš and Šmilauer, 2003).

Second, we searched for which of the above-mentioned soil and light parameters explained the most variation in the native community and in hogweed performance. Specifically, in the univariate analyses, as responses we used native species richness and native productivity (site means, $n = 20$) obtained during vegetation surveys in 2011 as described above (Dostál et al., 2013). As a parameter of the hogweed performance we used its cover (in %) measured in the field. We also used hogweed biomass from a common garden experiment conducted during 2010–2011. In this experiment, hogweed was cultivated in soil inocula from the sites where the above-described soil and light parameters were measured. Brief description of this experiment can be found in Appendix 2 and more details are present in Dostál et al. (2013). We decided to use this additional measure of hogweed performance because hogweed eradication started at six sites in 2011 (see Appendix 1) and the information on hogweed cover from these localities could not be used in the analyses. The second reason for using the experimental results was that we could assess the effects of soil chemical and biological characteristics on hogweed performance separately for plants cultivated in sterile (mean total biomass per inoculum origin, $n = 20$) and non-sterile inocula (mean total biomass per inoculum origin, $n = 18$). Significant effects of soil biological characteristics on hogweed performance were expected for the latter but not former treatment since Dostál et al. (2013) found hogweed biomass to decrease with the soil inoculum collected in the older hogweed stands but only if not treated by sterilization.

To avoid multi-collinearity in the analyses, only factors with correlations less than 0.7 were used as predictors (as suggested by Gujarati, 1995; see correlation matrix in Appendix 3). This reduced the potential explanatory variables to 8 parameters: pH (KCl), conductivity, extractable phosphorus, nitrogen, carbon/nitrogen ratio, Δ PAR and composition of soil microbial communities expressed by the site scores of the first and the second axes of principal component analysis, PCA axis 1 and PCA axis 2. For each response variable (field native richness and productivity, field hogweed cover, experimental hogweed biomass) we thus started with all factors (full model) and eliminated non-significant ones by likelihood-ratio test to achieve the minimum adequate model. We used linear mixed-effects models with the above-listed factors as fixed terms and area ($n = 4$; Appendix 1) as a random term. Factors were standardized to zero mean and unit variance to facilitate comparisons of effect size estimates (Schielzeth, 2010).

We also performed multivariate redundancy analysis (RDA) of native plant and soil microbial composition. In RDA of native plant composition we used identical factors as in the above-described univariate analyses. In the case of RDA of soil microbial

composition we used PCA axis 1 and PCA axis 2 site scores of vegetation, in addition to the soil chemical and light characteristics described above. The forward selection was used to test the significance of each factor by a Monte Carlo permutation test (with 999 permutations within blocks defined by areas). Only significant variables ($P \leq 0.05$) were included in the final RDA model. Data centering and standardization by samples (*sensu* Lepš and Šmilauer, 2003) was performed prior to the analyses.

All univariate analyses were performed in R version 2.14.2 (R Development Core Team, 2012). Mixed-models were done with help of R package *lme4* (Bates et al., 2012). Multivariate analyses were performed using CANOCO 4.5 (Ter Braak and Šmilauer 2002).

3. Results

3.1. Effect of hogweed invasion and its invasion history on soil chemical and biological characteristics and light availability

Hogweed invasion or its history significantly, or marginally significantly, influenced seven of the 19 soil and light characteristics measured (Table 1). The soil pH (water, KCl) was higher at invaded (pH (KCl): 5.67 ± 0.10) than intact sites (5.07 ± 0.21 ; mean \pm SE) whereas R/FR ratio decreased at invaded sites (0.47 ± 0.03 vs 0.69 ± 0.07 at uninvaded sites; mean \pm SE). Δ PAR was also reduced by 56% on average in hogweed stands in comparison with uninvaded sites but it changed during invasion history: according to the model with linear time including a threshold, Δ PAR dropped at the beginning of invasion (i.e. at sites invaded for 11 years) but increased at sites invaded for a longer time (Table 1, Fig. 1).

The model with linear time was top-ranked in predicting change in conductivity and phosphorus as both parameters increased with longer residence time of hogweed (although its effect on phosphorus was only marginally significant; Table 1, Fig. 1). Fungal/bacterial ratio changed according to a quadratic model as it increased until hogweed residence time of 28 years, when it started to decline (Table 1, Fig. 1).

Regarding the composition of soil microbial communities, the first two principal components (PCA axis 1 and PCA axis 2) explained 94.4% of the variation (Fig. 2; Appendix 4). However, the hogweed presence or hogweed invasion history were not significant predictors of differences in soil microbial community as found by RDA (not shown).

