

Can enemy release explain the invasion success of the diploid *Leucanthemum vulgare* in North America?

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Abstract Enemy release is a commonly accepted mechanism to explain plant invasions. Both the diploid *Leucanthemum vulgare* and the morphologically very similar tetraploid *Leucanthemum ircutianum* have been introduced into North America. To verify which species is more prevalent in North America we sampled 98 *Leucanthemum* populations and determined their ploidy level. Although polyploidy has repeatedly been proposed to be

associated with increased invasiveness in plants, only two of the populations surveyed in North America were the tetraploid *L. ircutianum*. We tested the enemy release hypothesis by first comparing 20 populations of *L. vulgare* and 27 populations of *L. ircutianum* in their native range in Europe, and then comparing the European *L. vulgare* populations with 31 *L. vulgare* populations sampled in North America. Characteristics of the site and associated vegetation, plant performance and invertebrate herbivory were recorded. In Europe, plant height and density of the two species were similar but *L. vulgare* produced more flower heads than *L. ircutianum*. *Leucanthemum vulgare* in North America was 17 % taller, produced twice as many flower heads and grew much denser compared to *L. vulgare* in Europe. Attack rates by root- and leaf-feeding herbivores on *L. vulgare* in Europe (34 and 75 %) was comparable to that on *L. ircutianum* (26 and 71 %) but higher than that on *L. vulgare* in North America (10 and 3 %). However, herbivore load and leaf damage were low in Europe. Cover and height of the co-occurring vegetation was higher in *L. vulgare* populations in the native than in the introduced range, suggesting that a shift in plant competition may more easily explain the invasion success of *L. vulgare* than escape from herbivory.

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Introduction

Comparative studies assessing performance of invasive alien plant species under field conditions revealed that they often perform better in their introduced than in their native ranges (Hinz and Schwarzlaender 2004; Parker et al. 2013). One of the most prominent hypotheses explaining their increased size and abundance in their introduced range is the enemy release hypothesis (Keane and Crawley 2002; Colautti et al. 2004). It is based on the assumptions that populations in the native range are regulated by their associated natural enemies and that, when introduced into new ranges, they escape from their specialist natural enemies. The decreased regulation by natural enemies in the introduced range is expected to result in an increase in plant growth, reproduction and abundance. However, plants in the introduced range may not completely escape from herbivores since specialist herbivores might have been co-introduced with them or specialists of closely related native congeners might switch to attack the introduced plant species (Keane and Crawley 2002). In addition, resident generalist herbivores may start exploiting the new food source (Maron and Vilà 2001). Previous studies have found that invasive plants generally experience reduced attack by herbivores or are attacked by fewer species of herbivores in the invaded compared to the native range (Colautti et al. 2004; Liu and Stiling 2006; Heger and Jeschke 2014).

Herbivores do not always have negative effects on species performance in their native range (Prior et al. 2015) and only few studies tested if the observed differences in damage between ranges have an impact in regulating plant populations (DeWalt et al. 2004; Williams et al. 2010; Roy et al. 2011). Theoretically, exotic plants that experience high herbivore attack in their native range are more likely to escape top-down regulation and become invasive in the introduced range than plant species that experience only low levels of herbivory in their native range. Beside an escape from natural enemies, invasive plants may also profit from a release from competition with neighbouring plants (Crawley 1986; Callaway et al. 2011) or from more favourable climatic conditions in the introduced ranges (Erfmeier and Bruelheide 2004; Cripps et al. 2010). To gather support for any of these mechanisms that might explain invasion success, it is necessary to apply a biogeographic approach by

comparing invasive plants in their native and introduced ranges (Hierro et al. 2005).

Polyploidy has been proposed to be associated with invasiveness in plants (Müller-Schärer et al. 2004; Pandit et al. 2011, 2014; te Beest et al. 2012; Hahn et al. 2012a), through, for instance, increased phenotypic variation, fixed heterosis or reduced inbreeding depression, which may pre-adapt polyploids to become invasive or increase their ability to adapt to novel conditions post-introduction (Soltis and Soltis 2000; Comai 2005; te Beest et al. 2012, Hahn et al. 2012b). Polyploidy has been found to be over-represented in invasive plants (Pandit et al. 2011, 2014) and in various taxa with more than one ploidy level in the native range, only polyploids have become invasive (e.g. Lafuma et al. 2003; Kubátová et al. 2008; Schlaepfer et al. 2008; Treier et al. 2009). Furthermore, polyploids are expected to exhibit increased concentrations of secondary metabolites compared to their diploid progenitors and may therefore experience greater levels of herbivore resistance (Levin 1983; Dhawan and Lavanina 1996).

In this study we surveyed two closely related plant species, the diploid *Leucanthemum vulgare* (Vaill.) Lam. (Asteraceae) and the tetraploid *Leucanthemum ircutianum* DC in their native (Europe) and introduced (North America) ranges. Both species are very similar in their morphology and have often been treated as a species complex (in the following referred to as “*L. vulgare* s.l.”) together with various other species (Heywood 1976; Hegi 1987; Greuter (2006). Oberprieler et al. (2011) described *L. ircutianum* as an allopolyploid with *L. vulgare* and possibly *L. virgatum* (Desr.) Clos as parental species. In their native range (Europe and western Asia), *L. vulgare* and *L. ircutianum* are both widely distributed, but *L. ircutianum* is reported to be more common than *L. vulgare* (Zelený 1982; Vogt 1991; Zelený 2004; Oberprieler et al. 2011). *Leucanthemum vulgare* s.l. has been introduced to North America as ornamental and seed contaminant and now invades pastures, meadows, roadside areas and forest openings (Olson and Wallander 1999; Clements et al. 2004). In North America, it was reported to be naturalized in Québec and in the north-eastern USA by the eighteenth century (Fernald 1903; Lavoie et al. 2012). Nowadays, it is common in the north-eastern and north-western states of the USA and in the south-eastern and south-western provinces

of Canada (Olson and Wallander 1999; Clements et al. 2004). Beside North America, *L. vulgare* s.l. has also been introduced to many other parts of the world, including South America, Australia, New Zealand and India (Holm et al. 1979; Khuroo et al. 2010). To suppress *L. vulgare* s.l. or to stimulate the growth of competing vegetation, application of herbicides or fertilizer, respectively can be effective (Olson and Wallander 1999; Clements et al. 2004); however, this is not feasible over large areas. A biological control programme for *L. vulgare* s.l. was therefore initiated in 2008, but no agents have been released so far (McClay et al. 2013). Morphological surveys and chromosome counts from the eastern part of North America indicate that in this area *L. vulgare* might be more common than *L. ircutianum* (Fernald 1903; Mulligan 1958). However, western parts of North America have not been surveyed yet and the relative abundance of the two species across their introduced range remains unclear.

