Journal of Biogeography (*J. Biogeogr.*) (2006) **33**, 2107–2119

ORIGINAL ARTICLE

Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges

Michael G. Cripps[1]*, Mark Schwarzländer[1], Jessica L. McKenney[1], Hariet L. Hinz[2] and William J. Price[3]

[1]Division of Entomology, Department of Plant Soil and Entomological Sciences, University of Idaho, Moscow, ID 83844-2339, USA, [2]CABI Bioscience, Switzerland Centre, 1 Rue des Grillons, Delémont CH-2800, Switzerland and [3]Statistical Programs, College of Agriculture, University of Idaho, Moscow, ID 83844-2337, USA

ABSTRACT

Aim To examine the composition and structure of the arthropod community on the invasive weed *Lepidium draba* in its native, expanded and introduced ranges, in order to elucidate the lack of a biotic constraint that may facilitate invasion.

Location Europe and western North America.

Methods Identical sampling protocols were used to collect data from a total of 35 populations of *L. draba* in its native (Eastern European), expanded (Western European) and introduced (western US) ranges. A bootstrapping analysis was used to compare herbivore richness, diversity and evenness among the regions. Core species groups (monophages, oligophages and polyphages) on the plant were defined and their abundances and host utilization patterns described.

Results Species richness was greatest in the native range, while species diversity and evenness were similar in the native and expanded range, but significantly greater than in the introduced range of *L. draba*. Specialist herbivore abundance was greater in the native and expanded compared with the introduced range. Oligophagous Brassicaceae-feeders were equally abundant in all three ranges, and polyphagous herbivore abundance was significantly greater in the introduced range. Overall herbivore abundance was greater in the introduced range. Host utilization was more complete in the two European ranges due to monophagous herbivores that do not exist in the introduced range. Root feeders and gall formers were completely absent from the introduced range, which was dominated by generalist sap-sucking herbivores. However, one indigenous stem-mining weevil, *Ceutorhynchus americanus*, occurred on *L. draba* in the introduced range.

Main conclusions This is, to our knowledge, the first study documenting greater herbivore abundance on an invasive weed in its introduced, compared with its native, range. However, greater abundance does not necessarily translate to greater impact. We argue that, despite the greater total herbivore abundance in the introduced range, differences in the herbivore community structure (specialist vs. generalist herbivory) may contribute to the invasion success of *L. draba* in the western USA.

Keywords

Arthropods, Brassicaceae, community structure, core species, enemy-release hypothesis, Europe, herbivore diversity, invasive species, niche saturation, western North America.

*Correspondence: Michael G. Cripps, Field Service Centre, PO Box 84, Lincoln University, Canterbury, New Zealand.
E-mail: crippsm2@lincoln.ac.nz

INTRODUCTION

Invasive plants often reach higher densities and biomasses per unit area, persist longer, and occupy a wider set of environmental conditions compared with conspecifics in their native range (Crawley, 1987; Hinz & Schwarzlaender, 2004). One of the most common explanations for the increased vigour of invasive plants is the release from natural enemies (Elton,

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2006.01560.x

1958; Maron & Vilà, 2001; Keane & Crawley, 2002). The enemy-release hypothesis (ERH) asserts that upon introduction to an exotic range, plants experience a decrease in natural enemy pressure that facilitates their dispersal and increased abundance. The hypothesis is based on two assumptions: (1) herbivores are able to regulate plant populations, and (2) plants experience reduced herbivore pressure, particularly from specialists, when introduced into a new range. Studies comparing herbivore levels and the herbivorous communities in native and introduced ranges have found reduced herbivory, lower overall diversity, and a shift from specialists to generalists and from endophagous to exophagous arthropods in the introduced range of invasive plants (Goeden, 1974; Memmott *et al.*, 2000; Colautti *et al.*, 2004; Hinz & Schwarzlaender, 2004). Studies investigating the impact of natural enemies on plant population dynamics have yielded mixed results, with the outcome appearing to depend on the life history of the plant, the herbivores involved, and environmental conditions (Louda, 1983, 1994; Crawley, 1989; Louda & Potvin, 1995; Root, 1996; Maron & Gardner, 2000). Although the role of arthropod herbivory in plant regulation is dependent on a variety of factors, many of which are still unresolved (Crawley, 1989; McEvoy, 2002), the differences in the community structure and composition of generalists vs. specialists may provide insights into mechanisms that facilitate plant invasions (Keane & Crawley, 2002). For invasive plant species, the ERH specifically predicts that (1) specialist enemies will be absent in the introduced range, (2) host switching by specialists of native congeners will be rare, and (3) generalist herbivores will have a greater impact on native species relative to introduced species (Keane & Crawley, 2002).

Most field studies that compared invasive weeds in their native and introduced ranges recognized the importance of comparing levels of herbivore damage, or incidence of herbivory (e.g. percentage seedheads infested), but did not compare the actual herbivore community composition and structure between the ranges (Weiss & Milton, 1984; Paynter *et al.*, 1996; Sheppard *et al.*, 1996; Woodburn & Sheppard, 1996; Fenner & Lee, 2001; Wolfe, 2002; DeWalt *et al.*, 2004; Jakobs *et al.*, 2004; Prati & Bossdorf, 2004; Vilà *et al.*, 2005). Other studies that have compared phytophagous communities have relied on literature records to supply species composition data for one of the ranges (Wilson *et al.*, 1990; Jobin *et al.*, 1996; Syrett *et al.*, 1999; Imura, 2003); fewer studies have used the same sampling protocol in both native and introduced ranges to quantify herbivore community composition and structure (Goeden, 1974; Sobian & Zwölfer, 1985; Ashbourne & Putman, 1987; Memmott *et al.*, 2000). However, such biogeographical studies of the herbivorous arthropod communities in both native and introduced ranges are essential for elucidating potential invasion mechanisms of introduced plant species (Maron & Vilà, 2001; Hinz & Schwarzlaender, 2004; Hierro *et al.*, 2005).

Here we report on a biogeographical comparison of the herbivorous arthropod communities associated with the herbaceous perennial mustard *Lepidium draba* L. in its native Eastern European, expanded Western European, and introduced US ranges. We collected data from a total of 35 different *L. draba* populations, using identical sampling protocols in each range. In accordance with existing, but rarely tested, theory we predicted that (1) species richness, diversity and evenness would increase toward the centre of origin of *L. draba*. In accordance with the ERH, we also predicted that (2) toward the centre of origin the number of specialist herbivores and the degree of host utilization would be greater, and (3) the overall abundance of herbivores would be greater.

METHODS

Study system

Lepidium draba L. [=*Cardaria draba* (L.) Desv.] is a perennial mustard (Brassicaceae) indigenous to south-western (Caucasus region) and central Asia (Caspian Sea region) (Mulligan & Frankton, 1962), and the European coastal regions of the Mediterranean and Black Seas (Ball, 1964). It spread to the rest of Europe at least 300 years ago, presumably moving west along stream corridors, and is now naturalized throughout continental Europe (Hegi, 1986). Currently, *L. draba* occurs on every continent except Antarctica (Scurfield, 1962), where it is classified as either adventive or naturalized. Introduction of *L. draba* to North America occurred in the mid- to late 1800s as seed in ship ballast (Bellue, 1933) and contaminated alfalfa seed from central Asia (Groh, 1940). In North America, *L. draba* is recorded from the east to the west coast, but is considered particularly problematic throughout the west, where it is declared as noxious in 16 states and three Canadian provinces (Rice, 2005; USDA, NRCS, 2006). *Lepidium draba* commonly occurs on neutral-to-alkaline soils in a wide range of disturbed habitats, including cultivated land, rangeland, pastures, roadsides and waste areas, and particularly thrives in riparian or irrigated areas (Scurfield, 1962). The plant reproduces by rhizomes and seeds. Rhizomes comprise 56% of below-ground biomass, and are important for colonization of a site. The production of seeds, which requires insect pollination, is important for dissemination of the plant (Mulligan & Findlay, 1974). Seeds are produced in silicles, most of which contain two seeds; single shoots produce up to 850 silicles (Corns & Frankton, 1952). Two subspecies of *L. draba* are recognized (*L. draba* ssp. *draba* and *L. draba* ssp. *chalapense*), and the closest related species to *L. draba* is *Lepidium appelianum* Al-Shehbaz [=*Cardaria pubescens* (C.A. Mey.) Jarm.] (Al-Shehbaz *et al.*, 2002). Both species, including subspecies, are invasive weeds in western North America (Rice, 2005; USDA, NRCS, 2006), and there are current efforts investigating the potential for biological control of this weed complex (H.L. Hinz, unpublished data). *Lepidium draba* ssp. *draba* is by far the most widespread species in the regions surveyed (Lyons, 1998; Gaskin *et al.*, 2005), and was the only species encountered. A 2-year biogeographical survey of *L. draba* found no difference in population size between the native and introduced ranges. However, density, cover, biomass and individual plant size of *L. draba* were consistently greater in the introduced range, but cover of other vegetation was reduced (McKenney, 2005).