3.2. Factors correlated with native plant community structure and with hogweed performance

3.2.1. Univariate analyses

Variation in native species richness measured in the field was influenced by two factors. Specifically, diversity declined with increasing pH (KCl) and increased with greater Δ PAR. Differences in native productivity were related to the differences in soil microbial communities as productivity decreased with higher PCA axis 2 scores of soil microbial composition. The fatty acids 10Me-16:0 (actinobacteria), 16:1 ω 7 and cy17:0 (both G⁻ bacteria; Appendix 4) were found to be important due to their high PCA axis 2 scores.

Hogweed cover measured in the field was positively related to pH (KCl) but negatively to conductivity (Table 2; Fig. 3). Composition of soil microbial communities influenced hogweed performance in the common garden experiment. Specifically, the biomass of hogweed cultivated in non-sterile soil inocula was negatively correlated with PCA axis 1 scores of the communities. The high PCA axis 1 scores were found for 16:0, cy19:0 (G⁻ bacteria), i15:0 and i15:0 (both G⁺ bacteria; Appendix 4) fatty

Table 1
 Δ AICc scores for candidate models testing the effect of hogweed presence (Hogweed) or of its residence time (Time) on soil chemical and biological characteristics and light availability. Time was entered as a linear term only or as linear and quadratic terms. Six environmental parameters were also examined by the model with linear time including a threshold. Soil chemical characteristics were measured at 24 study sites and soil microbial composition and light conditions at 20 sites differing in hogweed presence and its invasion history (age of hogweed populations ranging from 11 to 48 years). Asterisks (or NS) indicate the best model (i.e., model with Δ AICc = 0) and the significance of that model is provided (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; (*), $0.05 < P < 0.10$; NS, non-significant).

	Intercept	Hogweed	Time	Time, Time ²	Time + threshold	Adjusted R ² for the best model
<i>Soil chemical characteristics</i>						
pH (H ₂ O)	1.316	(*)	1.961	1.719	2.353	0.113
pH (KCl)	4.159	*	2.159	1.957	2.918	0.212
Conductivity	11.498	9.268	***	2.905	–	0.419
Phosphorus	1.416	3.685	(*)	2.176	4.238	0.117
Carbon	NS	2.592	2.352	5.068	–	NS
Nitrogen	NS	2.599	2.244	4.724	–	NS
Carbon/nitrogen ratio	NS	2.628	2.599	5.395	–	NS
<i>Light conditions</i>						
Δ Photosynthetically active radiation	11.659	2.693	13.954	5.057	***	0.589
Red to far-red ratio	7.515	**	7.132	4.265	5.725	0.370
<i>Soil biological characteristics</i>						
NLFA16:1w5 (AM fungi)	NS	2.175	2.794	5.463	–	NS
Fungi	NS	2.790	2.673	5.656	–	NS
Bacteria	NS	2.188	2.020	5.130	–	NS
Actinobacteria	NS	0.412	2.169	4.933	–	NS
G+ bacteria	NS	1.785	2.097	5.129	–	NS
G– bacteria	NS	2.126	2.063	4.931	–	NS
Total PLFAs	NS	2.183	2.117	5.280	–	NS
F/B ratio	2.130	1.514	2.069	*	3.725	0.254
G–/G+ ratio	NS	2.793	2.670	4.767	–	NS
Ergosterol	NS	2.512	2.367	4.484	–	NS

acids, indicating their importance. Hogweed biomass was also greater in soil inocula from sites with larger Δ PAR but decreased with higher conductivity (Table 2; Fig. 3). Biomass of hogweed grown in sterile soil inocula was not related to any factor included in the model.

3.2.2. Multivariate analyses

Redundancy analysis (RDA) of vegetation composition identified Δ PAR ($F = 2.89$, $P = 0.002$) and pH (KCl) ($F = 2.21$, $P = 0.024$) to be the significant factors, explaining 19.2% and 8.6%, of the variation in vegetation composition, respectively.

