Can the enemy release hypothesis explain the success of *Rumex* (Polygonaceae) species in an introduced range?

Cristian-Andrei Costan · **William K. Godsoe** · **Jennifer L. Bufford** · **John W. M. Marris** · **Philip E. Hulme**

Abstract The enemy release hypothesis states that introduced plants have a competitive advantage due to their release from co-evolved natural enemies (i.e., herbivores and pathogens), which allows them to spread rapidly in new environments. This hypothesis has received mixed support to date, but previous studies have rarely examined the herbivore community, plant damage, and performance simultaneously and largely ignored below-ground herbivores. We tested for enemy release by conducting large scale field surveys of insect diversity and abundance in both the native (United Kingdom) and introduced (New Zealand) ranges of three dock (*Rumex*, Polygonaceae) species: *R. conglomeratus* Murray (clustered dock), *R. crispus* L. (curly dock) and *R. obtusifolius* L. (broad-leaved dock). We captured both above- and below-ground insect herbivores, measured herbivore damage, and plant biomass as an indicator for performance. In the introduced range, *Rumex* plants had a lower diversity of insect herbivores, all insect specialists present in the native range were absent and plants had lower levels of herbivore damage on both roots and leaves. Despite this, only *R. crispus* had greater fresh weight in the introduced range compared to the native range. This suggests that enemy release, particularly from below-ground herbivores, could be a driver for the success of *R. crispus* plants in New Zealand, but not for *R. conglomeratus* and *R. obtusifolius*.

Keywords Alien species · Native · Introduced · Herbivory · Plant invasion · Weeds

C.-A. Costan (✉) · W. K. Godsoe · J. L. Bufford · J. W. M. Marris · P. E. Hulme
Bio-Protection Research Centre, Lincoln, Canterbury 7647, New Zealand
e-mail: andrei.costan@far.org.nz

W. K. Godsoe
e-mail: William.godsoe@lincoln.ac.nz

J. L. Bufford
e-mail: Jennifer.bufford@lincoln.ac.nz

J. W. M. Marris
e-mail: John.marris@lincoln.ac.nz

P. E. Hulme
e-mail: Philip.hulme@lincoln.ac.nz

C.-A. Costan
Foundation for Arable Research, Templeton, Canterbury 7678, New Zealand

Introduction

The success of introduced plants is often credited to their escape from co-evolved natural enemies (Keane and Crawley 2002; Lake and Leishman 2004; Lambert and Casagrande 2006; Mukherjee et al. 2012). If plants experience enemy escape, then the Enemy Release Hypothesis (ERH) proposes that if plants are limited by herbivores in their native range, loss

of these natural enemies in the introduced range will increase their survival, biomass and fecundity (Williamson and Fitter 1996; Simberloff and Von Holle 1999; Richardson et al. 2000; Maron and Vila 2001; Kolar and Lodge 2001; Keane and Crawley 2002; Bruno et al. 2003; Daehler 2003; Duncan et al. 2003; Keane and Crawley 2002; Huang et al. 2018). Multiple studies, including a meta-analysis (Liu and Stiling 2006), have supported the ERH (Bigger and Marvier 1998; Colautti et al. 2004; Kater 2016; Torchin et al. 2001). In their native range, plants are exposed to pressures from both specialist and generalist herbivores, but specialist herbivores that have coevolved with the plant host rarely occur outside the native range of their host plant (Orians and Ward, 2010). As a result, plant species in the introduced range may have reduced herbivore pressure with mostly polyphagous generalist herbivores, while in their native range they may have both generalist and specialist natural enemies (Frenzel and Brandl 2003; Orians and Ward 2010; Van Lenteren et al. 2003). Studies comparing herbivore communities and the level of herbivory between the native and introduced ranges have found that plants in the introduced range often experience a lower overall diversity of natural enemies, a shift from specialists to generalist herbivores, and reduced herbivory (Colautti et al. 2004; Hinz and Schwarzlaender 2004; Willis et al. 2000), all indicative of enemy escape and possibly leading to enemy release. The success of biocontrol agents underscores the potential for natural enemies to control the population dynamics of their host plant, which can also be taken as evidence for the ERH (DeLoach 1995).