Sampling methods and division of regions

In April to early June 2002 and 2003, the arthropod community associated with *L. draba* was surveyed during the flowering period of the plant in Europe and the Pacific Northwest of the USA. At each field site, the arthropod community on *L. draba* was surveyed by beating plants into a sweep net for 30-s intervals. Nine to 10 30-s samples were collected at each site. In 2002, only Hemiptera (*sensu latu*) and Coleoptera were collected by aspirating all the Hemipteran and Coleopteran specimens from the sweep net. In 2003 the entire contents of the sweep net for each 30-s sample was emptied into sealed plastic bags and later transferred to vials of 70% ethanol. In addition, in both years *L. draba* plants (*c.* 90–180 shoots per site) were excavated at each site, stems and roots dissected, and an effort made to rear immature insect stages to adult for identification. All specimens collected from the sweep samples in both years were identified to family and morphospecies, and commonly occurring specimens were identified to species by expert taxonomists. Only herbivorous species were used in the analyses. The herbivore community was defined to encompass all phytophagous arthropods including species that feed on pollen and/or nectar, but excluded parasitic Hymenoptera that, as adults, may occasionally also feed on pollen and/or nectar. This broad inclusion of species may therefore include some pollinator species that facilitate seed set, and also pollinivorous herbivores that inhibit seed set. Inclusion in the herbivore community was based on the primary feeding habit known for the most refined taxonomic level available (family, genus or species) for each morphospecies. Therefore unidentified morphospecies were included only if congeneric or confamilial species are known phytophages. Morphospecies have been shown to be accurate surrogates for species estimates (Oliver & Beattie, 1996), and in this paper the term 'species' is used to indicate morphospecies. Voucher specimens of all identified material are deposited in the W.F. Barr Entomological Museum, University of Idaho.

The survey regions were divided into three ranges: Eastern Europe, Western Europe, and the USA (Table 1). The 'Eastern' region is east of the Carpathian Mountains in Bulgaria and Romania, the Crimean peninsula and south-eastern Ukraine. This is the Black Sea region, which is part of the native range of *L. draba*. The 'Western' region is Western Europe from south-western Germany to eastern Hungary. This area is considered to be part of the expanded range of *L. draba* (Hegi, 1986). The US region refers to the north-western states of Idaho, Oregon, Washington and Wyoming, where *L. draba* is one of the most prevalent invasive plant species. The sites in the three regions spanned similar latitudinal and longitudinal ranges, making the geographical areas comparable among the three regions (Table 1). In 2002, nine sites were surveyed in both the USA and Western Europe. In 2003, surveys were expanded to include seven sites in Eastern Europe, six sites in Western Europe, and 13 sites in the USA (Table 1). Surveys conducted over 2 years helped to determine the core species pool; all other analyses presented are based only on the 2003 sampling.

Core species selection and host utilization

For each range, a core species group (*sensu* Cornell & Lawton, 1992) of herbivorous arthropods found on *L. draba* was determined. Core species were defined using two criteria: (1) host-plant association (for monophages or oligophages), and (2) frequency and abundance of occurrence (for polyphages) (Magurran & Henderson, 2003; Magurran, 2004). Monophagous species were defined as having *L. draba*, its two subspecies, and *L. appelianum* (the former *Cardaria* genus) as primary hosts. Oligophagous species were defined as restricted to the family Brassicaceae, and polyphages were defined as feeding on plants in several families. Several monophagous and oligophagous feeders on *L. draba* occurred at low frequency and abundance but, based on their close association with *L. draba*, were considered part of the core species group (Magurran, 2004). Host utilization and specificity of monophagous and oligophagous arthropods collected on *L. draba* was determined from faunal records (Dieckmann, 1972; Freude *et al.*, 1983; Campobasso *et al.*, 1999), personal communication with specialists, and work conducted at the CABI Bioscience Switzerland Centre (H.L. Hinz, unpublished data). For the second inclusion criterion, consistent occurrence and high relative abundance, polyphagous species were included in the core species group when they occurred at least at half the sites in each range (four of seven for Eastern Europe; three of six for Western Europe; or seven of 13 for the USA) with an arbitrarily placed mean abundance threshold of at least 14 individuals per site (Magurran & Henderson, 2003). The remaining group of herbivorous species is referred to as the tramp species group (Cornell & Lawton, 1992). Following Lawton (1982), host-utilization matrices were constructed with the core species group for each range. Every core species was classified according to its feeding mode (chewing, sucking, mining, galling) and location (seeds, flowers, stems, foliage, roots) on *L. draba*. The location and pattern of resource utilization of a species in relation to other species in the community encapsulates a species' niche, and is therefore used to depict niche occupation (Putman, 1994). The term 'guild' is used here for a group of core species, regardless of taxonomic affiliation, that utilize similar food resources (Root, 1967). Thus columns in the host-utilization matrix represent herbivore guilds.

Analyses

Means and 95% confidence intervals (mean ± 1.96 × SE) for species richness, diversity and evenness were computed using a bootstrapping analysis that examined the effects of increasing sample size. Simulated samples began at one and continued to the maximum number of samples for a region.

Table 1 *Lepidium draba* populations sampled in Eastern Europe, Western Europe and the USA in 2002 and 2003

Site name	Country	Sampling year	Co-ordinates	Elevation (m)	Habitat*	Patch size (m^2)
Eastern European populations						
Petrich	Bulgaria	2003	41°25.143′ N, 023°12.770′ E	116	Roadside	360
Kocherinovo	Bulgaria	2003	42°04.426′ N, 023°02.462′ E	415	Roadside	450
South Sofia	Bulgaria	2003	42°36.985′ N, 023°27.452′ E	603	Roadside	284
Popricani	Romania	2003	47°16.417′ N, 027°29.899′ E	98	Orchard	168
Iaşi	Romania	2003	47°10.125′ N, 027°27.662′ E	53	Pasture	1,000,000
Schebetovka	Ukraine	2003	44°57.180′ N, 035°07.936′ E	139	Vineyard	550
Khomutivsky	Ukraine	2003	47°17.494′ N, 038°10.576′ E	34	Pasture	728
Western European populations						
Eisenstadt	Austria	2002	47°50.742′ N, 007°36.071′ E	139	Vineyard	3770
Sion	Switzerland	2002	46°12.793′ N, 007°19.030′ E	482	Roadside	300
Martigny	Switzerland	2003	46°07.662′ N, 007°03.645′ E	467	Roadside	480
Griessheim	Germany	2002, 2003	47°54.332′ N, 007°36.055′ E	224	Roadside	600
Taksony 1	Hungary	2002	47°19.167′ N, 019°05.661′ E	101	Roadside	375
Csanádpalota	Hungary	2002, 2003	46°12.861′ N, 020°44.296′ E	96	Roadside	500
Taksony 2	Hungary	2003	47°17.749′ N, 019°05.567′ E	103	Roadside	150
Tököl 1	Hungary	2002	47°18.123′ N, 018°56.906′ E	104	Ruderal	360
Tököl 2	Hungary	2002, 2003	47°17.802′ N, 018°56.389′ E	107	Ruderal	16,740
Ótompahát	Hungary	2002, 2003	46°30.416′ N, 020°24.067′ E	84	Roadside	4200
Mindszent	Hungary	2002	46°30.887′ N, 020°11.339′ E	85	Roadside	240
US populations						
Meridian	Idaho	2002, 2003	43°38.920′ N, 116°29.615′ W	766	Ruderal	3250
Lapwai	Idaho	2002, 2003	46°23.832′ N, 116°48.670′ W	461	Ruderal	1625
Boise	Idaho	2003	43°34.433′ N, 116°06.715′ W	869	Ruderal	2130
Lewiston	Idaho	2003	46°23.208′ N, 116°56.277′ W	403	Pasture	600
Kuna	Idaho	2002	43°29.368′ N, 116°16.469′ W	889	Ruderal	7500
Heath	Idaho	2002	44°45.44′ N, 116°51.83′ W	1272	Meadow	975
Vale	Oregon	2003	44°1.813′ N, 117°15.745′ W	695	Roadside	1200
Vale2	Oregon	2002, 2003	44°4.937′ N, 117°18.320′ W	713	Roadside	300
Vale2	Oregon	2002	44°4.937′ N, 117°18.320′ W	713	Roadside	300
Ontario	Oregon	2002, 2003	44°0.518′ N, 117°0.6473′ W	671	Pasture	240,000
Baker City	Oregon	2003	44°47.057′ N, 117°48.580′ W	1043	Ruderal	4200
Ritzville	Washington	2003	47°09.730′ N, 118°18.556′ W	563	Pasture	560
Yakima	Washington	2003	46°33.436′ N, 120°29.211′ W	299	Ruderal	11,700
Rosalia	Washington	2002	47°9.910′ N, 117°17.089′ W	769	Roadside	360
Garfield	Washington	2002	47°0.471′ N, 117°7.49′ W	2503	Ruderal	1200
Tensleep	Wyoming	2003	44°11.065′ N, 107°21.820′ W	2142	Meadow	180
Lander 1	Wyoming	2003	42°50.451′ N, 108°37.871′ W	1601	Pasture	2100
Lander 2	Wyoming	2003	42°41.731′ N, 108°32.477′ W	1720	Pasture	348

