LETTER

The impact of an invasive plant changes over time

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Abstract

Many exotic plant invaders pose a serious threat to native communities, but little is known about the dynamics of their impacts over time. In this study, we explored the impact of an invasive plant *Heracleum mantegazzianum* (giant hogweed) at 24 grassland sites invaded for different periods of time (from 11 to 48 years). Native species' richness and productivity were initially reduced by hogweed invasion but tended to recover after ~30 years of hogweed residence at the sites. Hogweed cover declined over the whole period assessed. A complementary common garden experiment suggested that the dynamics observed in the field were due to a negative plant–soil feedback; hogweed survival and biomass, and its competitive ability were lower when growing in soil inocula collected from earlier-invaded grasslands. Our results provide evidence that the initial dominance of an invasive plant species and its negative impact can later be reversed by stabilising processes.

INTRODUCTION

Exotic plant invasions may have detrimental impacts on native plant communities by reducing their native species diversity (Levine *et al.* 2003; Vilà *et al.* 2011). Exotic invaders can displace resident species through superior competitiveness or the production of novel allelochemicals (Vilà & Weiner 2004; Lankau *et al.* 2009; but see Dostál 2011). The dominance of exotic species at the expense of native plants is also often explained by the modification of nutrient and material fluxes within the invaded community (Ehrenfeld 2003; Levine *et al.* 2003).

The impact of an invasive species does not necessarily remain constant over the course of invasion (Strayer *et al.* 2006; Strayer 2012), and both ecological and evolutionary processes may increase or attenuate the impact of invaders on the resident community. For example, Mitchell *et al.* (2011) found fewer native species in older vs. younger stands of exotic cattails (*Typha* sp.) due to an increasing litter layer. In contrast, the cover of native woody species in the forest understory invaded by *Alliaria petiolata* increased in sites where invasive populations were present for a long time, which was attributed to them losing an advantage due to becoming less allelopathic (Lankau *et al.* 2009). Similarly, selection for native genotypes tolerant to allelopathy can equalise the fitness of invaders and that of resident species (Callaway *et al.* 2005).

Along with these equalising processes, the coexistence of resident and invasive species depends on stabilising processes such as the density-dependent specialist enemy attack (Janzen 1970; Connell 1971; Chesson 2000; MacDougall *et al.* 2009). The initial advantage of exotic species due to missing enemies may translate into improved performance (Keane & Crawley 2002; Reinhart *et al.* 2003; DeWalt *et al.* 2004) and, most likely, also into local dominance at the expense of native species. Over the course of invasion, however, specialist pathogens or herbivores, subsequently introduced

from the previous range (Zangerl & Berenbaum 2005) or recruited from native pests (Carroll *et al.* 2005), are expected to reduce the dominance of the invader, facilitating the recovery of the native species (Flory & Clay 2013). Simberloff & Gibbons (2004) list several examples of boom-and-bust cycles of invaders' populations in their new ranges together with changes in their impact, and hypothesise that diseases could be the proximal cause of the collapse of the invaders. To date, there are several examples of increased enemy richness and control over the performance of exotic species that have colonised novel ranges at an earlier time (Hawkes 2007; Diez *et al.* 2010; Mitchell *et al.* 2010). To our knowledge, however, there are no rigorous data documenting pest accumulation and a subsequent modification of the invaders' impact along an invasion chronosequence (see discussion in Strayer 2012).

Heracleum mantegazzianum Sommier & Levier (giant hogweed) is a stout, up to 5 m tall, monocarpic perennial umbellifer native to the western Greater Caucasus that was introduced to Europe in 1817 (Jahodová *et al.* 2007). Following its introduction, it became invasive in a number of European countries, including the Czech Republic (Pyšek *et al.* 2012). Giant hogweed predominantly invades grasslands, where it can form large and dense stands and significantly reduce native species richness (Thiele & Otte 2007; Hejda *et al.* 2009) due to the reduction in light availability and changes in soil properties (Thiele *et al.* 2010). Hogweed also produces allelopathic compounds (Junttila 1975), yet its significance in competitive interactions remains to be proven.

In this study, we used spatially explicit knowledge of the invasion of giant hogweed in the western part of the Czech Republic, which was derived from a sequence of aerial photographs previously used to analyse the dynamics of invasion in this region (Müllerová *et al.* 2005, 2013; Nehrbass *et al.* 2007). The mapping of invading populations in particular years made it possible to perform vegetation surveys at sites invaded for different periods of time. At the same

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sites, we also sampled soil inocula for an experiment to evaluate the effects of soil biota on hogweed and native species performance and competitive ability. Our goal was to test the hypothesis that native species richness and native biomass production will be most reduced in recently invaded communities but will recover in older hogweed stands. If true, we hypothesised that this pattern was driven by the accumulation of soil pathogens in the older hogweed stands, thus reducing hogweed performance and/or its competitive ability.