Most studies addressing the ERH that have undertaken field surveys have only examined one or two plant species (Meijer et al. 2016) and typically only look at above-ground natural enemies (Huang et al. 2018). The fact that below-ground insect herbivores have received so little attention is unfortunate, as they are pervasive in most terrestrial ecosystems and play a crucial role in moderating the spread and abundance of plants (Johnson and Rasmann 2015; van Dam 2009; Van Der Putten et al. 2009). Shoot herbivory can lead to a reduction of photosynthetic tissue (Hambäck 2001) and reproductive output (Karban and Strauss 1993; Zangerl et al. 2002). Root herbivory can reduce water and nutrient uptake and disrupt their transportation within the plant (Blossey and Hunt-Joshi 2003;

Zvereva and Kozlov 2012). Furthermore, shoot and root herbivory may interactively influence plant fitness (Johnson et al. 2016; Maron 1998).

In this study, we tested for both enemy escape and enemy release between the native (United Kingdom) and introduced (New Zealand) ranges of three species of *Rumex* (*R. conglomeratus* Murray, *R. crispus* L. and *R. obtusifolius* L.). Here, enemy escape is defined as the absence of specialists in the introduced range, whereas enemy release also implies that plants would have evolved as a results of this reduced specialist pressure. Each of the three plant species are native to Eurasia, occupy a wide range of natural and cultivated habitats across the world (Kubát 1990) and are considered problematic weeds in both the native and introduced environments (Bond et al. 2007). The three *Rumex* species serve as a good model for testing the ERH across a suite of related species because they: (i) have multiple specialist herbivores in the native range (Martinková and Honěk 2004); (ii) occupy similar habitats and often co-occur in both the native and introduced ranges; (iii) were introduced to New Zealand almost two centuries ago, which should have given them sufficient time to acquire natural enemies in their new environment (Atwood and Meyerson 2011); and (iv) were accidental introductions and thus not exposed to deliberate plant breeding that might influence plant traits such as size.

There are at least 32 species of insect herbivores that feed on *R. crispus* and *R. obtusifolius* in the native range (Cavers and Harper 1964). This includes several herbivores that are sufficiently specialized on, and damaging to *Rumex*, that they have been considered as potential biological control agents: the shoot herbivores *Gastrophysa viridula* (De Geer) (Coleoptera, Chrysomelidae) (Martinková and Honěk 2004), *Hypera rumicis* L. (Coleoptera, Curculionidae), species of *Apion* weevils (Grossrieder and Keary 2004) and the root herbivore *Pyropteron chrysidiformis* (Esper) (Lepidoptera, Sesiidae) (Hahn et al. 2016). In particular, *Gastrophysa viridula* can reduce *Rumex* species seed production (Bentley et al. 1980; DeGregorio et al. 1992), regeneration (DeGregorio et al. 1992), leaf and shoot growth (Cottam et al. 1986) and alter *Rumex* cover (Kohout and Kohoutova 1994; Kohout 1994). The larvae of clearwing moths, *Pyropteron* spp., can increase root decay and reduce the number of rosettes in *R. obtusifolius* (Hahn et al. 2016).

Here we tested three predictions of the ERH: (i) insect herbivore communities in the native range will be more diverse than in the introduced range; (ii) the introduced range contains fewer specialist herbivores than the native range; (iii) *Rumex* in the introduced range experience lower levels of herbivory and are larger than their counterparts in the native range.

Materials and methods

To quantify invertebrate herbivore abundance, particularly of specialist natural enemies, as well as leaf and root herbivory, field surveys were conducted in June and July of 2017 in the United Kingdom (UK, native range) and December 2017 and January 2018 in New Zealand (NZ, introduced range). These sampling periods represent the summer in both ranges, when plants were large and not yet senescent. We sampled across England and Scotland in the UK and across the South Island of NZ to encompass a similar array of climatic conditions in both ranges across a large latitudinal gradient as both climate and latitude can influence the strength of enemy release (Allen et al. 2017). For *R. crispus* and *R. obtusifolius*, 16 populations were surveyed from each range, but for *R. conglomeratus* only 12 populations were surveyed in the UK, as only four populations could be located in Scotland. The exact coordinates of the sampling locations can be found in the supplementary material.