* Habitat classifications: We defined ruderal as a site where the natural vegetation has been disturbed by humans. Roadsides are a further qualification of a ruderal site. Vineyards and orchards are agricultural sites that have also been disturbed. Pastures are areas that are actively grazed by domesticated animals. A meadow is a field that exhibits no evidence of grazing by domesticated animals or other agricultural use, and are relatively undisturbed.

At each simulated sample size, bootstrap samples were taken randomly with replacement. Mean and confidence limit values were subsequently obtained from the resulting bootstrap distribution for each metric (Efron & Tibshirani, 1998). Species richness is the most basic, direct comparison among communities, based simply on presence. The diversity (richness and relative abundance) among the three regions was compared using the Shannon (H') and Simpson (D) indices. These two indices are complementary, and calculating both provides a more robust comparison of community diversity (Hurlbert, 1971; Peet, 1974; Southwood & Henderson, 2000). To obtain a measure of community evenness (species relative abundance), we used the Simpson evenness index, E (Magurran, 2004). The sampling effort among the three regions was uneven: 69 in Eastern Europe; 60 in Western Europe; 129 samples in the USA. Therefore all comparisons among regions were made at the largest common sample size (60 samples).

The core species groups were also used to compare the overall abundance of herbivores classified as monophages, oligophages or polyphages among regions. A mixed-effects model, with region (native, expanded and introduced) as a fixed effect and populations within regions as random effects, was used. The same analysis was used to compare the abundance of core species occurring in all three regions. All mixed models were estimated with a restricted maximum-likelihood estimation technique (Hocking, 1985). To meet assumptions of normality, abundances were logarithmically ($\log_e$) transformed. For a significant region effect, pairwise differences were used to compare means among the regions. All statistical analyses were conducted using SAS Institute Inc. (2004).

RESULTS

Species richness, diversity and evenness

The total number of herbivorous species sampled in each region was 137, 112 and 104 for Eastern Europe, Western Europe and the USA, respectively. At the largest common sample size (60 samples), the species accumulation curves for each range appeared to reach an asymptote, indicating that nearly all the herbivorous species in the respective ranges had been collected (Fig. 1). At this sample size, the mean species accumulation (± CI) for Eastern Europe (135.18 ± 4.19), Western Europe (111.34 ± 1.85) and the USA (93.37 ± 5.65) all had non-overlapping confidence intervals (Fig. 1a), suggesting there were significant differences among regions. The means for the Shannon diversity index ($H'_{\mathrm{EE}} = 3.16 \pm 0.152$; $H'_{\mathrm{WE}} = 2.91 \pm 0.172$; $H'_{\mathrm{US}} = 1.71 \pm 0.279$); Simpson diversity index ($D_{\mathrm{EE}} = 14.11 \pm 2.99$; $D_{\mathrm{WE}} = 9.30 \pm 2.14$; $D_{\mathrm{US}} = 3.35 \pm 0.965$); and Simpson evenness index ($E_{\mathrm{EE}} = 0.645 \pm 0.0312$; $E_{\mathrm{WE}} = 0.617 \pm 0.0367$; $E_{\mathrm{US}} = 0.377 \pm 0.0618$) were all overlapping between the two European ranges, but differed significantly between European ranges and the USA (Fig. 1b–d).

Core species abundance, specialization and host utilization

Nineteen core species were collected in Eastern Europe, 21 in Western Europe, and 12 in the USA (Fig. 2). Four core species occurred in all three ranges: *Ceutorhynchus obstrictus* (Marsham), *Plutella xylostella* (L.), *Frankliniella occidentalis* (Pergande) and *Myzus persicae* (Sulzer). There was no significant difference in the abundance of *C. obstrictus* ($F_{2,5} = 3.83$, $P = 0.0979$) or the abundance of *M. persicae* ($F_{2,17} = 0.10$, $P = 0.907$) among the three ranges. However, *P. xylostella*, which is introduced to North America, was significantly more abundant in the USA compared with Eastern and Western Europe ($P = 0.0002$). The mean abundance of *F. occidentalis* was significantly greater in the USA

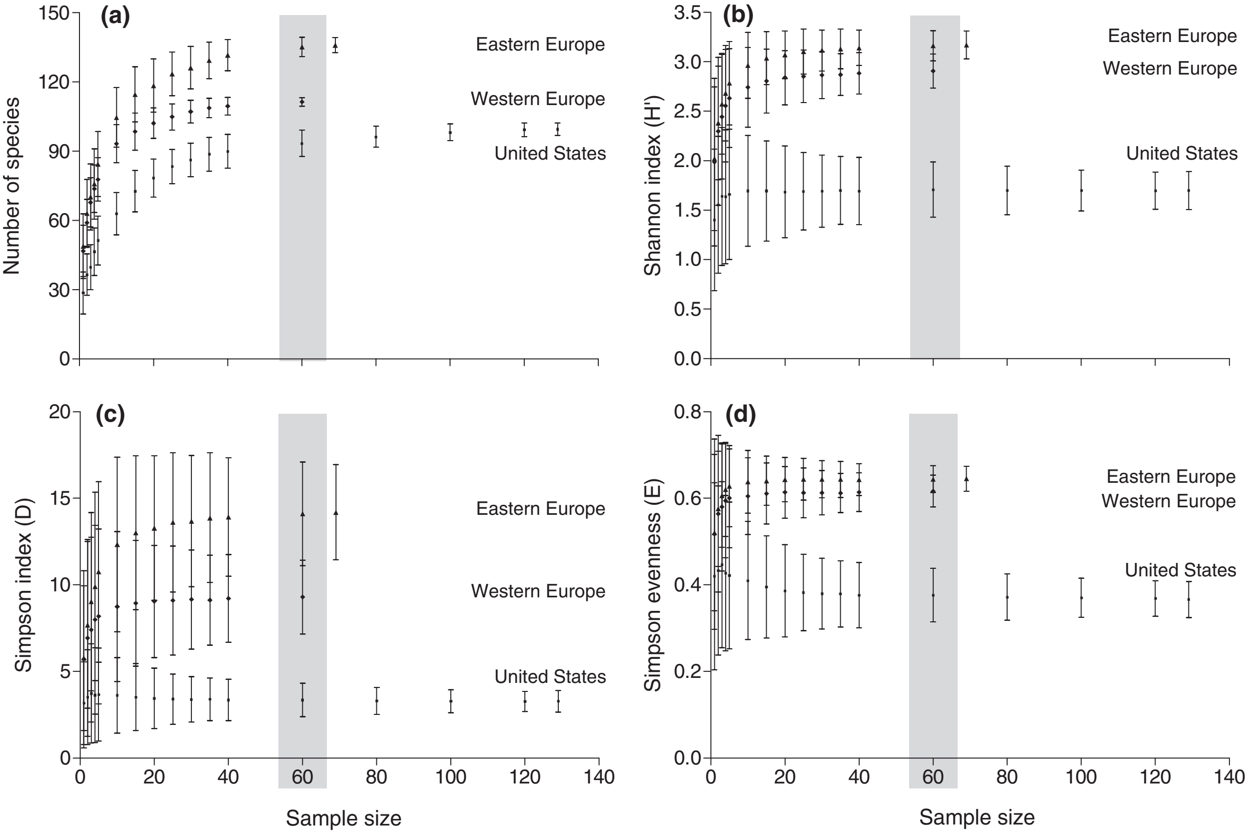

Figure 1 Bootstrapped sampling results of (a) number of species; (b) Shannon diversity index; (c) Simpson diversity index; (d) Simpson evenness index for the herbivorous arthropod communities on *Lepidium draba* in its native (Eastern Europe), expanded (Western Europe) and introduced (US) ranges surveyed in 2003. Means ± (1.96 × SE) approximates the 95% CI for a given sample level after 1000 bootstrap iterations. Mean and approximated 95% CI at 60 samples are highlighted (grey).