METHODS

Survey of plant communities

We performed vegetation surveys in the Slavkovský les Protected Landscape Area, which is located in the western part of the Czech Republic (Fig. 1). Hogweed was introduced to this region as an ornamental plant in 1862 but began to spread massively only after WWII, presumably as a consequence of the lack of appropriate grassland management after the displacement of the German popu-
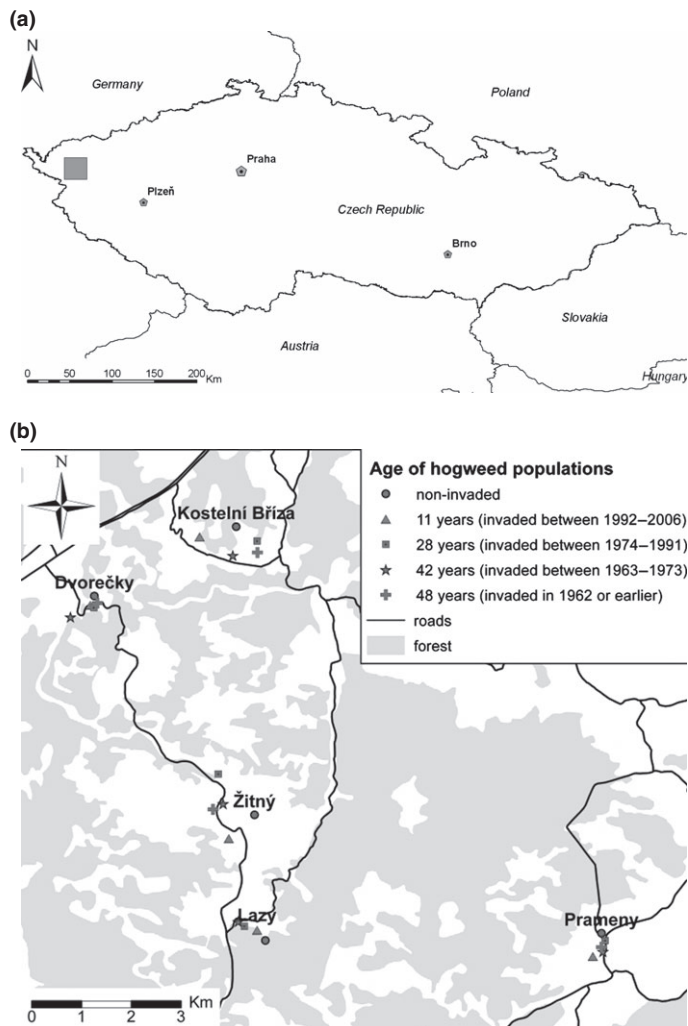

(a)

(b)

Figure 1 (a) Map of the Czech Republic with a square indicating the study location. (b) Map of the sites included in the study. Within each area, there were uninvaded grasslands and grasslands invaded for 11 to 48 years.

lation (Pyšek 1991). To obtain the information on sites invaded for different periods of time, we used data explored in the study by Müllerová *et al.* (2005, 2013), who reconstructed the hogweed invasion dynamics in this region over the past 50 years using a series of aerial photographs. We chose five areas (Fig. 1; Appendix S1) and in each of them identified grassland sites that were invaded (1) in 1962 or earlier, (2) between 1963 and 1973, (3) between 1974 and 1991, (4) between 1992 and 2006 and (5) were free of hogweed prior to 1962 and remained uninvaded until 2006. These intervals were further classified by the estimated mean age of the hogweed stands, yielding a chronosequence of invasive populations of differing age, i.e. (1) a minimum of 48 years, (2) 42 years, (3) 28 years, (4) 11 years and (5) 0 years (indicating hogweed-free sites). Mean age of 42 years, e.g. was calculated as $(2010-1963+2010-1973)/2$, with 2010 being the year when this study was initiated and 1963 and 1973 the years when aerial photographs were taken.

In 2010, sites were surveyed for the presence or absence of hogweed. In total, we included 24 sites of five different invasion histories as outlined above, each represented by five (or four) replicates (Fig. 1; Appendix S1). We assumed independent invasion dynamics within the individual areas; this assumption is justified by the maximum distance between sites within the areas being 1316 m (mean = 491.3 m; SD = 305.3 m) and the minimum distance between the area centres 2497 m (mean = 6935.3 m, SD = 2951.8 m). We also assumed that the sites involved in this study were similar in environmental conditions prior to the invasion because the historical aerial photographs indicate that the sites now colonised by hogweed used to be managed grasslands, as are the hogweed-free sites at present. However, as in all space-for-time-substitution studies, we cannot rule out the possibility that the pre-invasion differences in the abiotic and community characteristics also influenced the hogweed invasion and its temporal dynamics (see Appendix S2 for more details).

During the vegetation peak in June 2011, we determined plant species composition and species cover (in %). At each of the 24 sites, we installed three transects separated by a distance of 7 m, with three 2×2 m plots per transect; the centres of the neighbouring plots were 7 m apart. At the sites with hogweed populations present, we located the grid in the middle of the hogweed stands. 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 nine or six plots per site.

The species data collected in all plots at a particular site were pooled for further analyses. For each site, we calculated the cumulative number of native species (S, species richness), the Shannon diversity index (H') and evenness (J'), which was calculated as $H'/\ln S$ (Magurran 1983). Shrub and tree species were excluded from the data set ($n = 11$ species), as were the four neophytes (alien species introduced since the end of the Medieval Period) from a set of 155 species that were recorded during a vegetation survey. The mean species cover was used for the calculation of H' and J'. Diversity of sites represented by six plots was not significantly different from diversity of sites where nine plots were sampled ($P > 0.5$ in all three diversity parameters).

At the same time, we also harvested the native species biomass 2 cm above the ground in 25×25 cm squares located in each plot. The biomass was then dried to a constant mass at 70 °C. In addition, we harvested the hogweed biomass in three 2×2 m plots

at the invaded sites for a total productivity analysis (i.e. sum of mean native and hogweed biomass), with the value recalculated for an area of $0.0625 \ m^2$. The biomass sampling was performed prior to the any mowing or grazing applied by managers at the hogweed-free sites.