Insect and leaf collection in the native and introduced ranges

In each range, insect and leaf samples were collected from 10 individual plants per population (Fig. 1). Although all three *Rumex* species are widespread in both the UK and NZ, we targeted populations that
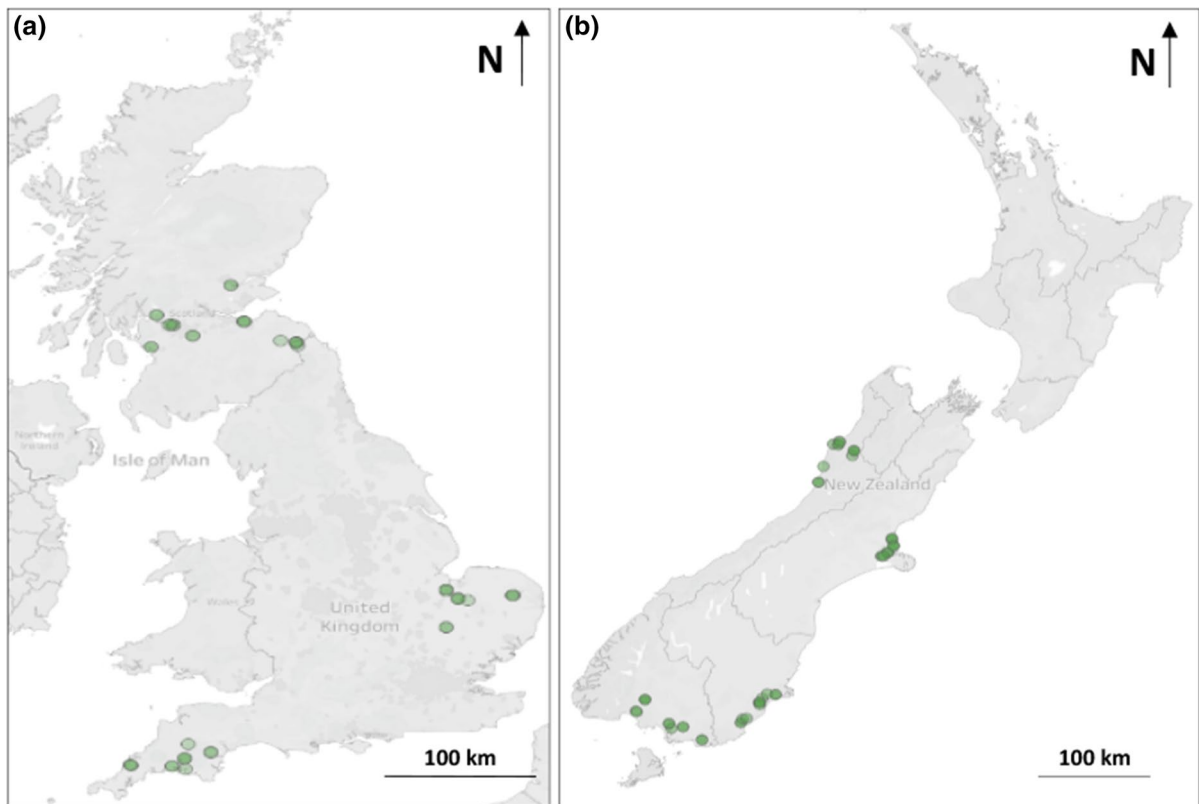

Fig. 1 Populations of three *Rumex* species sampled for herbivorous insect abundance and diversity, leaf and root damage and plant biomass from **a** the United Kingdom (native range) and **b** New Zealand (introduced range). The different shades of green are as a result of overlapping sites

had at least 30 individuals growing in close proximity. In both the UK and NZ, populations were sampled across a range of temperature and precipitation environments which largely overlapped across the two ranges (Carlin 2022). All populations were located below 300 m elevation, at least 1 km away from the coast in open habitat and at least 3.5 km away from other surveyed conspecific populations (mean = 38 km, range = 3.5 to 120.8 km). For the most part, each location only contained a single *Rumex* species, but a few sites in both the native and introduced range contained two species. Since multiple *Rumex* species were often found growing in close proximity to each other, prior to collection, each plant was examined to confirm species identity and exclude obvious hybrids based on morphological traits. In both ranges, we only collected from plants that were either flowering or beginning to set seed, to standardize plant life stage and available herbivore habitat.