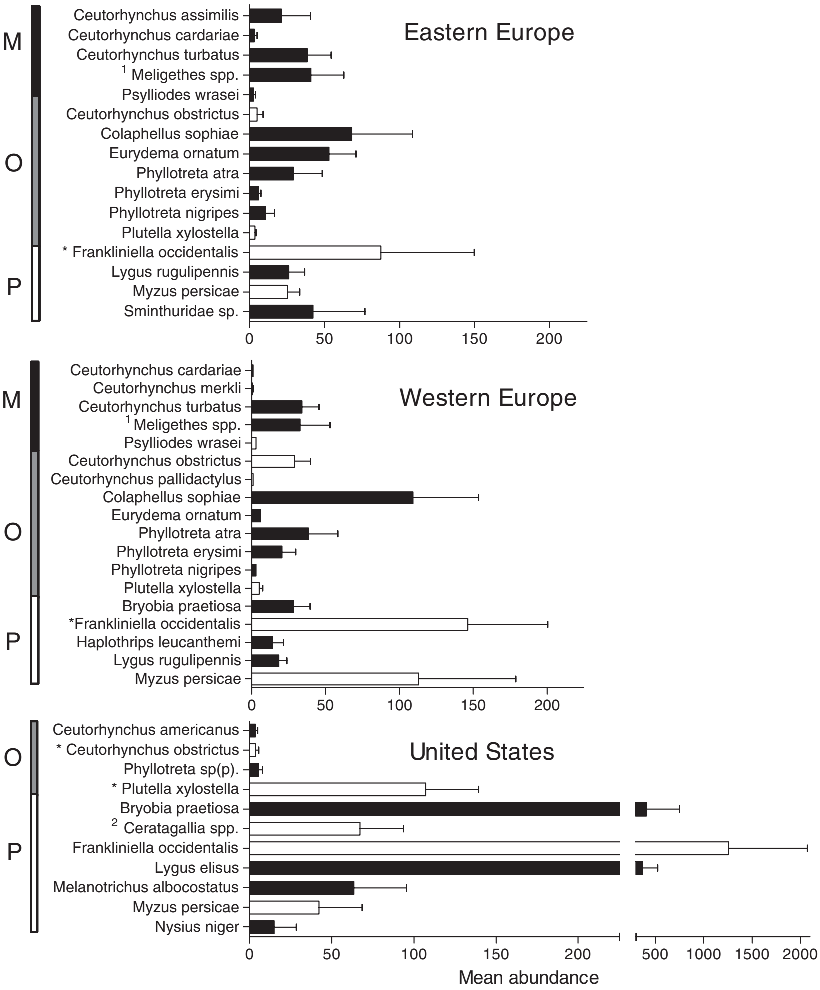

Figure 2 Core species (see text for details) and their respective mean (± SE) abundances for each range surveyed in 2003. White bars indicate species that occurred in all three ranges. Species in each range are grouped according to feeding specialization (M, monophages; O, oligophages; P, polyphages). *Species that are known introductions to that range. 1, *Meligethes* species included specimens of *M. lepidii*, *M. aeneus*, *M. coracinus* and *M. kraatzi*. 2, *Ceratagallia* species included specimens of *C. curvata* and *C. viator*.

than in Eastern Europe ($P = 0.009$), but was not different from Western Europe.

When grouping core species by feeding specialization (Fig. 3), monophagous feeders ($n = 7$) were encountered only in the two European ranges, and their mean abundance did not differ ($F_{1,11} = 0.66$, $P = 0.434$). Oligophagous feeders were equally abundant in all three ranges ($F_{2,23} = 0.63$, $P = 0.540$), while polyphagous feeders occurred in similar numbers in the two European ranges ($P = 0.456$), but were significantly more abundant in the USA ($P = 0.033$) (Fig. 3). Polyphagous herbivores were also more abundant than monophagous or oligophagous herbivores, regardless of range ($P < 0.0001$). The mean total abundance of core individuals in the USA (2280 ± 1330) was significantly greater than in Eastern Europe (376 ± 124, $P = 0.026$), and marginally greater than in Western Europe (421 ± 121, $P = 0.067$).

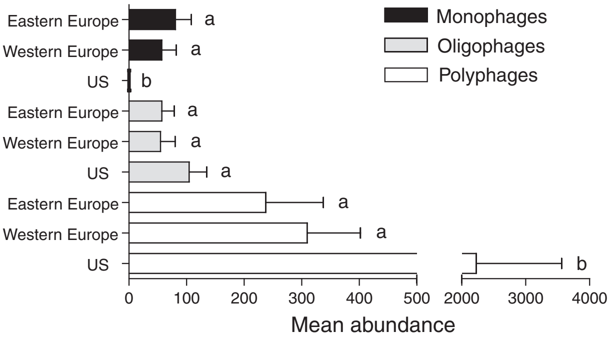

Figure 3 Mean (± SE) abundance of core species classified according to feeding specialization: monophages, oligophages or polyphages (Eastern Europe, $n = 7$; Western Europe, $n = 6$; USA, $n = 13$). See text for definitions of host specialization. Within a host specialization group, bars followed by different letters indicate a significant difference ($P < 0.05$). Statistical inferences are based on logarithmically ($\log_e$)-transformed means.

Host-utilization matrices depict a greater degree of plant utilization in the European ranges compared with the US range. All modes of feeding, except gall forming, were represented in the introduced range; however, only one endophagous feeder was found in the US range, compared with six in the European ranges, and the root-feeding guild was completely absent in the USA (Fig. 4). In the US host-utilization matrix, the chewing mode of feeding was represented by oligophagous feeders (*P. xylostella*, *C. obstrictus*, *Phyllotreta* sp.), and the remaining species were polyphagous