The first objective of our study was to assess the relative abundance of the diploid *L. vulgare* and the tetraploid *L. ircutianum* in North America by using flow cytometry to identify the ploidy level of 98 sampled populations. In our second objective, we tried to find indications whether enemy release may help explain the invasion success of *L. vulgare* in North America, which was found to be far more common than the tetraploid *L. ircutianum*. To assess whether herbivore attack is higher on *L. vulgare* than on *L. ircutianum* in their native range, and whether *L. vulgare* might therefore profit more from enemy release in the introduced range, we compared the herbivore communities and attack rates between *L. vulgare* and *L. ircutianum* in two regions in Europe surveying a total of 47 populations. We also recorded plant performance and site characteristics to assess whether they could explain potential differences in herbivory. We then compared the performance and herbivore attack of *L. vulgare* between the native and introduced range, by surveying 31 *L. vulgare* populations in North America. We hypothesized that (1) in their native European range, *L. vulgare* has higher herbivore attack rates than *L. ircutianum*, (2) herbivore attack rates are reduced in the invaded compared to the native range, and (3) *L. vulgare* populations in North America are denser and plants larger than in the native range.

Materials and methods

Ploidy screening

To investigate the relative abundance of *L. vulgare* and *L. ircutianum* in their introduced range, a total of 98 populations were sampled from 2008 to 2013. Thirty-one of the populations were sampled during our own field surveys (Online Resource 1) and 67 populations were sampled by colleagues (Online Resource 2). Because *L. vulgare* and *L. ircutianum* are similar in morphology, seeds were separately collected from one to ten plants with a minimum distance of 2 m and used for subsequent ploidy level determination using flow cytometry (for number of plants analysed, see Online Resource 1 and Online Resource 2). Since in the native range mixed-ploidy populations are rare (Zelený 1982), we analysed two bulk samples per population each containing two seeds from up to five plants but we separately analysed plants with atypical morphology. Previous analyses revealed that analyses of bulk samples with two seeds from five plants still allowed us to reliably detect mixed ploidy levels within a sample. The seeds were transferred into small Petri dishes together with a few drops of general-purpose buffer and chopped with a sharp razor blade following the protocol of Loureiro et al. (2007). After this, 950 µl of the buffer were added and the mix was incubated for approximately 1 min and then filtered through a 30-µm nylon filter. Afterwards, 30 µl of a staining solution composed of RNase (1 %) and propidium iodide (1 %) was added. The extracted and stained nuclei were analysed with a Partec Cyflow SL cytometer equipped with a green laser functioning at 532 nm. Seeds from a *L. vulgare* plant whose ploidy level was known from previous analyses were used to adjust the laser.

Field surveys

Sampling design

To compare plant performance, herbivore communities, herbivore attack rates and site characteristics, a total of 78 *L. vulgare* and *L. ircutianum* populations were surveyed in Europe and North America in 2013 (Fig. 1, Online Resource 1). In Europe, 24 populations were sampled across the Czech Republic and adjacent