To collect insect herbivores, each *Rumex* plant was cut at ground level, placed in a bag and vigorously shaken to cause insects to drop into the bag. The plant was also inspected for insects that did not fall after shaking. In the UK, stem burrowing weevils, such as *Apion violaceum* Kirk can be found in their larval state on *Rumex* from mid-May to mid-June (Freese 1995). This means that sampling in the native range took place after they emerge into adulthood, which is why stems were not inspected for weevil larvae but adults were nevertheless collected on the plants. All insects were stored in 70% ethanol for later identification. This technique is similar to the beat sheet method which is fast, has low variability (Turnipseed 1974) and is effective for counting mobile insects (Deutscher et al. 2003). The roots of each plant were also collected to check for any root feeders inside the central tap root and were scored as damaged by disease (evidence of root rot) and/or herbivory (present/absent).

The five largest leaves from each surveyed plant were collected and photographed to determine the percentage of leaf area damaged by herbivores. The photos were analysed using the image processing program BioLeaf (Machado et al. 2016). To test for differences in performance, we measured fresh biomass by cleaning and weighing the above- and below-ground parts of the collected plants on the same day as collection. Biomass is correlated with

seed production in short-lived herbaceous species like *Rumex* (Pino et al. 2002; Grime et al. 2007).

All herbivorous insect specimens were separated into morphospecies and a representative from each of these groups was identified to order and family (where possible) (Coleoptera: Brentidae, Curculionidae, Elateridae, Nitidulidae, Scarabaeidae; Diptera: Tipulidae; Forficulidae; Hemiptera: Aphidae, Cercopidae, Coreidae, Miridae, Pentatomidae, Psillidae; Lepidoptera: Sesiidae; and Thysanoptera). Known *Rumex*-specialist insects and any insects found in both the native and introduced ranges were identified to the species level: *Gastrophysa viridula* (De Geer), *Hypera rumicis* (L), *Coreus marginatus* (L), *Pyropteron chrysidiforme* (Esper), *Philaenus spumarius* (L) and *Closterotomus norwegicus* (Gmelin). We chose to group insects by morphospecies because they are accurate surrogates for estimates of species numbers (Oliver and Beattie 1996) and the large number of individuals collected meant identifying each to species was not feasible. Morphospecies were classified by feeding mode as chewers or sap-suckers. Chewing insects cause damage that can be visually quantified on leaves and typically include the orders Coleoptera (adults and larvae), Lepidoptera (larvae), Symphyta (sawfly larvae), Orthoptera and Phasmatodea (Elliott et al. 1998). Phloem feeders can remove as much biomass as chewers, but damage from sap-sucking insects is less obvious and more difficult to quantify (Leigh 1997). Sap-sucking insects belong to the orders Hemiptera and Thysanoptera (Elliott et al. 1998).

Statistical analyses

To test whether insect communities differed between the native and introduced ranges, we compared insect abundance across common orders. We tested whether the abundance of insects in each order in NZ was significantly different from what we would expect based on observations in the UK using a chi-squared test. This analysis included four insect orders (Thysanoptera, Lepidoptera, Hemiptera, Coleoptera) and "Others", which due to the very low number of insect individuals (< 20 per order), included all other orders.

Differences in the diversity of insect herbivore morphospecies found on *Rumex* plants between the native (UK) and introduced (NZ) ranges were

calculated using an unpaired *t*-test of the Shannon index entropy at the population level $(H') = -\sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportion of individuals of species i divided by the total number of individuals across all species. The number of species is *s*. Morphospecies richness (the number of insect morphospecies) and total abundance of chewing and sucking insects per plant was modelled using generalized linear mixed effects models with a Poisson distribution. Each model had fixed effects of range (UK or NZ) and total plant fresh weight, which was centred and scaled (Schielzeth 2010), and population was included as a random effect.

To assess whether *Rumex* species herbivore damage differed between the native and introduced ranges, we compared rates of damage for both above- and below-ground plant parts across ranges. To analyse the proportion of roots diseased or damaged within a population we used generalized linear models with a binomial distribution and range (UK or NZ) as the predictor. For the analyses of the percentage of leaf area lost to herbivory and of total plant fresh weight, we used linear mixed effects models with a Gaussian distribution, where range (UK or NZ) was included as a fixed effect and population as a random effect. Percentage of leaf area lost was calculated as the average across five leaves per plant.