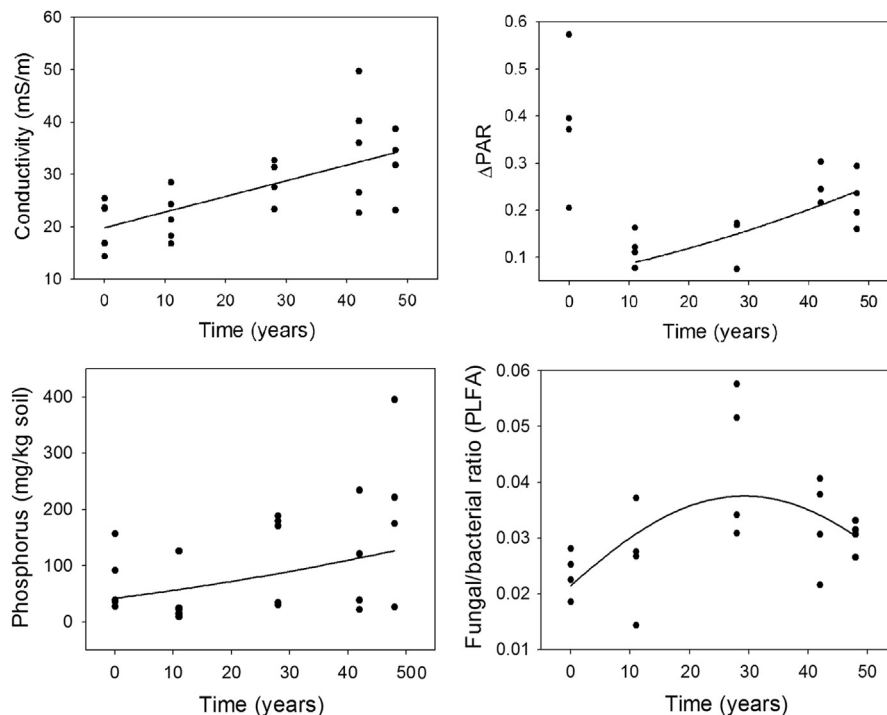


Fig. 1. Effect of hogweed invasion history on four selected characteristics measured at uninvaded (hogweed residence time = 0 years) and invaded sites (residence time from 11 to 48 years). Points are site means and fitted lines come from the top candidate model with the lowest AIC (see Table 1). Δ PAR, relative amount of photosynthetically active radiation measured as ratio of light available at 5 cm above-ground and light available above vegetation.

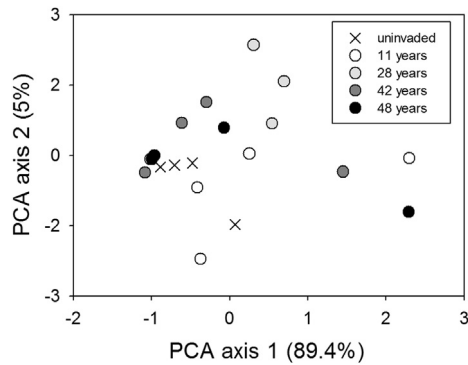


Fig. 2. PCA results for PLFA analysis of soil microbial communities of 20 sites differing in hogweed invasion history. Uninvaded sites as well as sites invaded for 11–48 years were sampled. PCA Axis 1 described 89.4% and PCA Axis 2 5.0% of variation in the data. Invasion history was not a significant predictor of the composition of soil microbiota (based on redundancy analysis).

RDA of the composition of soil microbial communities identified the carbon/nitrogen ratio ($F = 2.83$, $P = 0.043$) to be the only significant factor and explained 15.9% of the variation in the data.

4. Discussion

In this study we demonstrated significant changes in several ecosystem characteristics following the invasion of an exotic plant species, *Heracleum mantegazzianum*. Importantly, there were significant differences not only between uninvaded and invaded sites, but in several parameters the sites also differed depending on how recently they were invaded. The results of the second part of this study further suggest that some of these ecosystem properties underlie the changes in native plant communities and hogweed performance.

Table 2

An overview of minimum adequate models showing significant factors explaining variation in native species richness and productivity and in hogweed biomass. Native species richness and productivity and hogweed cover were measured at 20 study sites of 4 areas; hogweed biomass comes from a common garden experiment that used soil inocula collected at the same study sites (see Methods for more details). Factors were selected out of 8 parameters: pH (KCl), conductivity, phosphorus, nitrogen, carbon/nitrogen ratio, Δ photosynthetically active radiation, PCA axis 1 and PCA axis 2 of fatty acids compositions detected by PLFA/NLFA analysis.