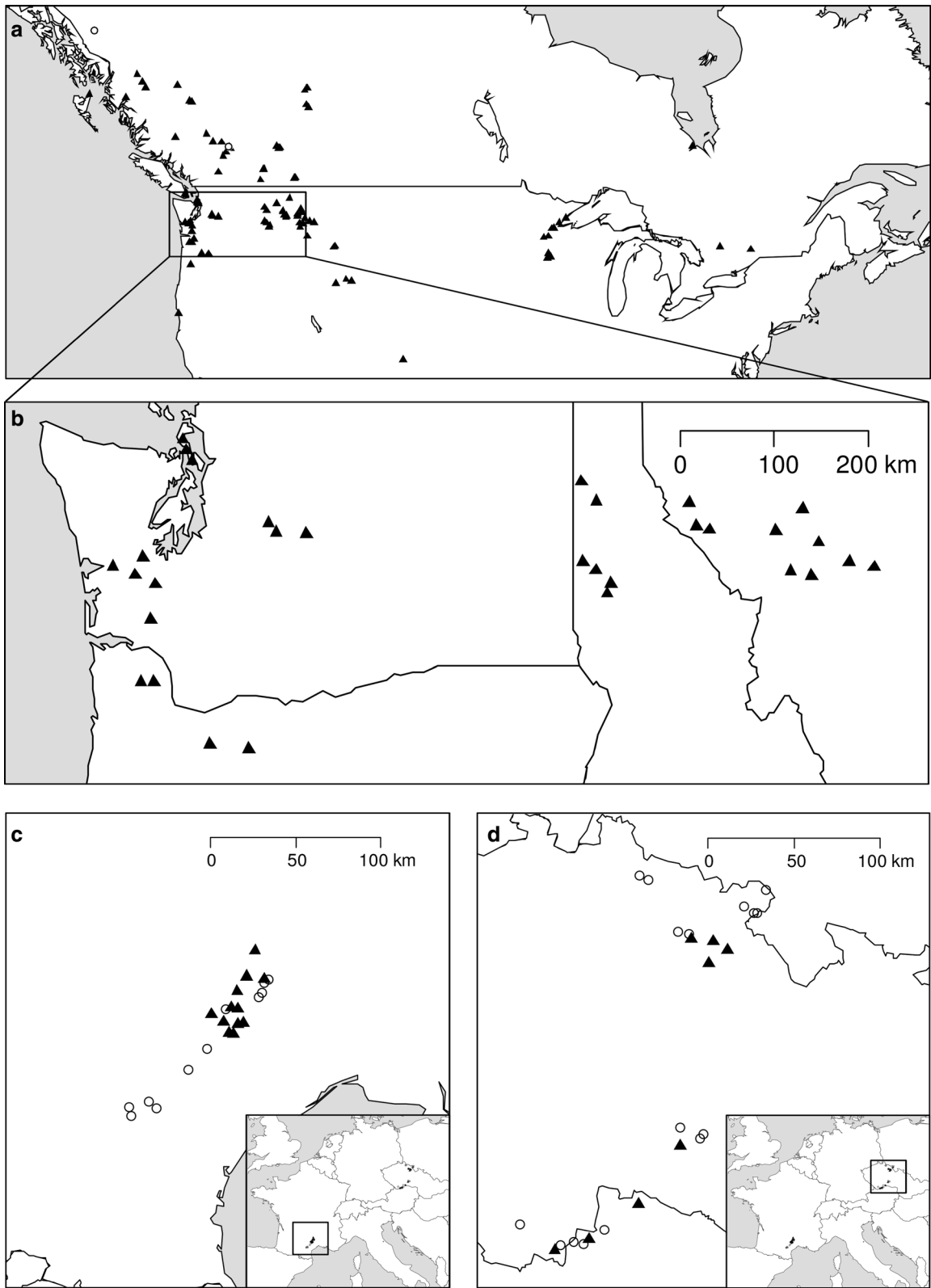


Fig. 1 Locations of populations of *L. vulgare* (triangles) and *L. ircutianum* (circles) surveyed in the invaded (North America) and native (Europe) range. **a** Populations surveyed for ploidy level in North America. **b, c, d** Populations surveyed for ploidy level, herbivores, plant performance and site characteristics in Washington, Oregon, Idaho and Montana (**b**), in France (**c**) and in the Czech Republic and adjacent parts of Austria (**d**)

parts of northern Austria and 23 populations in southern France. These two regions were selected because herbarium records and previous surveys revealed that both *L. vulgare* and *L. ircutianum* occur there. In North America, 15 sites were sampled in western Washington and north-western Oregon and 16 sites in northern Idaho and north-western Montana. The minimum distance between surveyed populations was 2 km in Europe and 12 km in North America. With the exception of two North American sites, only populations which had not been mown or grazed during the previous months were included in the surveys. All surveys were conducted towards the end of the flowering period of the plants when the shoots had reached their maximum height. Populations in Europe were sampled from 12 to 18 June (Czech Republic and Austria) and from 24 to 29 June (southern France) and populations in North America were sampled from 25 July to 4 August.

Geographic location and climatic data

To compare the climatic conditions of the native and invaded range, climatic data were obtained from the National Climatic Data Center (<http://www.ncdc.noaa.gov/>). Weather stations that were closest to the 78 sampled populations were chosen and mean annual temperature, mean minimum temperature of the coldest month, mean maximum temperature of the warmest month, and mean annual precipitation were calculated for the years 1998–2012. Coordinates and altitude for each sampled population were recorded in the field using a GPS.

Plant performance

To estimate population density, five 1 m × 1 m quadrats were placed every 7 m along a transect and all *Leucanthemum* shoots as well as all rosettes were counted in the quadrats. From each population 20 flowering plants were randomly chosen along the

transect with a maximum distance of 1 m from the transect and a minimum distance of 2 m between the plants. Of these, we measured the length of the longest shoot and counted the number of shoots and flower heads per plant. The number of flower heads per shoot was then used to compute the density of flower heads per square meter. Whenever available, seeds were collected from each of the selected plants for subsequent ploidy level determination (see above).

Herbivory

Damage by leaf herbivores was estimated for each collected plant using the following scoring system (after Lewis et al. 2006): 0 = no damage; 1 = minimal damage with no more than approximately 5 % of any leaf damaged; 2 = minimal damage plus some leaves with 5–10 % damage; 3 = 10–50 % damage on multiple leaves, but fewer than half of all leaves affected; 4 = at least half of all leaves with 10–50 % damage and multiple leaves with more than 50 % damage. The roots of the selected plants were dissected and all root-attacking herbivores were recorded. To estimate the proportion of plants with attack by root herbivores we also recorded whether the roots showed mining damage from previous attack. In addition, all flower heads were dissected and attack by the most abundant herbivores was recorded. Dissections were done directly in the field for North American populations, whereas plants from European populations were dissected using a microscope in the laboratory.

Site characteristics

All field sites were assigned to one of the following habitat types: roadside, grassland, forest or ruderal (defined as sites with soil disturbance, but not grazed or mown, e.g. waste areas or landfills). It was estimated whether the site was mown or grazed in the preceding year (by looking for dried flowering stalks dating from the preceding year and for livestock manure or by consulting the farmers), and we recorded whether there were any signs of soil disturbance. In addition, the following vegetation parameters were determined within each of the five 1 m × 1 m quadrats placed along the transect: (1) visual estimates of vegetation cover (excluding *Leucanthemum*), (2) species richness of forbs and grasses and (3) average

vegetation height in the centre of each of the five quadrats, estimated by placing a hand lightly on the vegetation at the level reached by about 80 % of the vegetation (“direct measurement method” after Stewart et al. 2001). Also, since *L. vulgare* has been reported to prefer calcareous-rich sites (Oberprieler et al. 2011), two soil samples were collected from each sampled population at a depth of 5–7 cm and the pH was recorded in the field using a soil pH tester (Luster Leaf Products, Inc. Woodstock, Illinois).