To determine the significance of the range effect, a Wald *Z* test or a Wald Chi-squared test were used.

Each *Rumex* species was modelled separately. Residual plots and diagnostics were checked for all analyses to ensure the validity of the model assumptions. All statistical analyses were performed in R (R Core Team 2019) and mixed models were run using 'lme4' R package v.1.1–19 (Bates et al. 2015).

Results

Abundance and diversity of insect herbivores between native and introduced ranges

The abundance of insects across orders in NZ was significantly different from what would be expected based on the abundance of insects across orders in the UK: *R. conglomeratus* ($\chi^2 = 1705$, df = 4, $p < 0.001$), *R. crispus* ($\chi^2 = 2544$, df = 4, $p < 0.001$) and *R. obtusifolius* ($\chi^2 = 3606$, df = 4, $p < 0.001$). In the introduced range, all three *Rumex* species had fewer Coleoptera and Thysanoptera individuals (Fig. 2). In both ranges, Hemiptera individuals were highly abundant and Lepidoptera individuals were uncommon (Fig. 2).

There was a significantly greater Shannon entropy of herbivorous insect morphospecies in the native range for *R. conglomeratus* ($p < 0.001$) and *R. obtusifolius* ($p = 0.032$), but not for *R. crispus* ($p = 0.796$) (Fig. 3). *Rumex conglomeratus, R. crispus* and *R. obtusifolius* all had significantly greater abundance