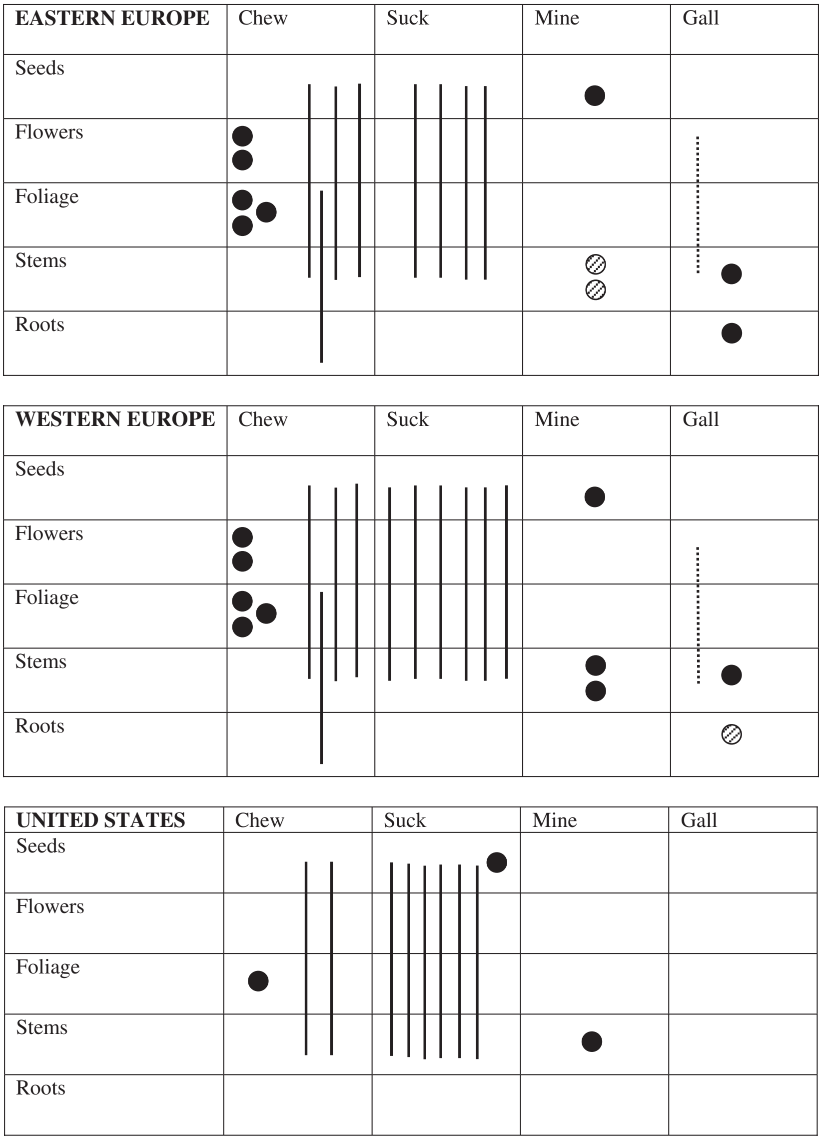

Figure 4 Host-utilization matrices for the core species pools in each of three regions sampled in 2002 and 2003 (after Lawton, 1982). See Fig. 2 for list of core species. Each dot or line in a matrix represents one species. Dots indicate a more restricted feeding niche; lines indicate a wider niche breadth. A shaded dot or dashed line indicates that the species was not actually present in the analysed samples, but was collected or reared from shoots harvested in the respective region.

phloem sap-sucking species. The stem-mining niche in the USA was occupied by an indigenous North American weevil, *Ceutorhynchus americanus* Buchanan.

DISCUSSION

Community richness, diversity and evenness

As predicted, species richness, diversity and evenness were greatest in the area of origin of *L. draba*, slightly reduced in the expanded range, and lowest in the introduced range. Considering that *L. draba* has most probably existed as a distinct lineage since the end of the Pleistocene (*c.* 11,000 years) in its native range (K. Mummenhoff, personal communication), whereas in the expanded Western European range herbivores have encountered the species for only *c.* 300 years (Hegi, 1986), species richness and diversity were more similar than expected. The similarity between Western and Eastern Europe may have been due to the inclusion of Hungary in the Western region. Although Hungary is considered part of the expanded range (Ball, 1964), *L. draba* has certainly occurred there longer than in more western localities. The westerly spread of *L. draba*, as suggested by Hegi (1986), has probably resulted in a gradient of diversity increasing towards the true native region. Increased travel and commerce in Europe have also probably facilitated the spread of the plant and associated herbivores, which explains the presence of many herbivorous species in both European ranges. Herbivores dispersing within continents have less formidable geographical barriers (e.g. mountain ranges) to overcome than species spreading to other continents (e.g. crossing oceans). One of the specialist herbivores on *L. draba*, the seed-feeding weevil, *Ceutorhynchus turbatus* Schultze, has been documented following its host plant to Western Europe (Morris, 1982; van den Berg & van de Sande, 1999).

In the introduced range, herbivores have encountered *L. draba* for approximately 150 years (Mulligan & Frankton, 1962; Mulligan & Findlay, 1974). The most common species colonizing *L. draba* in the USA are highly polyphagous, which is in accordance with the predictions for arthropods colonizing introduced plants (Strong *et al.*, 1984; Fraser & Lawton, 1994). The widespread distribution of *L. draba* and its functional similarity to other plants native to North America also contributes to the richness of herbivores found in this range. There are 37 endemic Brassicaceae genera in North America comprising over 600 native species, most of which are distributed primarily in western North American (Al-Shehbaz, 1984), which undoubtedly allows functionally pre-adapted species to utilize *L. draba*. Similarly, other comparative studies have also found a greater total number of herbivorous species in the native range, but a substantial number of highly polyphagous species in the introduced range (Goeden, 1974; Wilson *et al.*, 1990; Jobin *et al.*, 1996; Memmott *et al.*, 2000).

Both the Shannon (H') and the Simpson (D) indices showed that the arthropod community diversity increased toward the centre of origin of *L. draba* (Fig. 1b,c). While species richness contributed to the differences in diversity among the three regions, the difference in diversity between the USA and the European ranges is most strongly influenced by evenness (Fig. 1d). This is due to the arthropod community in the USA being dominated by a few generalist species [*F. occidentalis*, *Lygus elisus* Van Duzee and *Bryobia praetiosa* (Koch)], while the community tends to be more evenly balanced towards the centre of origin.

The majority of species collected on *L. draba* in each range are infrequent, and belong to the tramp species pool (Fig. 1a–d). It is unclear why the richness of the tramp species pool increases towards the centre of origin. However, *c.* 10% of the total herbivorous communities in Europe were flower-feeders (M.G. Cripps, unpublished data). It may be that, in its native range, *L. draba* serves as important pollen/nectar source for herbivorous species in early spring when few herbaceous species are flowering. Furthermore, *L. draba* typically occurs in smaller patches in its native range and is usually present in more diverse plant communities than in the invaded US range (McKenney, 2005). Therefore the higher overall herbivore richness in the native range may be due to complex, multifaceted attributes of greater ecosystem diversity. Although the overall herbivore community is more rich, diverse and even in the native range, this does not necessarily translate to greater impact on *L. draba* (Maron & Vilà, 2001; Agrawal & Kotanen, 2003; Agrawal *et al.*, 2005). The tramp species pool is unlikely to have a regulating influence on *L. draba*, as this group consists of mostly polyphagous species with variable occurrence (Cornell & Lawton, 1992).

Specialization, host utilization and the enemy-release hypothesis

The lack of specialist herbivores in the invaded range of *L. draba* (Figs 2–4) documented in this study provides strong support for the first prediction of the ERH (Keane & Crawley, 2002). Specialized, monophagous feeders were found exclusively in the European ranges of *L. draba*. It is commonly hypothesized that specialized insect–plant relationships are a result of long co-evolutionary histories (Ehrlich & Raven, 1964; Strong *et al.*, 1984; Thompson, 1994; Iwao & Rausher, 1997). Consequently, it is not surprising that a greater number of specialized feeding niches (e.g. mining and galling) are occupied in the native range of *L. draba*. Comparison of the core species pools of *L. draba* show a clear shift from specialized endophagous herbivores in the native range to generalist exophagous herbivores in the introduced range, similar to the results of the few other studies comparing natural enemies of plants in the native and introduced ranges (see reviews by Colautti *et al.*, 2004; Hinz & Schwarzlaender, 2004). Furthermore, the core species groups in the European ranges are largely comprised of oligophagous species, which is in accordance with other work documenting that oligophages are predominant on Brassicaceae plants in Europe (Frenzel & Brandl, 1998). While Frenzel & Brandl (2003) found that species diversity was similar on native and introduced Brassicaceae plants in Poland, in our study core species in the US range were predominantly polyphages. Considering that their study was conducted close to the centre of origin of the Brassicaceae, it is not surprising that family-level specialists were able to utilize introduced Brassicaceae plants. It is unclear whether the introduced plants used in their study represent species that have expanded their range, rather than intercontinental introductions.

Secondly, the ERH predicts that host switching by specialists of native congeners will be rare (Keane & Crawley, 2002). However, in this study the native North American weevil *C. americanus* was commonly found mining in the stems of invasive *L. draba* (McKenney, 2005). The host affinity of *C. americanus* is unknown, except that it has been collected on *Brassica* and *Lepidium* species, *Medicago sativa* (alfalfa), and at least one specimen was reared from *Lepidium virginicum* (Buchanan, 1937; Scheibner, 1963). In addition, this species was never listed as a pest on *Brassica* crops (Bonnemaison, 1965; Lamb, 1989), suggesting that its host range may be restricted, possibly only including *Lepidium* and species in closely related genera. It is unclear why more specialist host switches were not found. It may be that, despite the wide radiation of the genus *Lepidium* in the western USA (Rollins, 1993), there are few insect herbivores associated with plants in the genus, supported by the fact that literature and database searches did not reveal any specialist herbivores. Alternatively, it may be that *L. draba* has not been in North America long enough for more host switches to occur (Andow & Imura, 1994). Widespread distribution is thought to have promoted novel arthropod host switches to soybean crops (Kogan & Turnipseed, 1987), and has probably also facilitated the switch of *C. americanus* to *L. draba*. Most native *Lepidium* species have very restricted distributions (USDA, NRCS, 2006), which might also account for the lack of specialized arthropod herbivores. Host switches to introduced plants by native arthropod species have been documented in other cases (Thomas *et al.*, 1987; Novotny *et al.*, 2003); however, lack of host switching by specialists of native congeners to an introduced plant was noted by Olckers & Hulley (1991). We are aware of only one other documented case of a native stem miner utilizing a non-indigenous host (Creed & Sheldon, 1995). Thus new host associations could be rare, or it may simply be that researchers have not looked for specialists of native congeners on introduced plants (Maron & Vilà, 2001).