We also used the same plots to calculate the mean hogweed cover at the invaded sites. All invaded sites were free of any management during the community selection in 2010, but a hogweed eradication campaign was initiated at six sites in 2011 prior to data collection (see Appendix S1). We included native community measurements but not hogweed cover measurements (and total biomass) from these six sites in our further analyses.

Common garden experiment

In addition to the vegetation survey, at 20 sites, we sampled soil blocks along four transects (5 m apart) with 10 sampling points each (5 m apart) during late June 2010 (Appendix S1; soil sampling was not performed in the 'Lazy' area). The sampled blocks were approximately $10 \times 10 \times 8$ cm in size. At certain sites, we were able to install two transects only; in such cases, the soil was sampled at 20 sampling points per transect.

The soil from the same site was then bulked, homogenised and sieved through a 10-mm mesh to remove large stones and roots. Half of the soil from each site was sterilised by 25 kGy gamma irradiation, and the other half was left untreated; both were mixed with sterile sand in a 2 : 3 ratio. The sterilization treatment was crossed with the addition of activated carbon to control for possible hogweed allelopathic effects (Junttila 1975), adding 20 g of carbon per litre of substrate mixture (particle size of 0.075 mm; Resorbent, Ostrava, Czech Republic). The factorial manipulation of sterilization and activated carbon gave four soil treatments.

The soil treatments were combined with three planting schemes. In 2.5 l pots, we added either (1) one hogweed seedling alone, (2) a mixture of native seed or (3) one hogweed seedling along with the native seed mixture. Hogweed seedlings were obtained in the field and their roots were surface-sterilised with 2% bleach for one hour. Each seedling was also measured for root length and width to estimate its below-ground biomass; the product of the two measured parameters effectively predicted the root biomass ($R^2 = 0.737$, $P < 0.001$; based on $n = 20$ seedlings). The native seed mixture consisted of forbs *Plantago lanceolata* and *Centaurea jacea* (10 seeds each) and 20 seeds of *Dactylis glomerata* (grass). These are native grassland species observed to occur in the study area, with *D. glomerata* being the most abundant and *C. jacea* the rarest plant species. *Dactylis glomerata* was found in all of the communities whereas *P. lanceolata* and *C. jacea* tended to occur at uninvaded sites or at those harbouring old hogweed stands. The native seeds used in the experiment had no prior contact with hogweed (purchased from Planta Naturalis, Sobotka, Czech Republic), i.e. the results of the experiment were not confounded by possible evolutionary adaptations of the native species to hogweed.

The experiment was initiated in early July 2010 and consisted of 480 pots (20 sites of soil origin × four soil treatments × three planting schemes × two replicates) randomly placed in beds of the experimental garden of the Institute of Botany in Průhonice, Czech Republic (49°99′N, 14°57′E). In addition, we prepared four replicates per site that were left untreated and without native seed addition to check for the presence of the three native species in the

soil inoculum; no seedlings of the native mixture germinated in these controls. The experiment was maintained by watering, if necessary, and by fertilization using 0.25-strength Hoagland solution, 100 mL per litre of substrate, which was performed biweekly until the end of September 2010 and again from early May 2011 until mid-July 2011, when the experiment was terminated. The hogweed seedlings that died during the first month of the experiment were replanted. The pots were weeded regularly to remove non-sown species.

We recorded the number of native germinants by the end of August 2010 and hogweed survival by mid-October 2010, early May 2011 and mid-July 2011. We separately harvested the above-ground biomass for each species in mid-October 2010. In mid-July 2011, we performed the final harvest and sampled the above-ground biomass separately for each species and the below-ground biomass separately for hogweed and the natives. The biomass was dried at 70 °C. Herein, we report the total native and hogweed biomass and the hogweed survival recorded during the final harvest.

Statistical analyses

Survey of plant communities

First, we analysed the effect of hogweed invasion (i.e. of hogweed presence/absence at the sites) on native species richness and productivity. Within invaded sites, we tested the effect of hogweed cover on richness and productivity. We used linear mixed models with area as random effect.

Second, we tested the effect of invasion history (time since community invasion) on the native species diversity (expressed as the species richness, H' and J'), native productivity and total productivity. In addition, we tested whether the invasion history was a significant predictor of the variation in native species composition. For the latter, we used detrended correspondence analysis (hereafter DCA) to calculate the axis 1 and axis 2 (that explained 19.8 and 12.0% of the variance respectively) site scores from the species composition data (with species cover included). We also analysed hogweed cover at sites differing in invasion history.

We ran three models for each of the above eight response variables (see also Appendix S3), one with the time variable entered as a linear term only, another one with both linear and quadratic terms for time, and the third one with intercept only. We used linear mixed models to test for the fixed effects of time, with area included as a random effect. The statistical significance of the fixed effects was estimated using likelihood ratio tests, and the model with the best fit was also identified based on Akaike's Information Criterion.

Common garden experiment

We searched for effects of soil origin (i.e. for differences between soils with different invasion histories measured as time since the site was invaded), sterilization, the addition of activated carbon, and competition on the performance of hogweed and that of native plants. We analysed hogweed survival and total biomass, separately for hogweed and the native species, harvested in mid-July 2011.