Statistical analyses

Climate, altitude and latitude

To investigate whether mean annual temperature, average minimum temperature of the coldest month, average maximum temperatures of the warmest month, mean annual precipitation, altitude and latitude of the sampled *L. vulgare* populations differed between the two ranges *t* tests were performed.

Plant performance

Generalized linear mixed models and linear mixed models with plant population nested in four geographic regions (Czech Republic and Austria, France, Washington and Oregon, Idaho and Montana) as random factor were performed to test whether the number of shoots per plant, the number of flower heads per plant, the number of flower heads per shoot and the length of the longest shoot differed between native *L. vulgare* and *L. ircutianum* plants and between native and introduced *L. vulgare* plants. To analyse whether the number of rosettes, shoots and flower heads per square meter differed between plant species and range, we carried out linear mixed models on population means with geographic region as random factor. The number of flower heads per shoot, and the number of *Leucanthemum* rosettes, shoots and flower heads per square meter were $\log_e(X)$ transformed to meet underlying assumptions of linear mixed models. To explore whether the observed differences in the performance of *L. vulgare* between ranges are still significant when controlling for climatic differences, we also included mean annual temperature, average maximum temperatures of the warmest month, mean annual precipitation, altitude and latitude as fixed effects in the models comparing *L. vulgare* in the

native and introduced range. The average minimum temperature of the coldest month was highly correlated with the mean annual temperature ($r = 0.92$) and therefore not included in the models. The best-fitted models were selected based on likelihood ratio tests.

Site characteristics

ANOVAs were performed to determine whether species richness and vegetation height differed between native *L. vulgare* and *L. ircutianum* populations and between native and introduced *L. vulgare* populations. Because the assumptions for ANOVA were not met for data on soil pH and vegetation cover, non-parametric Kruskal–Wallis tests were carried out instead. χ^2 tests were performed to test for differences in the proportions of populations that were mown or grazed and the proportions of populations with soil disturbance.

Pearson’s product moment correlation tests were used to explore whether the performance of *L. vulgare* (shoot density, plant height, number of flower heads per plant) is correlated with differences in plant competition (vegetation cover, vegetation height and number of plant species). The data were analysed separately for native and introduced *L. vulgare* populations. Two sites in North America that were grazed by cattle or horses and where vegetation parameters could not be accurately estimated were excluded from these analyses.

Herbivory

χ^2 tests were performed to compare the frequency distribution of leaf damage scores of native *L. vulgare* and *L. ircutianum* populations and of native and introduced *L. vulgare* populations. Generalized linear mixed models with plant population nested within geographic region as random effect and continent as fixed effect were used to compare the proportion of native and introduced *L. vulgare* plants attacked by root herbivores. To analyse if the proportion of plants attacked by root herbivores (total attack and attack by the three most abundant root herbivores) and the total number of root-attacking larvae and pupae found per plant (herbivore load) differs between *L. vulgare* and *L. ircutianum* in Europe and whether plant performance and site characteristics could explain potential differences in herbivory we used generalized linear

mixed models. Plant population nested within geographic region was included as random effect and *Leucanthemum* species, the number of shoots per plant, shoot density and vegetation height were included as fixed effects. For the analyses of herbivore load, plants in which only mining but no larvae or pupae were found were assigned to have a herbivore load of one. The best-fitted models were selected using likelihood ratio tests. To assess the significance of each parameter included in the best-fitted model, models with and without the respective parameter were compared.

All analyses were performed with the software R version 3.1.2 (R Core Team 2014). Linear mixed models (for normally distributed data) were done using the function `lme` in the `nlme` package (Pinheiro et al. 2014) and generalized linear mixed models (for binomial and count data) were done using the function `glmer` in the `lme4` package (Bates et al. 2014). Binomial distribution was used on proportions, Poisson distribution was used on counts and Gaussian distribution was used for normally distributed dependent variables. Separate analyses were conducted to compare European *L. vulgare* with *L. ircutianum* and European with North American *L. vulgare* populations.

Results

Ploidy level determination

Flow cytometric analyses revealed that all except for two populations from the introduced range were diploid and thus *L. vulgare* (Fig. 1a, b, Online Resource 1 and 2). Eight of the 24 sites sampled in central Europe (Czech Republic and Austria) and 12 of the 23 sites sampled in western Europe (southern France) were *L. vulgare*, the remaining European populations were *L. ircutianum* (Fig. 1c, d, Online Resource 1). In all of the populations only one ploidy level was detected.

Climate, altitude and latitude

For the sampled sites, mean annual temperature was higher in Europe than in North America (9.9 ± 0.3 °C vs. 8.4 ± 0.5 °C, $t = 3.1$, $P = 0.003$), whereas average maximum temperature of the warmest month was

higher in North America (27.5 ± 0.5 °C vs. 26.1 ± 0.2 °C, $t = 2.7$, $P = 0.009$) (Online Resource 1). All other climatic variables as well as altitude and latitude were similar between both ranges ($P > 0.05$).

Plant performance

In Europe, *L. vulgare* had on average 60 % more shoots and flower heads than *L. ircutianum*, whereas plant height, rosette-, shoot-, and flower head densities were similar between the two species (Table 1, Online Resource 3: Table S1). In the introduced range, *L. vulgare* were significantly taller, had a similar number of shoots per plant but produced twice as many flower heads compared to their native counterparts. Rosette density of *L. vulgare* was ten times higher, shoot density three times higher and flower head density five times higher in populations from the introduced compared to the native range (Table 1). Differences in plant performance and density of *L. vulgare* populations between the introduced and native ranges remained highly significant when climatic variables were included as covariates in the analyses (Online Resource 3: Table S2).