Fig. 2 Relative abundance of morphospecies across different insect orders found on *Rumex conglomeratus, R. crispus and R. obtusifolius* in their native (UK) and introduced (NZ) ranges. The abundance of each order was calculated as the percentage of the total insect individuals found per range
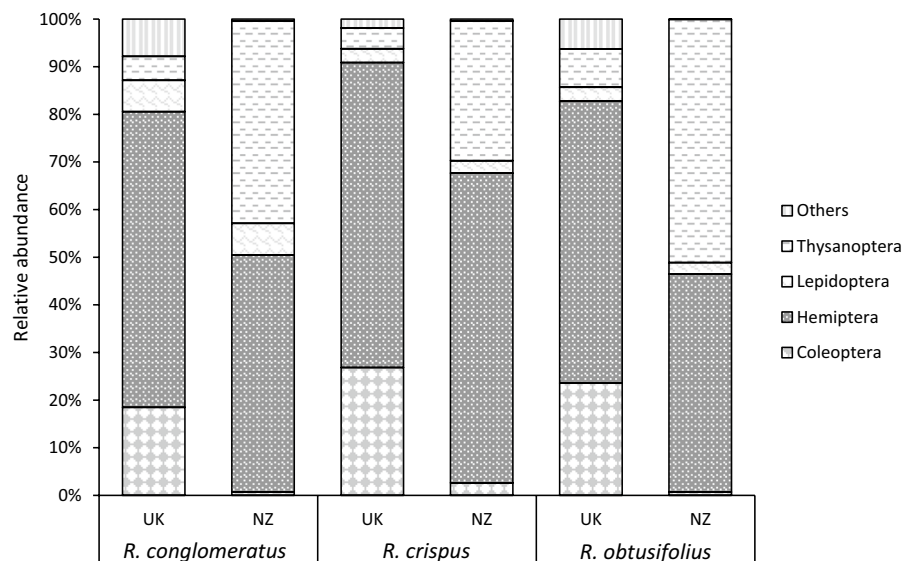
Fig. 3 Mean Shannon entropy of herbivorous insect morphospecies found per plant in populations of *Rumex conglomeratus, R. crispus* and *R. obtusifolius* in their native (UK) and introduced (NZ) ranges. *$P < 0.05$; ***$P < 0.001$. Error bars ± 1SE
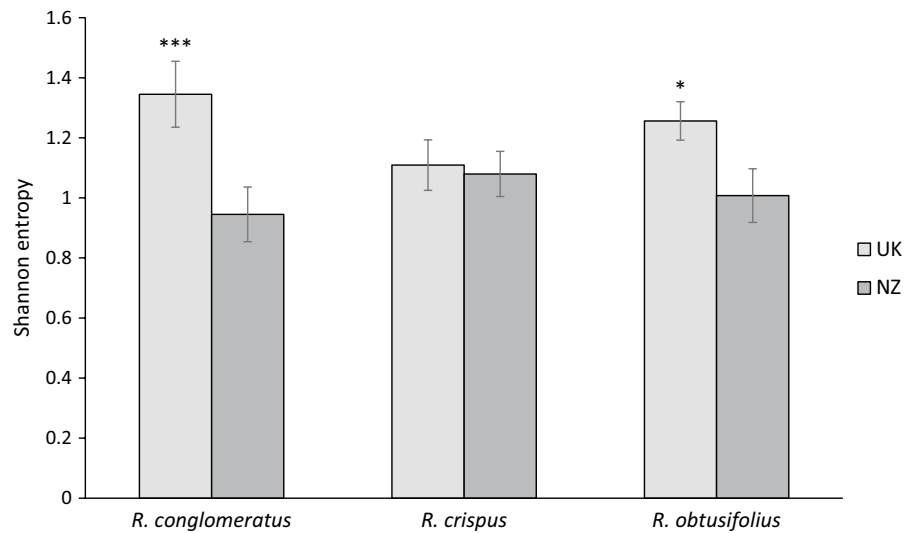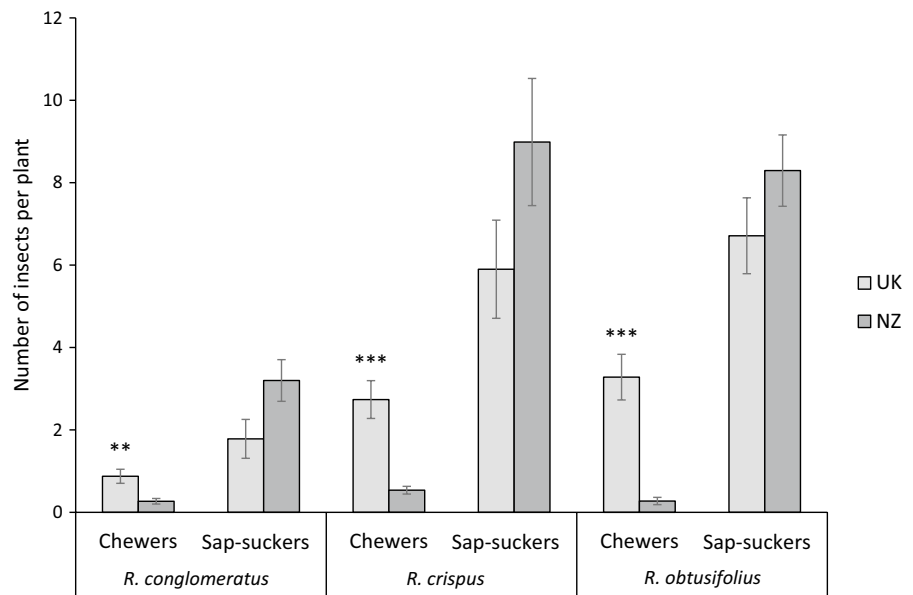
Fig. 4 Mean number of insect herbivores per plant found on *Rumex conglomeratus*, *R. crispus* and *R. obtusifolius* plants in the native (UK) and introduced (NZ) ranges. **$P < 0.01$; ***$P < 0.001$. Error bars ± 1SE

of chewing insects in the native range than in the introduced range ($p \leq 0.004$, Fig. 4). However, no differences between ranges in sap-sucking insect abundance were detected for any *Rumex* species ($p \geq 0.17$) (Fig. 4).

In the native range, the leaf specialist *Gastrophysa viridula* was found on 3% of *R. conglomeratus* (mean ± 1SE 0.09 ± 0.06 insects per plant), 10% of *R. crispus* (0.94 ± 0.32) and 16% of *R. obtusifolius* (1.26 ± 0.45) and the root specialist *Pyropteron chrysidiforme* was found on 2% of *R. conglomeratus*

(mean ± 1SE insects per plant 0.02 ± 0.01), and 6% of *R. crispus* and *R. obtusifolius* (0.06 ± 0.02). No specialist insect herbivores were found in the introduced range. However, two generalist hemipteran species native to Europe, *Philaenus spumarius* and *Closterotomus norwegicus*, were present in large numbers on plants in both ranges.