We constructed a full model that included all four treatments as the main and interacting effects (entered as fixed effects), producing a four-way interaction model. Area and site nested within area were included as random effects. Likelihood ratio tests were used to estimate the statistical significance of main effects and their interactions,

and to obtain a minimum adequate model. Binomial errors were used in the models for hogweed survival.

For the total hogweed biomass, we ran an additional model using the mean biomass per site of inoculum origin (instead of the biomass from individual pots used in the above-described models). Time, sterilization and their interaction were used as predictors (fixed effects), with area included as random effect.

In the analyses of hogweed survival and biomass, the initial root biomass of the hogweed seedlings from early July 2010 was entered as a covariate, $\log(x \times 1000)$-transformed.

The hogweed total biomass was square-root-transformed to meet the assumptions of homoscedasticity and normality of residuals. The outliers [determined by the $1.5 \times$ interquartile range (IQR) rule] for the hogweed ($n = 5$ values) and native total biomass values ($n = 3$) were replaced by the mean values. Alternative models with outliers retained or removed yielded similar results (data not shown) as those with outliers replaced by the mean. The native mixtures initially planted with hogweed that died by May 2011 were entered in the analysis as hogweed-free (competition-free) pots based on the observation that hogweed had no effect on the native above-ground biomass during the harvest in mid-October 2010 ($p = 0.387$). Raw data can be found in Appendix S5.

Mixed-effects models were developed using R version 2.14.2 (R Development Core Team 2012), specifically with the R packages *lme4* and *nlme* (Bates *et al.* 2012; Pinheiro *et al.* 2012). Marginal R^2 (proportion of variance explained by the fixed factors alone) and conditional R^2 (proportion of variance explained by both the fixed and random factors) were calculated according to Nakagawa & Schielzeth (2013). DCA was performed using CANOCO (ter Braak & Šmilauer 2002).

To assess the native community recovery in invaded sites, we used measurements at uninvaded sites as a reference point. We also included soil inocula from uninvaded sites in the experiment to estimate the effects of initial soil conditions. Including uninvaded sites could, however, prevent the detection of temporal changes within invaded sites as the dynamic view of invasion impacts predicts (Strayer *et al.* 2006). To overcome this problem, we repeated the analyses with measurements from invaded sites only, and also with plants grown in soil inocula originating from there.

RESULTS

Survey of plant communities

Hogweed invasion was correlated with low native species richness: we found 40.8 ($\pm$ 1.4 SE) species at hogweed-free sites, whereas communities colonised by *H. mantegazzianum* hosted an average of 31.3 ($\pm$ 1.6 SE) species (t-value $= -2.975$, $P = 0.004$). The invaded communities were also less productive in terms of native biomass (18.2 $\pm$ 2.2 g vs. 10.8 $\pm$ 1.2 SE g of dry biomass/0.0625 m^2 (mean $\pm$ SE) in uninvaded vs. invaded communities; t-value $= -3.122$, $P = 0.004$) but not in terms of the total biomass (18.2 $\pm$ 2.2 g vs. 16.4 $\pm$ 1.3 g of dry biomass/0.0625 m^2 (mean $\pm$ SE) in uninvaded vs. invaded communities; t-value $= -0.516$, $P = 0.54$). Within invaded sites, greater
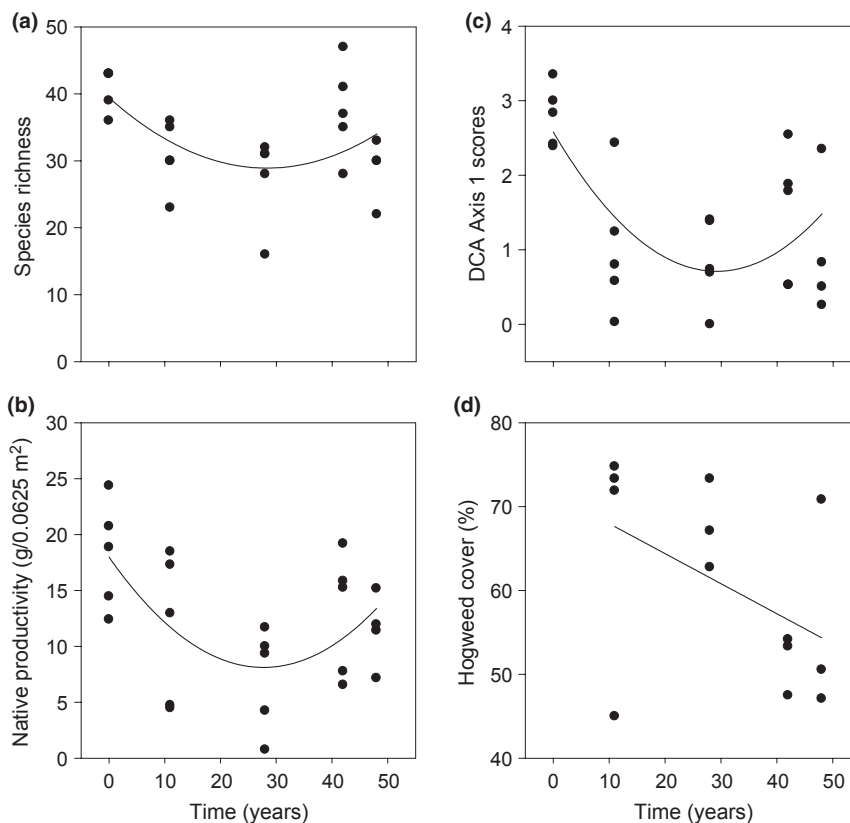

Figure 2 Regression of species richness (a), native productivity (b), community composition (as DCA axis 1 scores; c) and hogweed cover (d) against the time since the sites ($n = 24$) were invaded by hogweed *Heracleum mantegazzianum*. The best fits included linear and quadratic terms for time (both always significant at $P \leq 0.05$) in (a–c) and a linear term for time ($P = 0.046$) for (d). Time $= 0$ years indicates uninvaded sites.

hogweed cover reduced both the species richness (*t*-value = −1.983, *P* = 0.088) and native productivity (*t*-value = −2.288, *P* = 0.056), though the effect was only marginally significant.