Habitat and site characteristics

In Europe, all measured site characteristics were similar for populations of *L. vulgare* and *L. ircutianum* (Table 2, Online Resource 3: Table S3, Online Resource 4). Soil pH was similar between *L. vulgare* sites in North America and Europe while vegetation cover, vegetation height, and forb and grass species richness were significantly lower in North America (Online Resource 4: Table S4). In both ranges, the majority of populations were sampled from grasslands (Online Resource 4). The proportion of populations with soil disturbance and the proportion of populations which were grazed in the year preceding our survey were similar between European and North American *L. vulgare* populations ($P > 0.1$, Online Resource 4) but North American populations were less often mown than European *L. vulgare* populations (34.8 vs. 75.0 %, $\chi^2 = 10.0$, $P = 0.002$).

The number of flower heads per plant and the density of *L. vulgare* shoots were negatively associated with vegetation cover (number of flower heads: $r^2 = 0.18$, $P = 0.02$; density: $r^2 = 0.4$, $P < 0.001$) in the introduced but not in the native range. They were

Table 1 Mean values (\pm SE) of plant and population traits of *L. vulgare* and *L. ircutianum* populations in the native (Europe, EU) and invaded (North America, NA, only *L. vulgare*) range

	<i>L. ircutianum</i> (EU)	vs.	<i>L. vulgare</i> (EU)	vs.	<i>L. vulgare</i> (NA)
Maximum shoot height (cm)	49.1 \pm 1.6	n.s.	45.5 \pm 1.6	*	54.5 \pm 1.6
Number of shoots	1.6 \pm 0.1	***	2.6 \pm 0.4	n.s.	3.0 \pm 0.3
Number of flower heads	1.9 \pm 0.2	**	3.3 \pm 0.5	***	6.2 \pm 0.9
Number of flower heads/shoot	1.2 \pm 0.0	n.s.	1.3 \pm 0.1	*	2.1 \pm 0.1
Number of shoots/m ²	16.6 \pm 4.8	n.s.	11.2 \pm 1.9	*	33.2 \pm 5.0
Number of rosettes/m ²	6.9 \pm 2.3	n.s.	3.3 \pm 0.9	*	32.1 \pm 5.4
Number of flower heads/m ²	19.5 \pm 5.1	n.s.	15.1 \pm 2.9	*	74.7 \pm 14.0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, mixed effect models; separate analyses were performed to compare European *L. vulgare* and *L. ircutianum* populations and European and North American *L. vulgare* populations, respectively

Table 2 Mean values (\pm SE) of site characteristics of *L. vulgare* and *L. ircutianum* populations in the native (Europe, EU) and invaded (North America, NA, only *L. vulgare*) range

	<i>L. ircutianum</i> (EU)	vs.	<i>L. vulgare</i> (EU)	vs.	<i>L. vulgare</i> (NA)
Vegetation cover (%) ^a	92.9 \pm 1.5	n.s.	92.3 \pm 2.0	*	75.9 \pm 3.1
Mean vegetation height (cm) ^a	37.7 \pm 2.8	n.s.	38.3 \pm 3.9	***	22.1 \pm 1.8
Number of forb species ^a	10.4 \pm 0.3	n.s.	9.8 \pm 0.4	***	4.1 \pm 0.3
Number of grass species	2.5 \pm 0.1	n.s.	2.4 \pm 0.1	***	1.7 \pm 0.1
Total number of species ^a	12.9 \pm 0.3	n.s.	12.2 \pm 0.4	***	5.7 \pm 0.3
Soil pH	6.8 \pm 0.1	n.s.	7.0 \pm 0.1	n.s.	7.0 \pm 0.1

^a Of vegetation other than *Leucanthemum*

* $P < 0.05$; *** $P < 0.001$, Kruskal–Wallis tests (for soil pH and vegetation cover) or ANOVAs (for all other variables). Separate analyses were performed to compare European *L. vulgare* and *L. ircutianum* populations and European and North American *L. vulgare* populations, respectively

not correlated with the number of co-occurring plant species ($P > 0.05$). The average height of *L. vulgare* was positively correlated with vegetation height in the native ($r^2 = 0.30$, $P = 0.01$) and introduced ($r^2 = 0.31$, $P = 0.002$) ranges but was not associated with vegetation cover or the number of co-occurring plant species.

Herbivores

Comparison of European *L. vulgare* and *L. ircutianum*

In Europe, the frequency distribution of leaf damage scores was similar between *L. vulgare* and *L. ircutianum* ($\chi^2 = 0.9$, $P = 0.9$) and the majority of plants had low leaf damage scores of 1 or 2 (Fig. 2a). The

best-fitted models to explain the proportion of plants attacked by root herbivores (Fig. 2b) and the number of root herbivores found per plant (herbivore load) revealed a positive correlation with the number of shoots per plant for both response variables ($z = 4.64$, $P < 0.001$ and $z = 9.5$, $P < 0.001$) but did not include *Leucanthemum* species, shoot density or vegetation height as explanatory variables (Online Resource 3: Table S5). Herbivore load was low for both plant species (0.41 ± 0.04 vs. 0.28 ± 0.02). The root-mining weevil *Diplapion stolidum* (Germar) was the most abundant root herbivore on both plant species. Furthermore, we found larvae of the root-feeding weevil *Cyphocleonus trisulcatus* (Herbst) in southern France and larvae and pupae of the root-galling tephritid fly *Oxyna nebulosa* (Wiedemann) in the