	Coefficient estimate	SE	t-value	P
<i>Field measurements</i>				
Native species richness				
Intercept	33.835	1.507	22.449	<0.001
pH (KCl)	-4.462	1.369	-3.260	0.006
Δ Photosynthetically active radiation	2.898	1.336	2.168	0.048
Native productivity				
Intercept	11.965	1.533	7.806	<0.001
PCA 2 (PLFA)	-2.922	1.232	-2.372	0.032
Hogweed cover				
Intercept	58.771	3.527	16.665	<0.001
pH (KCl)	8.177	1.975	4.141	0.006
Conductivity	-5.126	2.130	-2.406	0.052
<i>Common garden experiment</i>				
Hogweed biomass (non-sterile inocula)				
Intercept	3.296	0.301	10.921	<0.001
Conductivity	-0.399	0.134	-2.984	0.012
Δ Photosynthetically active radiation	0.362	0.154	2.348	0.039
PCA 1 (PLFA)	-0.410	0.167	-2.457	0.032
Hogweed biomass (sterile inocula)				
Intercept	5.057	0.201	25.142	<0.001

As the study was based on an observational approach, we cannot distinguish whether the modification of ecosystem characteristics was due to the invasion of the exotic species with its novel traits (e.g. Wolfe and Klironomos, 2005; Wardle et al., 2011), or rather due to the loss of native species displaced from invaded communities, a phenomenon previously documented for this study system (Pyšek and Pyšek, 1995; Thiele and Otte, 2007; Hejda et al., 2009; Dostál et al., 2013). We also cannot rule out the possibility that the invasion dynamics have been determined by the environmental differences already present before the invasion started. We consider this possibility less likely, however, as invaded and uninvaded sites were shown to be similar in elevation (m a.s.l.), yearly sum of solar radiation (kWh m^{-2}) and topographic wetness index (unitless) (Dostál et al., 2013).

There are several traits of *Heracleum mantegazzianum* that differentiate this species from native plants, and by being novel to the invaded communities they could contribute to the observed ecosystem changes. First, no native grassland species from the study system reaches comparable biomass: with stem height of 200–500 cm and leaves up to 250 cm in length, it is the largest European forb (Tiley et al., 1996), restricting access to light for co-occurring plants. Second, hogweed can reach high dominance at invaded sites with cover up to 75% (Dostál et al., 2013). It is a monocarpic, deep-rooting perennial and non-clonal forb whereas intact grasslands are typically dominated by clonal perennial grasses (e.g. *Dactylis glomerata*, *Festuca* spp. and *Poa* spp.). Such contrasting life-history strategies can be associated with differences in litter decomposition rates or with variation in phenology and the vertical distribution of nutrient uptake, although direct measurements of these processes in native dominants and hogweed have not been undertaken so far. Finally, *H. mantegazzianum* produces a great diversity of secondary compounds, e.g. flavonoids, essential oils and furanocoumarins (Tiley et al., 1996; Hattendorf et al., 2007) and some of these metabolites are likely to be novel to the invaded communities. These three distinct characteristics and possibly others not mentioned here (see Pyšek et al., 2007a for a summary of traits contributing to this species' invasion success) could have been responsible for the modification of the soil environment and light conditions in the invaded communities.

4.1. Effect of hogweed presence and its invasion history on soil chemical and biological characteristics and light availability

Though the majority of measured parameters, namely those describing soil biological characteristics, were not altered by hogweed invasion, there were three principal trends with respect to the post-invasion temporal changes. First, parameters such as R/FR ratio or pH decreased and increased, respectively, in response to hogweed invasion but did not further change during the ongoing invasion. Second, invasion induced a change and this divergence from pre-invasion conditions continued as the invasion proceeded. This scenario was observed for conductivity and phosphorus. Finally, some of the measured parameters (Δ PAR, fungal/bacterial ratio) were initially altered by the hogweed invasion but tended to return to pre-invasion conditions in older hogweed stands. These different trends demonstrate that considering differences between invaded and uninvaded plots without reference to invasion history can yield a misleading picture of the invasion's impact on ecosystem characteristics. Below we discuss in detail some ecosystem parameters in the context of hogweed invasion.