The impact of hogweed changed during its invasion history. The best fit models in the analysis of hogweed impact included both linear and quadratic terms for the time since community invasion. Specifically, the native species richness and productivity consistently decreased with time from the beginning of invasion; they were most strongly reduced in the 28-year-old stands but increased again in the older populations (Fig. 2a, b; Appendix S3). This unimodal pattern was also found for Shannon diversity *H′* and DCA axis 1 scores of the community composition data (Fig. 2c). Evenness *J′*, total productivity and DCA axis 2 scores were, however, similar across the sites of different invasion history (Appendix S3).

Maximum hogweed cover (66.2 ± 7.1%, mean ± SE) was recorded in the earliest invasion stage, in 11-year-old stands, but declined linearly with the time since invasion (*P* = 0.046), reaching 56.2 ± 7.4% in the 48-year-old populations (Fig. 2d; Appendix S3).

Common garden experiment

Of the 320 hogweed seedlings that were initially planted, one hundred and sixty-one survived until mid-July 2011. The survival was reduced by competition (*z*-value = −6.121, *P* < 0.001; Appendix S4), the effect of which was further modified by sterilization (competition × sterilization: *z*-value = 4.149, *P* < 0.001): without competition, more plants survived in the sterile (*n* = 59 plants) than non-sterile substrate (*n* = 44 plants). In the presence of native species, twice as many hogweed plants survived under the non-sterile condition than in pots with the sterile inoculum (38 vs. 20 plants). Although the biomass of native species grown with hogweed was larger in sterile than non-sterile inocula (18.7 ± 0.8 g vs. 13.4 ± 0.7 g, mean ± SE) and could thus have a more detrimental effect on hogweed survival, the effect of sterilization treatment remained significant even if the native biomass was used as a covariate (*z*-value = 2.272, *P* = 0.023). Survival was also less likely in the substrate with activated carbon (*z*-value = −2.198, *P* = 0.028).

Consistent with our hypothesis, soil inocula collected at sites with longer invasion history had a greater negative effect on the survival of hogweed plants. Importantly, this trend was found in pots with non-sterile inoculum only (time × sterilization: *z*-value = −2.515, *P* = 0.012; Fig. 3a). Addition of activated carbon modified this relationship (see Fig. S1 in Appendix S4) as indicated by a marginally significant three-way interaction (activated carbon × time × sterilization: *z*-value = −1.896, *P* = 0.058). When analysed separately, a significant time × sterilization interaction was detected in pots without addition of activated carbon but not in pots with carbon (Appendix S4).

The hogweed total biomass was smaller in pots with the non-sterile (13.8 ± 1.6 g) than sterile inoculum (28.8 ± 2.4 g, mean ± SE; *t*-value = −4.698, *P* < 0.001) and was also reduced by the competition with native species (*t*-value = −8.407, *P* < 0.001; Appendix S4). When the hogweed total biomass (taken as the mean per site of inoculum origin) was regressed against the invasion history in an additional model, a pattern similar to that for hogweed survival was found: plant size decreased with the soil inoculum collected in the older hogweed stands but only if not treated by sterilization (a marginally significant time × sterilization interaction: *t*-value = −1.960, *P* = 0.059; Fig. 3b, Appendix S4).
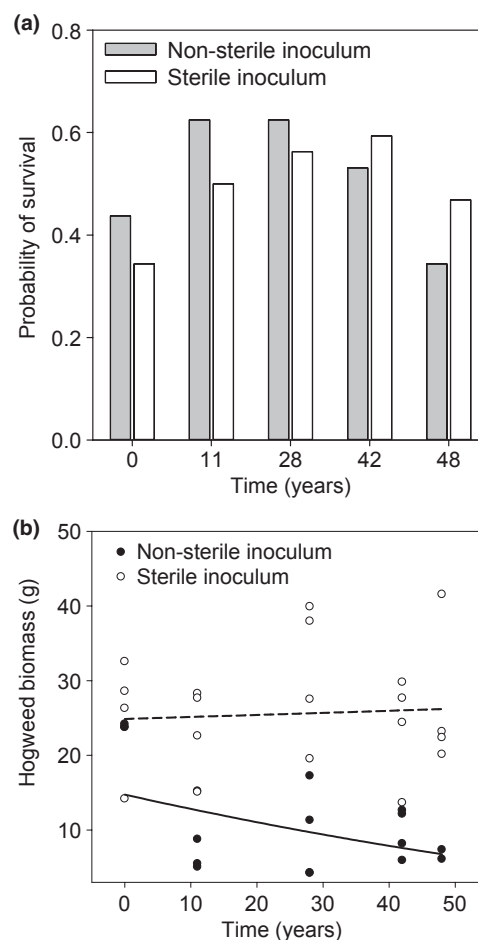

Figure 3 Survival probabilities (a) and total biomass (b) of hogweed plants by July 2011 in the common garden experiment. The plants were grown in substrates that included non-sterile and sterile soil inocula sampled from sites with different invasion histories (including uninvaded sites and sites invaded for 11 to 48 years). In (a), hogweed plants were less likely to survive in non-sterile inocula sampled at sites invaded for longer time (*P* = 0.012 of time × sterilization interaction). In (b), biomass (mean per site of inoculum origin) decreased with longer invasion history, but in non-sterile (full line) rather than sterile inocula (dashed line; *P* = 0.059 of time × sterilization interaction).