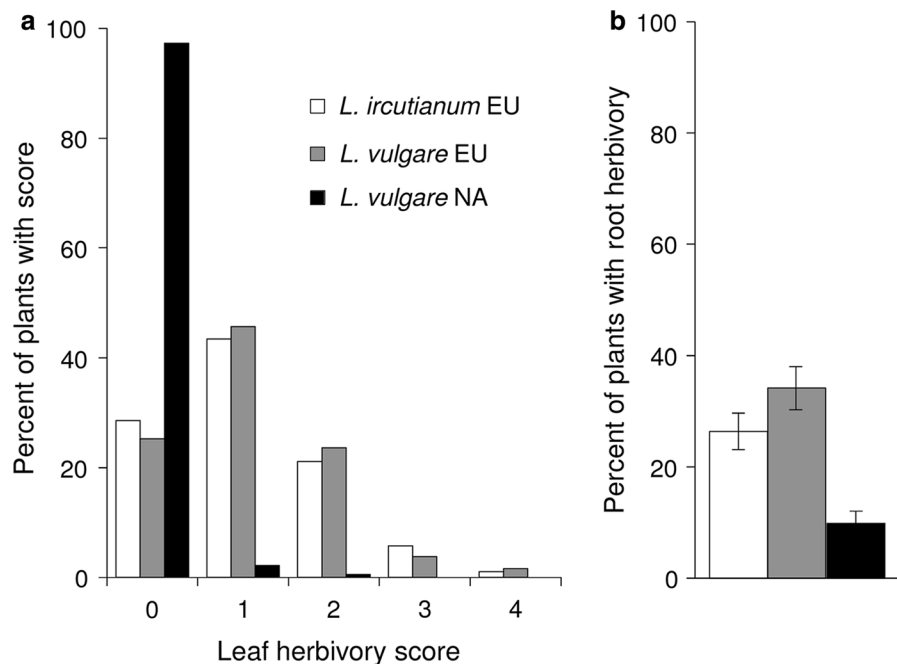


Fig. 2 **a** Leaf herbivory scores and **b** mean (\pm SE) proportions of plants attacked by root herbivores for *L. vulgare* and *L. ircutianum* plants sampled in the native (Europe, EU) and invaded (North America, NA, only *L. vulgare*) range. 0 = no damage; 1 = minimal damage with no more than about 5 % of any leaf damaged; 2 = minimal damage plus some leaves with 5–10 % damage; 3 = 10–50 % damage on multiple leaves, but fewer than half of all leaves affected; 4 = at least half of all

leaves with 10–50 % damage, and multiple leaves with more than 50 % damage. In EU, the frequency distribution of leaf damage scores and the proportion of plants attacked by root herbivores were similar between *L. vulgare* and *L. ircutianum* ($\chi^2 = 0.9$, $P > 0.05$) but *L. vulgare* plants in NA had significantly lower leaf and root herbivory than those in EU ($P < 0.001$)

Czech Republic. In addition, a few larvae of other herbivores such as *Dichrorampha* spp. and of the family Mordellidae were found in the roots of both plant species. The best-fitted models to explain the proportions of plants attacked by *D. stolidum* and *C. trisulcatus* both included *Leucanthemum* species and the number of shoots per plant as explanatory variables. *Leucanthemum vulgare* plants were more often attacked by *D. stolidum* and by *C. trisulcatus* than *L. ircutianum* ($z = -3.56$, $P < 0.001$ and $z = -2.05$, $P = 0.04$, Fig. 3a) and attack by both herbivores was positively associated with the number of shoots per plant ($z = 3.44$, $P < 0.001$ and $z = 2.25$, $P = 0.02$) (Online Resource 3: Table S5). The best-fitted model for *O. nebulosa* included *Leucanthemum* species and vegetation height as explanatory variables. *Leucanthemum vulgare* plants were less often attacked by *O. nebulosa* than *L. ircutianum* ($z = 2.22$, $P = 0.03$, Fig. 3a) and attack by *O. nebulosa* was negatively correlated with vegetation height

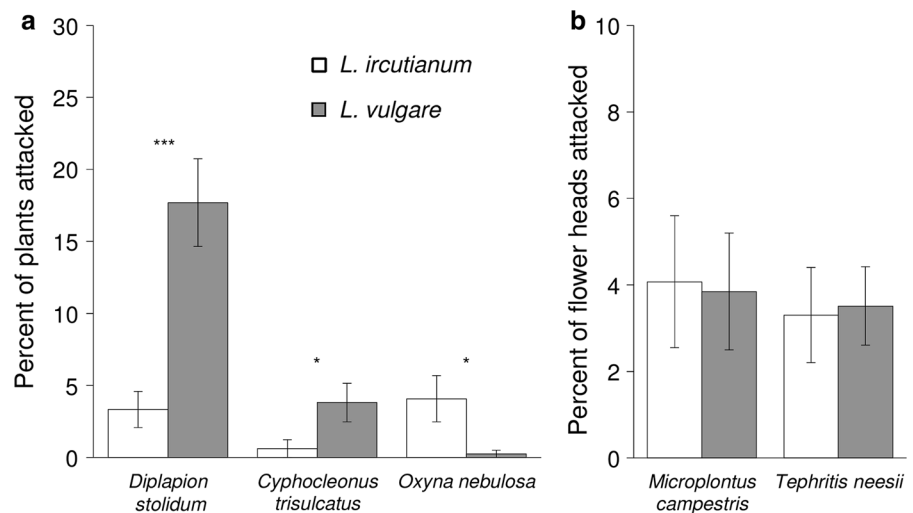
($z = -2.24$, $P = 0.03$) (Online Resource 3: Table S5).

In Europe, on average 3.5 % of the *Leucanthemum* flower heads per population were attacked by *Tephritis neesii* Meigen and 3.8 % by *Microplontus campestris* (Gyllenhal). Attack by these two herbivores was similar on *L. vulgare* and *L. ircutianum* (Fig. 3b). Seeds were frequently attacked by an unidentified gall midge [potentially *Contarinia chrysanthemi* (Kieffer)] but they were not included in the analyses because we were not able to reliably verify their presence or absence. In addition, 1.7 % of the flower heads were attacked by Lepidopteran larvae [*Dichrorampha acuminatana* (Lienig & Zeller) and others].