The decrease in light availability (i.e. Δ PAR) and light quality (i.e. R/FR ratio) was among the most profound changes detected at invaded sites. Our findings correspond with other studies documenting reduced light levels in the understory of invasive plants (e.g. Standish et al., 2001; Reinhart et al., 2006). Dense and

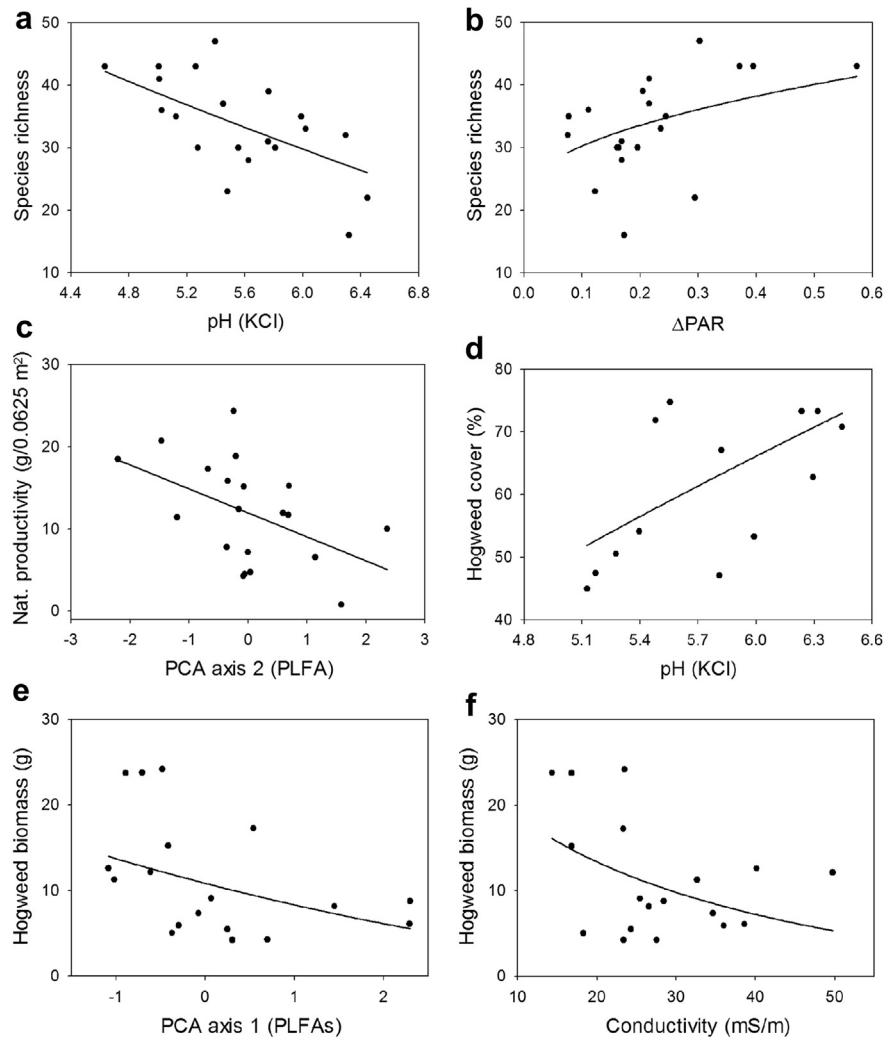


Fig. 3. Relationship of native species richness (a, b), native productivity (c), hogweed cover (d) measured in the field and hogweed performance from a common garden (e, f), and the environmental factors. Lines are fits from the minimum adequate models (all predictors significant at $P \leq 0.05$; for more details see Table 2). In the common garden experiment, hogweed was grown in non-sterile soil inocula that were sampled at sites where soil chemical and biological characteristics and light conditions were measured. Δ PAR, relative amount of photosynthetically active radiation measured as ratio of light available at 5 cm above-ground and light available above vegetation. PCA Axis 1 and Axis 2 (PLFA), site scores of soil microbial communities determined by PLFA.

extensive populations and large size resulted in only a small fraction of full light, in the most extreme conditions as little as 7.5%, reaching the ground in hogweed stands. Δ PAR tended to increase in older hogweed stands, and that likely reflects decreasing hogweed cover found in the field (Dostál et al., 2013). It must be noted, however, that in the second part of this study we failed to prove the significant relationship between hogweed cover and Δ PAR, probably due to a small sample size ($n = 13$ invaded communities).

Given the large biomass of hogweed plants we also expected an increase in soil nitrogen and carbon (Ehrenfeld, 2003; Liao et al., 2008; Vilà et al., 2011). Nitrogen and carbon content did not, however, change following the invasion. The likely reason is that although hogweed productivity compensated for the post-invasion decrease in native biomass, it did not increase the overall productivity at invaded sites (Dostál et al., 2013). It must be noted, however, that we measured the content of soil nitrogen and carbon only once during the vegetation period. Although invaded and uninvaded sites were similar in soil nitrogen and carbon, there could still be differences in the nutrient supply and uptake dynamics linked to, for example, differences in the phenology of dominant

natives and that of invasive species (Myras and Junttila, 1981; Dickens et al., 2013). Nevertheless, Dassonville et al. (2008), who analyzed soil nutrients altered by invasion of several species including *H. mantegazzianum*, also failed to find a consistent increase in soil carbon, nitrogen and other nutrients. They rather showed a site-specific impact, with nutrients increasing and decreasing at nutrient-poor and -rich sites, respectively.