The native total biomass was reduced in pots with the non-sterile (13.5 ± 0.5 g, mean ± SE) compared to the sterile inoculum (18.9 ± 0.5 g, mean ± SE; *t*-value = −7.683, *P* < 0.001). Hogweed presence also decreased the biomass of native species (*t*-value = −2.526, *P* = 0.012), but its competitive effect was dependent on the origin of the soil inoculum. Specifically, when grown with the invader, the native biomass increased with inocula collected at sites with longer invasion history (time × competition: *t*-value = 2.382, *P* = 0.018; Fig. 4, Appendix S4). The significant time × competition interaction associated with native biomass was mostly due to plants grown in sterile rather than non-sterile inocula (Appendix S4). Further, the effect of time on the biomass of native species was independent of the biomass of hogweed plants (treated as a covariate) growing together with natives (*t*-value = 2.262, *P* = 0.045).

Re-analysing the data with invaded communities only

When uninvaded sites were excluded from the analyses of field community measurements, evenness *J′* (Fig. S1 in Appendix S3) and
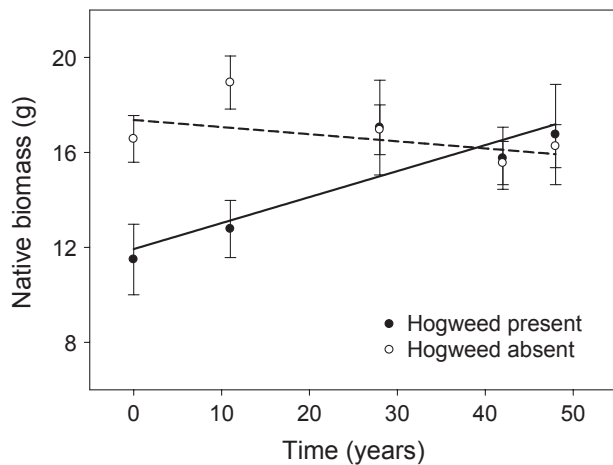
Figure 4 The native total biomass (mean ± SE) grown with (full line) and without (dashed line) hogweed in a common garden experiment. The presence of hogweed significantly (*P* = 0.012) reduced the native biomass, but its competitive effect was dependent on the invasion history of the community from which the soil inoculum was sampled (*P* = 0.018 of time × competition interaction).

Shannon diversity index increased with the age of hogweed stands (although the effect was only marginally significant in case of the latter parameter). Variation in all other parameters including species richness and composition (DCA axes scores) was not, however, related to the invasion history (Appendix S3).

Regarding the experiment, similar temporal trends as those found for a complete data set were indicated for hogweed survival and native species' biomass but not for hogweed total biomass (with mean per site of inoculum origin; Appendix S4).

DISCUSSION

The rapidly growing interest in biological invasions is closely associated with their potential impact on native communities (Levine 2008). In most studies, the impact is usually derived from a comparison of invaded and invasion-free plots of presumably similar environmental conditions (e.g. Hejda *et al.* 2009) without further reference to the invasion history. However, such an approach cannot properly estimate the long-term effects of the invader on the native community, as these can change over time (reviewed by Strayer *et al.* 2006). In accordance with this argument, we found that the hogweed impact on the diversity and productivity of native species is dynamic: the invader exerted the strongest effect on native communities in the early stages of invasion, up to approximately 30 years, with the impact diminishing after 40–50 years since the beginning of invasion. We showed that temporal changes occurred also within invaded sites only as the evenness and Shannon diversity index increased linearly since the beginning of the invasion. There was, however, little evidence for an increase of species richness or change in species composition in older hogweed stands when uninvaded sites were excluded from the analyses.

Changes in the hogweed impact are likely associated with the decreasing dominance of this species in the invaded communities over time. Our results indicate that hogweed cover in the oldest populations (48 years old) was smaller by 10% than at the begin-

ning of invasion (11 years), with 66% cover on average. Müllerová *et al.* (2005) analysed the same chronosequences derived from aerial photographs and recorded that hogweed patches reached their maximum size after 20–25 years but decreased later on. Nehrbass *et al.* (2006) used a modelling approach and demonstrated that the probability of sampling negative population growth of hogweed increased with time since first invasion, which also supports observed declines in hogweed cover over time. The ongoing process of native community recovery in less dense hogweed stands corresponds to findings of Thiele *et al.* (2010) who showed that cover of 50% (i.e. similar to that in the oldest stands of our study) was the threshold above which the adverse effects of hogweed on native species richness start to manifest. Studies from other invaded communities also support the view of a greater negative impact being associated with increasing exotic dominance (e.g. Ortega & Pearson 2005).