Comparison of *L. vulgare* between Europe and North America

Leucanthemum vulgare plants in the introduced range had significantly lower levels of damage by leaf

Fig. 3 **a** Mean (\pm SE) proportions of European *L. vulgare* and *L. ircutianum* plants per population attacked by the three most abundant root herbivores and **b** mean (\pm SE) proportions of flower heads per population attacked by *Microplontus campestris* and *T. neesii*. * $P < 0.05$; *** $P < 0.001$, generalized linear mixed model with binomial error distribution



herbivores than *L. vulgare* plants in the native range ($\chi^2 = 109.3$, $P < 0.001$, Fig. 2a). In North America, only 3 % of the plants were attacked by leaf herbivores while in Europe, 75 % of the *L. vulgare* plants showed at least some attack. In the introduced range a lower proportion of *L. vulgare* plants were attacked by root herbivores than in the native range ($z = 3.7$, $P < 0.001$, Fig. 2b, Online Resource 3: Table S6) and no herbivores were found in any of the mined roots. None of the 4000 flower heads that were sampled from the 31 *L. vulgare* populations in North America was attacked by herbivores.

Discussion

Our results from the ploidy screening of *Leucanthemum* populations in North America demonstrate that *L. vulgare* is by far more abundant in the introduced range than *L. ircutianum*. This is in accordance with surveys that had been conducted by Fernald (1903) and Mulligan (1958) in eastern North America where only a few populations of *L. ircutianum* were found. The higher invasion success of the diploid *L. vulgare* is in contrast to studies that found a positive association between polyploidy and invasiveness in plants (Lafuma et al. 2003; Kubátová et al. 2008; Schlaepfer et al. 2008; Treier et al. 2009; Pandit et al. 2011, 2014; te Beest et al. 2012). The higher abundance of *L. vulgare* in the introduced range could potentially be explained by differences in introduction pressure

between the two species. However, both species largely overlap in their native range where *L. ircutianum* is more common than *L. vulgare* (Zelený 1982; Vogt 1991; Zelený 2004; Oberprieler et al. 2011). In addition, flow cytometric analyses which were conducted with 13 commercially sold seed sources purchased from twelve US and one Canadian seed companies revealed that only one of them was *L. vulgare*, all others were *L. ircutianum* (Stutz et al. unpublished data). Based on this, *L. ircutianum* had a higher chance to naturalize and spread in North America than *L. vulgare*.

Comparison of European *L. vulgare* and *L. ircutianum*

In the native range, both *Leucanthemum* species were predominantly collected from grasslands and the vegetation height and cover, soil pH as well as plant species richness were similar in populations of both species. The two species are reported to have slightly different habitat preferences in their native range: *L. vulgare* is more abundant on dry calcareous grasslands and in more natural plant communities while *L. ircutianum* prefers nutrient-rich meadows and is more often found on disturbed sites and less specialised regarding ecological requirements and geological substrate (Zelený 1982; Hegi 1987; Vogt 1991; Oberprieler et al. 2011). In addition, *L. vulgare* is reported to be more thermophilous than *L. ircutianum* (Hegi 1987). Levin (1983) proposed that

polyploidization leads to increased resistance to herbivores, because polyploids should have higher concentrations of secondary metabolites than diploids. We therefore hypothesized that in its native range *L. vulgare* would be more attacked by herbivores than *L. ircutianum* and that it would therefore be more likely to escape regulation by herbivores and become invasive in the introduced range. However, the similar herbivore attack rate and herbivore load between the two species do not support this hypothesis. Nevertheless, we found differences in the composition of the herbivore communities between the two *Leucanthemum* species. The two root-feeding weevils *D. stolidum* and *C. trisulcatus* were both more often found in *L. vulgare* than in *L. ircutianum* populations while the opposite pattern was found for the root-galling tephritid fly *O. nebulosa*. Yet, in contrast to a generally larger plant size of polyploids (Ramsey and Ramsey 2014), the diploid *L. vulgare* produced more shoots and flower heads than the tetraploid *L. ircutianum* and our results suggest that the higher number of shoots of *L. vulgare* contributed to the higher attack rates of *L. vulgare* by *D. stolidum* and *C. trisulcatus*. Several field studies found differences in herbivore attack between closely related taxa differing in ploidy level (Thompson et al. 1997; Nuismer and Thompson 2001; Münzbergová 2006; Arvanitis et al. 2008; Halverson et al. 2008; Arvanitis et al. 2010; Richardson and Hanks 2011; Münzbergová et al. 2015). However, depending on plant taxa, herbivore species or even the population examined, polyploid taxa were either less, more or equally attacked by herbivores than the closely related diploids. For some taxa, differences in plant size or habitat preferences between cytotypes have been suggested to contribute to the differences in herbivory under field conditions (Münzbergová 2006; Arvanitis et al. 2007; Arvanitis et al. 2008; Richardson and Hanks 2011; König et al. 2014). For example, stem height has been suggested to be the main reason for the higher abundances of the leaf-galling fly *Asteromyia carbonifera* (Osten Sacken) and the aphid *Uroleucon nigrotuberculatum* (Olive) on hexaploid compared to sympatric diploid or tetraploid cytotypes of *Solidago altissima* L. in their natural habitat (Richardson and Hanks 2011). However, when grown in a common garden all cytotypes were similarly attacked by these herbivores, indicating that differences observed in the field were caused by habitat effects (Richardson and Hanks 2011). We

cannot exclude that site characteristics not recorded in our study may also help explaining the higher, respectively lower, densities of *D. stolidum*, *C. trisulcatus* and *O. nebulosa* on *L. vulgare*, since sympatric populations of *L. vulgare* and *L. ircutianum* are rare and were not encountered during this survey.

Comparison of *L. vulgare* in Europe and North America

As hypothesized, *L. vulgare* plants in the introduced range were taller and had more flower heads and the population density was higher than in the native range. These findings are consistent with a general pattern emerging from literature reviews indicating that invasive plants perform better in their introduced compared to their native range (Hinz and Schwarzaender 2004; Bossdorf et al. 2005; Parker et al. 2013). In our study, the populations surveyed in North America experienced higher mean and lower maximum temperatures than those in Europe, but differences in performance of *L. vulgare* between ranges remained significant even after we corrected for differences in these two climatic variables. A more benign climate does therefore not explain the better performance and higher density of *L. vulgare* in North America. Similarly, several other studies found better performance of invasive plants in their introduced compared to their native range and that these differences could not be explained by different environmental conditions between ranges (Jakobs et al. 2004; Ebeling et al. 2008; Hinz et al. 2012).