Thirdly, the ERH predicts that generalist herbivores will have a greater impact on native than on introduced species (Keane & Crawley, 2002). Several studies have documented greater herbivore damage on native compared with introduced species, supporting the ERH prediction (Schierenbeck *et al.*, 1994; Siemann & Rogers, 2003; Lankau *et al.*, 2004; Carpenter & Cappuccino, 2005). Conversely, studies have also shown that herbivore abundance, richness and damage do not differ between introduced and related native plants (Yela & Lawton, 1997; Agrawal & Kotanen, 2003; Agrawal *et al.*, 2005). While herbivore abundance does not necessarily translate into plant damage, we found no indication for reduced generalist herbivory on *L. draba* in the introduced range. This is the first study to document greater abundance of native generalist species on an invasive weed in its introduced range compared with its native range, which is contrary to our prediction. Similarly, our findings do not support the prediction by Tallamy (2004) that introduced plants might reduce native insect abundance, nor do our results support the third prediction of the ERH (Keane & Crawley, 2002). Memmott *et al.* (2000) found no significant difference in the abundance of generalist herbivores between native and introduced ranges of *Cytisus scoparius*. However, the authors noted that in the introduced range generalist feeders were dominant, and in the native range specialists were more abundant than generalists (Memmott *et al.*, 2000). In contrast, our study shows a greater abundance of generalist (polyphagous) herbivores compared with specialists (monophagous or oligophagous species), regardless of range.

Host utilization is not different between the native and expanded ranges, in contrast to our expectation, but it is greater in either European range compared with the introduced US range, as predicted. While our data indicate a relationship between time of *L. draba* naturalization and overall herbivore richness and utilization, herbivore abundance was highest in the most recently adopted range, which indicates no simple relationship between time of naturalization and abundance of herbivores. Similarly, Carpenter & Cappuccino (2005) found no relationship between time of invasive plant introduction and level of herbivory.

There is no simple explanation for the greater total abundance of herbivores in the US range. All the US polyphagous core species are native to the USA, and all the European polyphagous core species are native to Europe, except *F. occidentalis*, which is native to the western USA (Pergande, 1895; Priesner, 1928), and introduced to Europe in the early 1980s (Kirk & Terry, 2003). There is no established native range of *B. praetiosa* or *M. persicae*, but these two species are considered to have cosmopolitan distributions (Pritchard & Baker, 1955; van Emden *et al.*, 1969). There was no correlation between mean arthropod abundance and mean shoot density or biomass (M.G. Cripps, unpublished data), indicating no simple direct relationship between arthropod abundance and plant vigour. As all the US polyphagous core species are native to that range, release from natural enemies cannot explain their high abundances. However, the search for enemy-free space has been shown to facilitate herbivore shifts to novel host plants (Murphy, 2004), and therefore may play a role in the greater abundance of polyphagous species in the USA.

The differential impact of specialist vs. generalist herbivory in regulating plant populations is also unclear (Maron & Vilà, 2001; Keane & Crawley, 2002). In the European ranges of *L. draba*, there is a diverse group of specialist and generalist herbivores comprising multiple guilds, whereas in the US range, host utilization is predominantly by the generalist sap-sucking arthropods. Although the abundance of generalists is greater in the introduced range, the variety of feeding modes of generalists is similar in all three ranges. The core polyphagous species on *L. draba* in all three ranges primarily comprise three feeding modes: cellular sap ingestion by *F. occidentalis* (Kindt *et al.*, 2003) and *B. praetiosa* (Krantz, 1970; Jeppson *et al.*, 1975); mirid feeding that uses a macerate-flush feeding mode to exploit mesophyll and apical meristem tissue (Wheeler, 2000); and phloem feeding by cicadellids (*Ceratagallia* spp.) (Backus, 1985) and *M. persicae* (van Emden *et al.*, 1969). Since the feeding modes of the core polyphagous species are similar in all three ranges, these generalist species are probably not important regulators of *L. draba* populations. Therefore the specialist herbivores in the native range are of particular interest in the role they might play in regulating *L. draba* populations. Specialized herbivores such as *Psylliodes wrasei* Leonardi et Arnold can kill newly developing shoots (H.L.H., unpublished data); the eriophyid mite *Aceria draba* (Nalepa) can prevent seed development (Lipa, 1978; M.G. Cripps, personal observation); and the gall-forming weevils *Ceutorhynchus cardariae* Korotyaev and *Ceutorhynchus assimilis* (Marsham) form stem and root galls, which can act as nutrient sinks that stunt plant growth (Harris & Shorthouse, 1996). Therefore, if specialized herbivores are important *L. draba* population-regulators, the escape from specialist herbivores might facilitate its invasiveness in the USA.

In summary, the complete absence of specialist arthropod herbivores in the introduced range of *L. draba* reported here provides strong support for the first prediction of the ERH as outlined by Keane & Crawley (2002). There is evidence of an oligophagous stem miner switching to and utilizing *L. draba* as a host plant. Generalist herbivore abundance was much greater in the introduced US range than in both European ranges, but our data do not indicate that generalist herbivory is more damaging. We suggest that generalist herbivore abundance, and generalist herbivory is of little importance as a regulating factor for *L. draba* (Crawley, 1989; McEvoy, 2002). Conversely, we argue that specialized herbivores may contribute to the population regulation of *L. draba*, and that the absence of specialist natural enemies in the introduced range might contribute to *L. draba* invasiveness. The differential effects of generalist vs. specialist insect herbivory have, to our knowledge, not yet been rigorously tested in an invasive plant system. Manipulative biogeographical field studies in both the native and introduced ranges could provide important knowledge on the relative importance of generalist vs. specialist enemy release for plant invasions.

ACKNOWLEDGEMENTS

We are greatly indebted to A. Diaconu, A. Gumovsky, V. Fursov, R. Tomov and S. Töpfer for their assistance and hospitality during European field surveys. At the University of Idaho, R. Biggam, K. Marske and R. Sprague assisted with morphotyping work. James Johnson lent his insect taxonomy knowledge on many occasions, and Franck Merickel allowed access to the University of Idaho museum collections. We thank B. Korotyaev (Curculionoidea) and his colleagues for providing the bulk of the European species determinations. Other species determinations were provide by B. Gerdeman (Tetranychidae), A. Hamilton (Cicadellidae), J. Jelinek (Nitidulidae), K. Pike (Aphididae), A. Konstantinov (Chrysomelidae), L. Mound (Thysanoptera) and M. Schwartz (Miridae), for which we are extremely grateful. We also thank Sanford Eigenbrode, Marc Klowden, John Gaskin, Urs Schaffner, Bradford Hawkins, and an anonymous reviewer for helpful comments on the manuscript. This work was funded by a grant to M.S. from the USDA NRI Agreement no. IDA00108-CG. Additional funding was provided by grants to M.S. from the Idaho State Department of Agriculture and the Bureau of Indian Affairs. This is publication number 05P25 of the Idaho Agricultural Experiment Station.

REFERENCES

Agrawal, A.A. & Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters*, **6,** 712–715.

Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W. & Klironomos, J. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, **86,** 2979–2989.

Al-Shehbaz, A. (1984) The tribes of Cruciferae (Brassicaceae) in the southeastern United States. *Journal of the Arnold Arboretum*, **65,** 343–373.

Al-Shehbaz, I.A., Mummenhoff, K. & Appel, O. (2002) *Cardaria, Coronopus* and *Stroganowia* are united with *Lepidium*. *Novon*, **12,** 5–11.

Andow, D.A. & Imura, O. (1994) Specialisation of phytophagous arthropod communities on introduced plants. *Ecology*, **75,** 296–300.