The second, experimental part of our study indicated a possible explanation for hogweed decline and recovery of the native community. Specifically, we showed that the survival and biomass of hogweed decreased most markedly when growing in the soil from sites with the longest invasion history. Importantly, the relationship of hogweed performance and invasion history was detectable in the non-sterile rather than sterile soil. This indicates that hogweed performance was controlled by soil pathogens but their effect depended on the number of successive generations of hogweed occupying the same site (e.g. Packer & Clay 2004). As the negative plant–soil feedback is likely to develop slowly, hogweed can grow in high densities at sites invaded for a short time. With increasing number of hogweed generations, soil pathogens accumulate and increase their control over the hogweed performance. Alternatively, pathogens may have evolved a stronger virulence over time, reducing thus the hogweed density. A similar negative plant–soil feedback was demonstrated for *Sapium sebiferum*, a successful woody invader in southeastern USA, that showed less survival and biomass in soil collected near con- than heterospecifics (Nijjer *et al.* 2007). Nijjer *et al.* (2007) assume that this negative feedback may decrease *Sapium* persistence in invaded communities by limiting self-replacement, but unlike in our study, the authors do not provide a temporal framework of the expected invader's decline.

We hypothesise that the increasing hogweed dieback in soil with a long invasion history is a key for native species recovery. This process is likely to be further strengthened by decreasing competitive effects of hogweed, as native plants grown with the invader increased in soil occupied for a longer time. In this case, however, soil abiotic rather than biotic components drove the relationship as the variation in hogweed competitiveness was detected for sterile inocula only. These soil abiotic effects persisted in the pots fertilised by Hoagland solution, a treatment that we applied to control for chemical differences among different soil inocula as well as for side effects of soil sterilization (Troelstra *et al.* 2001). Still, soil chemical differences influenced the results, probably due to the relatively high ratio of soil inocula to sterile sand. The use of sterile field soil would probably be more appropriate in this case. There were also side effects of activated carbon intended to control for possible allelopathic effects (e.g. Callaway *et al.* 2005) that were previously documented for hogweed (Junttila 1975). We did not detect phytotoxicity in our study but the activated carbon reduced hogweed survival and modified the effect of soil inoculum on the survival. It is possible, although not proved yet that increased

hogweed mortality in pots with carbon was due to reduced infection with arbuscural mycorrhiza as reported for *Senecio inaequidens* (Weißhuhn & Prati 2009). These authors also found substantial changes in soil chemistry after carbon addition. These changes could also have direct negative effects on hogweed survival. Altered soil chemistry could also outweigh the invasion history-dependent effects of soil microbiota on hogweed performance. Therefore, these possible confounding effects of experimental treatments must be born in mind when interpreting the results of the common garden study.

Our results constitute a rare empirical demonstration that a negative plant–soil feedback (Bever *et al.* 1997), as an example of a stabilising process (Chesson 2000; MacDougall *et al.* 2009), can reverse the initial negative impact of an aggressive invader on native resident species, resulting in their coexistence later on (Flory & Clay 2013). These results provide more sophisticated guidance to prioritise populations for control than recommendations based simply on invader's cover or population size; sites with a shorter invasion history should be prioritised in hogweed management. This should not be taken as an incentive for a 'do-nothing' strategy in invasive plant management, based on the argument that sites with a longer invasion history would recover spontaneously. First, even less vigorous, older hogweed populations represent obstacles for landscape management since after 50 years they still reach rather high cover, and serve as a seed source for invasions of intact sites (Nehrbass *et al.* 2007). Second, given the coupled oscillatory population dynamics of plants and their pests (Olff *et al.* 2000; Van der Putten 2003), the ongoing decline in hogweed cover may be followed by pest retreat, which, in turn, may allow hogweed population recovery. Therefore, dynamic processes regulating hogweed populations can rather be utilised as a complementary tool in informing large-scale systematic management, but not a management approach to avoid persistent ecological damage.

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REFERENCES

Bates, D., Maechler, M. & Bolker, B. (2012). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. Available at: http://CRAN.R-project.org/package=lme4. Last accessed 12 October 2012.

Bever, J.D., Westover, K.M. & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J. Ecol.*, 85, 561–573.

ter Braak, C.J.F. & Šmilauer, P. (2002). *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca NY, USA.

Callaway, R.M., Ridenour, W.M., Laboski, T., Weir, T. & Vivanco, J.M. (2005). Natural selection for resistance to the allelopathic effects of invasive plants. *J. Ecol.*, 93, 576–583.

Carroll, S.P., Loye, J.E., Dingle, H., Mathieson, M., Famula, T.R. & Zalucki, M.P. (2005). And the beak shall inherit: evolution in response to invasion. *Ecol. Lett.*, 8, 944–951.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations.* (eds den Boer, P.J., Gradwell, G.R.). Centre for Agricultural Publishing and Documentation, Wageningen, The, Netherlands, pp. 298–312.

DeWalt, S.J., Denslow, J.S. & Ickes, K. (2004). Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta. Ecology*, 85, 471–483.

Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecol. Lett.*, 13, 803–809.

Dostál, P. (2011). Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *Am. Nat.*, 177, 655–667.

Ehrenfeld, J.G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6, 503–523.

Flory, S.L. & Clay, K. (2013). Pathogen accumulation and long-term dynamics of plant invasions. *J. Ecol.*, 101, 607–613.

Hawkes, C.V. (2007). Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *Am. Nat.*, 170, 832–843.

Hejda, M., Pyšek, P. & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.*, 97, 393–403.