Vegetation height, vegetation cover as well as species richness of co-occurring species were higher in *L. vulgare* populations in Europe than in North America, suggesting that invasive *L. vulgare* populations experience reduced competition. Similarly, other biogeographic studies comparing performance of plant species native to temperate grasslands in Eurasia and invasive in the prairies in North America revealed that the average cover of the co-occurring vegetation is lower in the introduced than in the native range (Callaway et al. 2011; Alba and Hufbauer 2012; Hinz et al. 2012). In a neighbour removal experiment, Callaway et al. (2011) detected higher competitive effects of the surrounding vegetation on *Centaurea stoebe* L. growth and reproduction in its native European range compared to its invaded US range. Our results are in line with these findings, suggesting

that reduced interspecific competition in the introduced range may contribute to the increased performance and density of *L. vulgare*. Further studies are needed to assess whether the significant negative correlation between vegetation cover and shoot density and number of flower heads per plant of *L. vulgare* populations in North America indicates negative impact of *L. vulgare* on co-occurring vegetation or suppression of *L. vulgare* by the co-occurring vegetation. The lack of a significant negative correlation between vegetation cover and *L. vulgare* performance in the native range is likely to be due to a considerably lower variation in vegetation cover compared to the invaded range (10 vs. 45 % of the sites had a vegetation cover of more than 80 %).

Leaf- and root herbivory was significantly reduced and flower head herbivores were completely absent in the invaded range, as predicted by the enemy release hypothesis. Reduced herbivore attack in the invaded compared to the native range has also been found by several other biogeographical studies (Wolfe 2002; Bossdorf et al. 2005; Vilà et al. 2005; Ebeling et al. 2008; Adams et al. 2009; Cripps et al. 2010; Alba and Hufbauer 2012; Castells et al. 2013; Maurel et al. 2013; Blaisdell and Roy 2014; Cronin et al. 2015). One reason for the low herbivore attack in the invaded range might be that there are no congeneric species native to North America (USDA, NRCS 2015), which decreases the probability for native specialist insect herbivores to extend their host range to include *L. vulgare* as a new host plant. It has been reported that larvae of two native North American generalist tortricid moths [*Argyrotaenia velutinana* Walk. and *Sparganothis sulfureana* (Clem.)] feed on the inflorescences of *L. vulgare* in the vicinity of Ottawa (Guillet and Arnason 1995). In addition, a few European insects known to attack *Leucanthemum* species have accidentally been introduced to North America, including the monophagous *Microplontus campestris* reported from Ontario and Quebec (Anderson and Korotyaev 2004; Douglas et al. 2013) and at least three European *Dichrorampha* species feeding in the roots of *Leucanthemum* species have accidentally been introduced to North America [*D. acuminatana*, *D. petiverella* (L.) and *D. sedatana* (Busck)] (Miller 1983; Dix et al. 1984; Roberts 1991; Roberts and Miller 2003]. However, all except *D. sedatana* are only reported from a restricted area in the eastern USA and none of these herbivores were found during our

North American surveys. Empty feeding tunnels observed in the roots of plants from the native and invaded ranges might have been caused by root-attacking larvae of *Dichrorampha* species or other herbivorous insects that left the roots for pupation prior to our surveys. In the native range, at least nine root-feeding *Dichrorampha* species are reported from *Leucanthemum* species (Razowski 2003) but only very few *Dichrorampha* larvae were found during our surveys. Most of the *Dichrorampha* species have one generation per year and adults fly from May to July. Larvae were therefore likely feeding in the leaves or shoots, which were not dissected, or too small to be detected during dissections.

Even though attack by herbivores was higher in the native range, most plants showed only minimal damage by leaf herbivores and only about one-third of plants was attacked by root herbivores and herbivore load was low. These results suggest that in the native range *L. vulgare* and *L. ircutianum* populations are not strongly regulated by herbivores. However, even if invasive plants are not regulated by natural enemies in their native range, they might still benefit from enemy escape in the introduced range. In the absence of enemies in the introduced range, plants may evolve to allocate fewer resources to defence, particularly defence against specialists, and more resources to growth or reproduction (Blossey and Nötzold 1995; Keane and Crawley 2002; Müller-Schärer et al. 2004; Broz et al. 2009, Hahn et al. 2012a). Studies are presently underway to identify whether the better performance of *L. vulgare* in the invaded compared to the native range is a plastic response or the result of post-introduction evolutionary changes.

While the overall herbivore load on *L. vulgare* in the native range was low, several root and flower head attacking herbivores were found during the surveys that are reported to be specialised on *Leucanthemum* species. Their suitability for biological control of *L. vulgare* in North America depends on their host specificity and how herbivore damage translates to plant fitness and whether the herbivores can reach high enough densities to reduce population densities of the target weed. Studies that assess the factors limiting the population growth rate of these biological control candidates in the native range may help predicting under which scenarios population outbreaks, a prerequisite for successful classical biological control

(Gassmann 1996; Müller-Schärer and Schaffner 2008), can be expected for these herbivores.

Conclusion

In summary, our biogeographic survey revealed comparable herbivore loads on *L. vulgare* and *L. ircutianum* in the native range, suggesting that differential escape from specialist herbivores does not explain the higher invasion success of *L. vulgare* compared to *L. ircutianum*. When comparing *L. vulgare* between the native and the introduced range, plants in North America had significantly lower levels of herbivory, grew taller and produced more flower heads than plants in Europe, which is in line with the predictions of the enemy release hypothesis. Yet, the low levels of herbivory found in the native range suggest that the increased performance of *L. vulgare* in the introduced range is not primarily caused by enemy release and that other factors such as a shift in plant competition may play a more important role.

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