Ashbourne, S.R.C. & Putman, R.J. (1987) Competition, resource partitioning and species richness in the phytophagous insects of red oak and aspen in Canada and the UK. *Acta Oecologica*, **8,** 43–56.

Backus, E.A. (1985) Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior. *The leafhoppers and planthoppers* (ed. by L.R. Nault and J.G. Rodriguez), pp. 163–194. John Wiley & Sons, New York.

Ball, P.W. (1964) *Cardaria* Desv. *Flora Europaea*, Vol. 1 (ed. by T.G. Tutin, V.H. Heywood, N.A. Burges, D.H. Valentine, S.M. Walters and D.A. Webb), p. 333. Cambridge University Press, Cambridge, UK.

Bellue, M.K. (1933) Hoary cress. *Monthly Bulletin, Department of Agriculture, State of California*, **22,** 287.

van den Berg, C. & van de Sande, J.C. (1999) *Ceutorhynchus turbatus* new for the Netherlands (Coleoptera: Curculionidae). *Entomologische Berichten, Amsterdam*, **59,** 157–159.

Bonnemaison, L. (1965) Insect pests of crucifers and their control. *Annual Review of Entomology*, **10,** 233–256.

Buchanan, L.L. (1937) A new species of *Ceutorhynchus* from North America (Coleoptera: Curculionidae). *Bulletin of the Brooklyn Entomological Society*, **32,** 205–207.

Campobasso, G., Colonnelli, E., Knutson, L., Terragitti, G. & Cristofaro, M. (1999) *Wild plants and their associated insects in the Palearctic region, primarily Europe and the Middle East*. ARS-147. US Department of Agriculture, Washington, DC.

Carpenter, D. & Cappuccino, N. (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology*, **93,** 315–321.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7,** 721–733.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61,** 1–12.

Corns, W.G. & Frankton, C. (1952) Hoary cress in Canada with particular reference to their distribution and control in Alberta. *Scientific Agriculture*, **32,** 484–495.

Crawley, M.J. (1987) What makes a community invasible?. *Colonisation, succession and stability* (ed. by A.J. Gray, M.J. Crawley and P.J. Edwards), pp. 429–453. Blackwell Scientific Publications, Oxford, UK.

Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, **34,** 531–564.

Creed, R.P. & Sheldon, S.P. (1995) Weevils and watermilfoil: did a North American herbivore cause the decline of an exotic plant? *Ecological Applications*, **5,** 1113–1121.

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.

Dieckmann, L. (1972) *Beiträge zur Insektenfauna der DDR, Coleoptera, Curculionidae, Ceutorhynchinae*, 22 (1). Institut für Pflanzenforschung (BZA) der Deutschen Akademie der Landwirtschaftswissenschaften, Berlin.

Efron, B. & Tibshirani, R. (1998) *An introduction to the bootstrap*. CRC Press, Boca Raton, FL.

Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, **18,** 586–608.

Elton, C.S. (1958) *The ecology of invasions of animals and plants*. Methuen, London.

van Emden, H.F., Eastop, V.F., Hughes, R.D. & Way, M.J. (1969) The ecology of *Myzus persicae*. *Annual Review of Entomology*, **14,** 197–270.

Fenner, M. & Lee, W.G. (2001) Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. *New Zealand Journal of Ecology*, **25,** 95–99.

Fraser, S.M. & Lawton, J.H. (1994) Host range expansion by British moths onto introduced conifers. *Ecological Entomology*, **19,** 127–137.

Frenzel, M. & Brandl, R. (1998) Diversity and composition of phytophagous insect guilds on Brassicaceae. *Oecologia*, **113,** 391–399.

Frenzel, M. & Brandl, R. (2003) Diversity and abundance patterns of phytophagous insect communities on alien and native host plants in the Brassicaceae. *Ecography*, **26,** 723–730.

Freude, H., Harde, K.W. & Lohse, G.A. (1983) *Die Käfer Mitteleuropas, Band 11, Rhynchophora*. Goecke & Evers Verlag, Krefeld, Germany.

Gaskin, J.F., Bon, M.-C. & Zhang, D.-Y. (2005) Invasion of *Lepidium draba* (Brassicaceae) in the western USA: distributions and origins of chloroplast DNA haplotypes. *Molecular Ecology*, **14,** 2331–2341.

Goeden, R.D. (1974) Comparative survey of the phytophagous insect faunas of Italian thistle *Carduus pycnocephalus*, in southern California and southern Europe relative to biological control. *Environmental Entomology*, **3,** 464–474.

Groh, H. (1940) Turkestan alfalfa as a medium of weed introduction. *Scientific Agriculture*, **21,** 36–43.

Harris, P. & Shorthouse, J.S. (1996) Effectiveness of gall inducers in weed biological control. *Canadian Entomologist*, **128,** 1021–1055.

Hegi, G. (1986) *Illustriertte Flora von Mitteleuropa. Spermatophyta, Band IV Teil 1. Angiospermae, Dicotyledones 2*. Paul Parey, Berlin.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93,** 5–15.

Hinz, H.L. & Schwarzlaender, M. (2004) Comparing invasive plants from their native and exotic range: what can we learn for biological control? *Weed Technology*, **18,** 1533–1541.

Hocking, R.R. (1985) *The analysis of linear models*. Brooks/Cole Publishing, Monterey, CA.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52,** 577–586.

Imura, O. (2003) Herbivorous arthropod community of an alien weed *Solanum carolinense* L. *Applied Entomology and Zoology*, **38,** 293–300.

Iwao, K. & Rausher, M.D. (1997) Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *The American Naturalist*, **149,** 316–355.

Jakobs, G., Weber, E. & Edwards, P.J. (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions*, **10,** 11–19.

Jeppson, L.R., Keifer, H.H. & Baker, E.W. (1975) *Mites injurious to economic plants*. University of California Press, Berkeley, CA.

Jobin, A., Schaffner, U. & Nentwig, W. (1996) The structure of the phytophagous insect fauna on the introduced weed *Solidago altissima* in Switzerland. *Entomologia Experimentalis et Applicata*, **79,** 33–42.

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

Kindt, F., Joosten, N.N., Peters, D. & Tjallingii, W.F. (2003) Characterisation of the feeding behaviour of western flower thrips in terms of electrical penetration graph (EPG) waveforms. *Journal of Insect Physiology*, **49,** 183–191.

Kirk, W.D.J. & Terry, L.I. (2003) The spread of the western flower thrips *Frankliniella occidentalis* (Pergande). *Agricultural and Forest Entomology*, **5,** 301–310.

Kogan, M. & Turnipseed, S.G. (1987) Ecology and management of soybean arthropods. *Annual Review of Entomology*, **32,** 507–538.

Krantz, G.W. (1970) *A manual of acarology*. Oregon State University Press, Corvallis, OR.

Lamb, R.J. (1989) Entomology of oilseed *Brassica* crops. *Annual Review of Entomology*, **34,** 211–229.

Lankau, R.A., Rogers, W.E. & Siemann, E. (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. *Ecological Entomology*, **29,** 66–75.

Lawton, J.H. (1982) Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology*, **51,** 573–595.

Lipa, J.J. (1978) Preliminary studies on *Aceria drabae* (Nal.) (Acarina, Eriophyiidae) and its usability in biological control of hoary cress (*Cardaria draba* L.) (Cruciferae). *Prace Naukowe Instytutu Ochrony Roslin*, **20,** 139–155.

Louda, S.M. (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology*, **64,** 511–521.

Louda, S.M. (1994) Experimental evidence for insect impact on populations of short-lived, perennial plants, and its application in restoration ecology. *Restoration of endangered species* (ed. by M.L. Bowles and C.J. Shelan), pp. 118–138. Cambridge University Press, Cambridge, UK.

Louda, S.M. & Potvin, M.A. (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology*, **76,** 229–245.

Lyons, K.E. (1998) *Elemental stewardship abstract for Cardaria draba* (L.) Desv. Heart-podded Hoary Cress, *Cardaria chalepensis* (L.) Hand-Maz., Lens-podded Hoary Cress and *Cardaria pubescens* (C.A. Meyer) Jarmolenko, Globe-podded Hoary Cress. The Nature Conservancy, Arlington, VA. Available from http://tncweeds.ucdavis.edu/esadocs/documents/card_sp.html

Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Science, Oxford, UK.

Magurran, A.E. & Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422,** 714–716.

Maron, J.L. & Gardner, S.N. (2000) Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia*, **124,** 260–269.

Maron, J.L. & Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95,** 361–373.