Jahodová, S., Trybush, S., Pyšek, P., Wade, M. & Karp, A. (2007). Invasive species of *Heracleum* in Europe: an insight into genetic relationships and invasion history. *Divers. Distrib.*, 13, 99–114.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.

Junttila, O. (1975). Allelopathy in *Heracleum laciniatum*: inhibition of lettuce seed germination and root growth. *Physiol. Plant.*, 33, 22–27.

Keane, R.M. & Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.*, 17, 164–170.

Lankau, R., Nuzzo, V., Spyreas, G. & Davis, A.S. (2009). Evolutionary limits ameliorate the negative impact of an invasive plant. *Proc. Natl Acad. Sci. USA*, 106, 15362–15367.

Levine, J.M. (2008). Biological invasions. *Curr. Biol.*, 18, 57–60.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B*, 270, 775–781.

MacDougall, A.S., Gilbert, B. & Levine, J.M. (2009). Plant invasions and the niche. *J. Ecol.*, 97, 609–615.

Magurran, A.E. (1983). *Ecological Diversity and its Measurement*. Croom Helm, London.

Mitchell, C.E., Blumenthal, D., Jarošík, V., Puckett, E.E. & Pyšek, P. (2010). Controls on pathogen species richness in plants introduced and native ranges: roles of residence time, range size and host traits. *Ecol. Lett.*, 13, 1525–1535.

Mitchell, M.E., Lishawa, S.C., Geddes, P., Larkin, D.J., Treering, D. & Tuchman, N.C. (2011). Time-dependent impacts of cattail invasion in a Great Lakes coastal wetland complex. *Wetlands*, 31, 1143–1149.

Müllerová, J., Pyšek, P., Jarošík, V. & Pergl, J. (2005). Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*. *J. Appl. Ecol.*, 42, 1042–1053.

Müllerová, J., Pergl, J. & Pyšek, P. (2013). Remote sensing as a tool for monitoring plant invasions: testing the effects of data resolution and image classification approach on the detection of a model plant species *Heracleum mantegazzianum* (giant hogweed). *Int. J. Appl. Earth Obs. Geoinf.*, 25, 55–65.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

Nehrbass, N., Winkler, E., Pergl, J., Perglová, I. & Pyšek, P. (2006). Empirical and virtual investigation of the population dynamics of an alien plant under the constraints of local carrying capacity: *Heracleum mantegazzianum* in the Czech Republic. *Perspect. Plant Ecol. Evol. Syst.*, 7, 253–262.

Nehrbass, N., Winkler, E., Müllerová, J., Pergl, J., Pyšek, P. & Perglová, I. (2007). A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. *Biol. Invasions*, 9, 383–395.

Nijjer, S., Rogers, W.E. & Siemann, E. (2007). Negative plant-soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.*, 274, 2621–2627.

Olff, H., Hoorens, B., de Goede, R.G.M., van der Putten, W.H. & Gleichman, J.M. (2000). Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. *Oecologia*, 125, 45–54.

Ortega, Y.K. & Pearson, D.E. (2005). Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecol. Appl.*, 15, 651–661.

Packer, A. & Clay, K. (2004). Development of negative feedback during successive growth cycles of black cherry. *Proc. R. Soc. Lond. B*, 271, 317–324.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team. (2012). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105. Last accessed 12 October 2012.

Pyšek, P. (1991). *Heracleum mantegazzianum* in the Czech Republic: dynamics of spreading from the historical-perspective. *Folia Geobot. Phytotaxon.*, 26, 439–454.

Pyšek, P., Chytrý, M., Pergl, J., Sádlo, J. & Wild, J. (2012). Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. *Preslia*, 84, 576–630.

R Development Core Team (2012). *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reinhart, K.O., Packer, A., Van der Putten, W.H. & Clay, K. (2003). Plant–soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecol. Lett.*, 6, 1046–1050.

Simberloff, D. & Gibbons, L. (2004). Now you see them, now you don't! – population crashes of established introduced species. *Biol. Invasions*, 6, 161–172.

Strayer, D.L. (2012). Eight questions about invasions and ecosystem functioning. *Ecol. Lett.*, 15, 1199–1210.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006). Understanding the long-term effects of species invasions. *Trends Ecol. Evol.*, 21, 645–651.

Thiele, J. & Otte, A. (2007). Impact of *Heracleum mantegazzianum* on invaded vegetation and human activities. In *Ecology and Management of Giant Hogweed (Heracleum mantegazzianum)*. (eds Pyšek, P., Cock, M.J.W., Nentwig, W. & Ravn, H.P.). CAB International, Wallingford, pp. 144–156.

Thiele, J., Kollmann, J., Markussen, B. & Otte, A. (2010). Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biol. Invasions*, 12, 2025–2035.

Troelstra, S.R., Wagenaar, R., Smant, W. & Peters, B.A.M. (2001). Interpretation of bioassays in the study of interactions between soil organisms and plants: involvement of nutrient factors. *New Phytol.*, 150, 697–706.

Van der Putten, W.H. (2003). Plant defense belowground and spatiotemporal processes in natural vegetation. *Ecology*, 84, 2269–2280.

Vilà, M. & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos*, 105, 229–238.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L. *et al.* (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, 14, 702–708.

Weißhuhn, K. & Prati, D. (2009). Activated carbon may have undesired side effects for testing allelopathy in invasive plants. *Basic Appl. Ecol.*, 10, 500–507.

Zangerl, A.R. & Berenbaum, M.R. (2005). Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. *Proc. Natl Acad. Sci. USA*, 102, 15529–15532.

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