The increase in phosphorus concentration at sites with a longer invasion history can be explained by nutrient uplift from deep soil layers by a deep-rooting species such as *H. mantegazzianum*, as reported by Dassonville et al. (2008). These authors also proposed that increased phosphorus can result from active mobilization by rhizospheric processes like those documented by Chapuis-Lardy et al. (2006), who found enhanced mineralization of phosphorus due to increased soil microbial activity at sites invaded by the exotic forb *Solidago gigantea*.

Similarly, conductivity also increased at sites invaded for a longer time. In a study of a related species, *Heracleum laciniatum*, elevated conductivity of root leachates was associated with phytotoxic effects (Myras and Junttila, 1981). Although here we

found greater conductivity in older hogweed stands, in a previous study from the same study sites Dostál et al. (2013) did not find the phytotoxic effects to be stronger in soil from invaded than uninvaded sites, or to increase with the residence time of giant hogweed in a site. Therefore, the link between conductivity and phytotoxicity remains unresolved.

In contrast to several previous studies (e.g. Kourtev et al., 2002; Elgersma and Ehrenfeld, 2011; Lankau, 2011) we did not find hogweed invasion or its invasion history to significantly modify the composition of soil microbial communities. The exception was fungal/bacterial ratio with a unimodal pattern during invasion history. Fungal/bacterial ratio is an important soil biological metric linked to carbon and nitrogen cycling, carbon storage and decomposition of soil organic matter (Six et al., 2006; Högberg et al., 2007; Cotrufo et al., 2009). In our study, differences in this ratio likely reflected changes in native communities and hogweed cover during its invasion history, with a linear decline of hogweed cover but unimodal change in native community richness and native productivity (Dostál et al., 2013). More experiments are needed to test, for example, how the fungal/bacterial ratio changes with varying proportions of hogweed and native species litter (e.g. Elgersma et al., 2011).

4.2. Factors correlated with native plant community structure and with hogweed performance

Whereas in the first part of this study we investigated whether and how invasion and its history changed ecosystem characteristics, in the second part we linked variation in these parameters with native community structure and hogweed performance, measured in the field and common garden experiment. We found that native species richness was positively related to aboveground resource availability, specifically to the availability of light (Δ PAR). This resource became much scarcer at the beginning of invasion but tended to increase as invasion proceeded. The increase in light availability probably explains the return of some grassland species that were initially displaced from invaded communities (Dostál et al., 2013). This explanation is supported by the significant effect of Δ PAR on vegetation composition. Soil pH, also shown to be altered by invasion, had the opposite effect on native species richness. Specifically, pH was positively correlated with hogweed cover but negatively with native species richness, and varied with native species composition. These effects on native community characteristics are hard to explain based on our data and require additional study.

Regarding hogweed performance in a common garden experiment, we showed that its biomass was negatively correlated with conductivity and positively with Δ PAR, i.e. light regimes at sites of soil inoculum origin. More importantly, the hogweed biomass was significantly related to the differences in soil microbial communities. In a previous study, Dostál et al. (2013) found decreasing hogweed biomass in non-sterile soil collected from sites with a longer invasion history but the decrease was not observed in sterile soil. We thus predicted that hogweed performance will change with the composition of soil microbiota, differentiated by the age of hogweed stands. Although the differences in the soil microbial communities were not driven by the invasion history, they significantly predicted the variation in hogweed biomass. The composition of soil microbiota was significantly related also to the productivity of native species, indicating the importance of soil biological characteristics for the variation in both the native community and invader performance. Our results, however, suggest that different microbial groups are involved in these relationships.

Findings of our study suggest that hogweed removal from the communities, although potentially complicated by a persistent soil seed bank (Moravcová et al., 2006) and long-distance seed

dispersal (Pergl et al., 2011), can immediately improve light conditions and thus favor the recovery of native species' richness. However, as we show here, native richness and productivity are also controlled by soil chemical and biological characteristics. In contrast to light availability, improvement of soil conditions following hogweed removal may be delayed, which is likely to prolong the full recovery of native communities (e.g. Zavaleta et al., 2001; Elgersma et al., 2011).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.soilbio.2013.10.014>.

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