McEvoy, P.B. (2002) Insect–plant interactions on a planet of weeds. *Entomologia Experimentalis et Applicata*, **104,** 165–179.

McKenney, J.L. (2005) *An inter-continental comparison of vigor and herbivory for the invasive plant Lepidium draba*. MSc Thesis, University of Idaho, Moscow, ID.

Memmott, J., Fowler, S.V., Paynter, Q., Sheppard, A.W. & Syrett, P. (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica*, **21,** 213–222.

Morris, M.G. (1982) *Ceutorhynchus turbatus* Schultze (Col., Curculionidae) in Dorset, Bedfordshire and North Essex. *Entomologists' Monthly Magazine*, **118,** 241.

Mulligan, G.A. & Findlay, J.N. (1974) The biology of Canadian weeds. 3. *Cardaria draba*, *C. chalepensis*, and *C. pubescens*. *Canadian Journal of Plant Science*, **54,** 149–160.

Mulligan, G.A. & Frankton, C. (1962) Taxonomy of the genus *Cardaria* with particular reference to the species introduced into North America. *Canadian Journal of Botany*, **40,** 1411–1425.

Murphy, S.M. (2004) Enemy-free space maintains swallowtail butterfly host shift. *Proceedings of the National Academy of Sciences USA*, **101,** 18048–18052.

Novotny, V., Miller, S.E., Cizek, L., Leps, J., Janda, M., Basset, Y., Weiblen, G.D. & Darrow, K. (2003) Colonising aliens: caterpillars (Lepidoptera) feeding on *Piper aduncum* and *P. umbellatum* in rainforests of Papua New Guinea. *Ecological Entomology*, **28,** 704–716.

Olckers, T. & Hulley, P.E. (1991) Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop. relative to indigenous *Solanum* species in Natal/KwaZulu and the Transkei. *Journal of the Entomological Society of South Africa*, **54,** 39–50.

Oliver, I. & Beattie, A.J. (1996) Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology*, **10,** 99–109.

Paynter, Q., Fowler, S.V., Hinz, H.L., Memmott, J., Shaw, R., Sheppard, A.W. & Syrett, P. (1996) Are seed-feeding insects of use for the biological control of broom? *Proceedings of the IX International Symposium on Biological Control of Weeds* (ed. by V.C. Moran and J.H. Hoffmann), pp. 495–501. University of Cape Town, Stellenbosch, South Africa.

Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5,** 285–307.

Pergande, T. (1895) Observation on certain Thripidae. *Insect Life, Washington*, **7,** 390–395.

Prati, D. & Bossdorf, O. (2004) A comparison of native and introduced populations of the South African Ragwort *Senecio inaequidens* DC. in the field. *Results of worldwide ecological studies* (ed. by S.W. Breckle, B. Schweizer and A. Fangmeier), pp. 353–359. Verlag Günter Heimbach, Stuttgart, Germany.

Priesner, H. (1928) *Die Thysanopteran Europas*. Verlag von Fritz Wagner, Wein, Austria.

Pritchard, A.E. & Baker, E.W. (1955) *A revision of the spider mite family Tetranychidae*. Pacific Coast Entomological Society, San Francisco, CA.

Putman, R.J. (1994) *Community ecology*. Chapman & Hall, New York.

Rice, P. (2005) *Invaders database system*. http://invader.dbs.umt.edu.

Rollins, R.C. (1993) *The Cruciferae of continental North America*. Stanford University Press, Stanford, CA.

Root, R.B. (1967) The niche exploitation pattern of the blue-grey gnat-catcher. *Ecological Monographs*, **37,** 317–350.

Root, R.B. (1996) Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*, **77,** 1074–1087.

SAS Institute Inc. (2004) *SAS Online Doc 9.1.2*. SAS Institute Inc., Cary, NC.

Scheibner, R.A. (1963) *A taxonomic study of the genus* Ceutorhynchus (Coleoptera, Curculionidae). PhD Thesis, Michigan State University, Ann Arbor, MI.

Schierenbeck, K.A., Mack, R.N. & Sharitz, R.R. (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, **75,** 1661–1672.

Scurfield, G. (1962) *Cardaria draba* (L.) Desv. (*Lepidium draba* L.). *Journal of Ecology*, **50,** 489–499.

Sheppard, A.W., Brun, L.A. & Lewis, R.C. (1996) A demographic comparison of common heliotrope, *Heliotropium europaeum* L.: southern Australia and southern France. *Proceedings of the 11th Australian Weeds Conference* (ed. by R.C.H. Shepherd), pp. 286–290. Weed Science Society of Victoria, Melbourne, Australia.

Siemann, E. & Rogers, W.E. (2003) Herbivory, disease, recruitment limitation, and success of alien and native tree species. *Ecology*, **84,** 1489–1505.

Sobian, R. & Zwölfer, H. (1985) Phytophagous insect species associated with flower heads of yellow starthistle (*Centaurea solstitialis* L.). *Zeitschrift für Entomologie*, **99,** 301–321.

Southwood, T.R.E. & Henderson, P.A. (2000) *Ecological methods*, 3rd edn. Blackwell Science, Oxford, UK.

Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on plants: community patterns and mechanisms*. Blackwell Scientific Publications, Boston, MA.

Syrett, P., Fowler, S.V., Coombs, E.M., Hosking, J.R., Markin, G.P., Paynter, Q.E. & Sheppard, A.W. (1999) The potential for biological control of scotch broom (*Cytisus scoparius*) (Fabaceae) and related weedy species. *Biocontrol News and Information*, **20,** 17–34.

Tallamy, D.W. (2004) Do alien plants reduce insect biomass? *Conservation Biology*, **18,** 1689–1692.

Thomas, C.D., Singer, M.C., Mallet, J.L.B., Parmesan, C. & Billington, H.L. (1987) Incorporation of a European weed into the diet of a North American Herbivore. *Evolution*, **41,** 892–901.

Thompson, J.N. (1994) *The coevolutionary process*. University of Chicago Press, Chicago, IL.

USDA, NRCS (2006) *The PLANTS database*, Ver. 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA.

Vilà, M., Maron, J.L. & Marco, L. (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia*, **142,** 474–479.

Weiss, P.W. & Milton, S. (1984) *Chrysanthemoides monilifera* and *Acacia longifolia* in Australia and South Africa: studies from North America and Europe. *Proceedings of the 4th International Conference on Mediterranean Ecosystems* (ed. by J.H. Brock, M. Wade, P. Pysek and D. Green), pp. 159–160. University of Western Australia, Perth.

Wheeler, A.G., Jr (2000) Plant bugs (Miridae) as pests. *Heteroptera of economic importance* (ed. by C.W. Schaefer and A.R. Panizzi), pp. 37–84. CRC Press, New York.

Wilson, C.G., Flanagan, G.J. & Gillett, J.D. (1990) The phytophagous insect fauna of the introduced shrub *Mimosa pigra* in northern Australia and its relevance to biological control. *Environmental Entomology*, **19,** 776–784.

Wolfe, L.M. (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *The American Naturalist*, **160,** 705–711.

Woodburn, T.L. & Sheppard, A.W. (1996) The demography of *Carduus nutans* as a native and alien weed. *Plant Protection Quarterly*, **11,** 236–238.

Yela, J.L. & Lawton, J.H. (1997) Insect herbivore loads on native and introduced plants: a preliminary study. *Entomologia Experimentalis et Applicata*, **85,** 275–279.

BIOSKETCHES

Michael Cripps recently completed his MSc in entomology at the University of Idaho under the supervision of Mark Schwarzländer. He carried out the European components of this research while stationed at CABI Bioscience, Switzerland. His general scientific interests are in biological control, invasive species ecology, community ecology, and assessing biodiversity. He is particularly interested in studying plant invasions from a biogeographical perspective.

Mark Schwarzländer is an assistant professor at the University of Idaho. His research focuses on biological control of weeds, bionomics of herbivore insects, insect–plant interactions, and non-target impacts of biocontrol agents.

Jessica McKenney recently completed her MSc in entomology at the University of Idaho under the supervision of Mark Schwarzländer. She carried out the American components of this research.

Hariet Hinz is a senior research scientist at CABI Bioscience, Switzerland. Her research focuses on classical biological control of weeds, and the ecology of invasive weeds.

William Price provides statistical and programming support to researchers in the College of Agriculture and Life Sciences at the University of Idaho.

Editor: Bradford Hawkins