Fig. 5 Percent of plants with damaged roots in a population **a** and percent leaf area damaged by herbivory **b** for *Rumex conglomeratus*, *R. crispus* and *R. obtusifolius* plants in the native (UK) and introduced (NZ) ranges. ***$P < 0.001$. Error bars ± 1SE
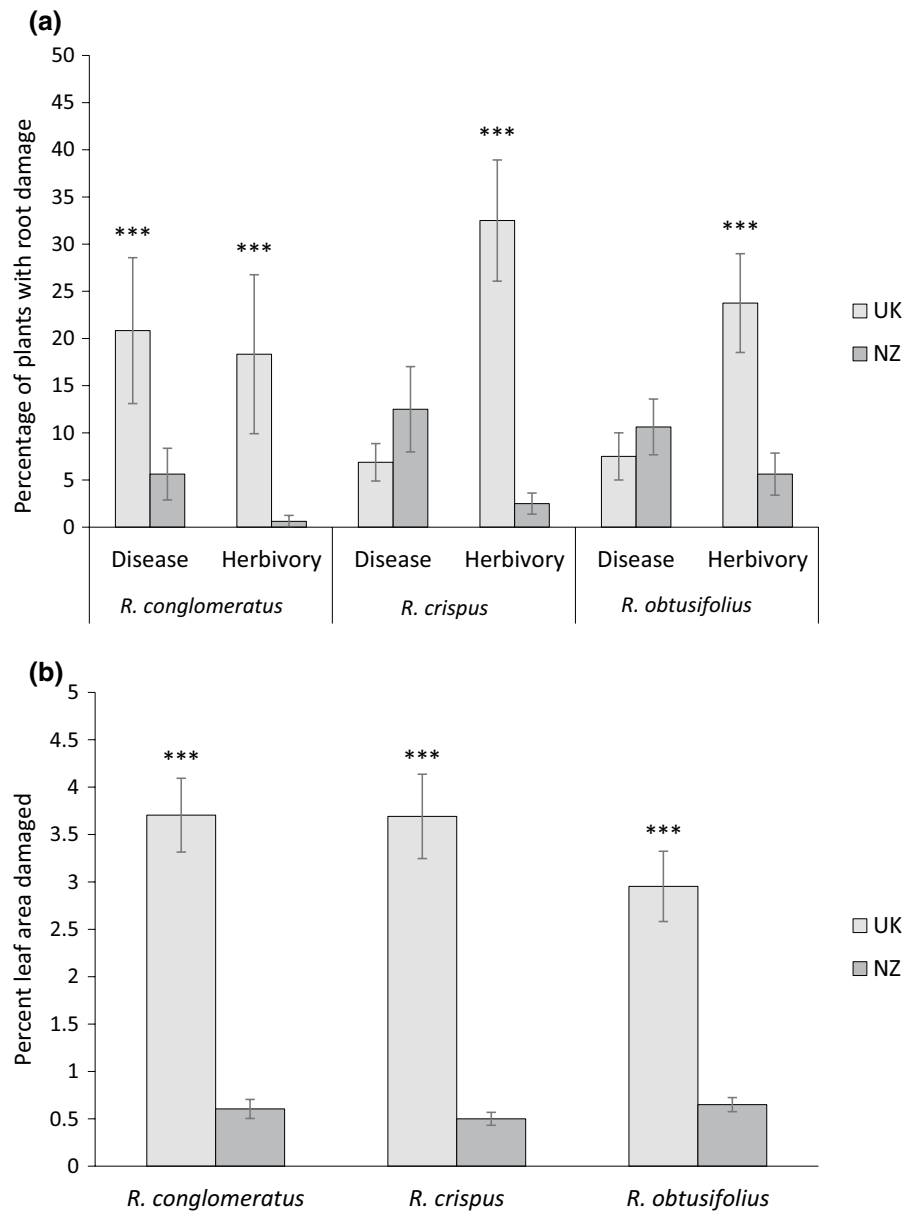
Root condition and leaf herbivore damage

The presence of root herbivory was significantly higher in *Rumex* plants in the native range than in the introduced range for all three study species (Fig. 5a). However, only *R. conglomeratus* plants had a significantly higher incidence of root disease in the native range ($p < 0.001$; Fig. 5a). Leaf damage in the native range was rarely more than 4%, but was on average six times greater (mean $\pm$ SE 3.43 ± 0.24) than in the
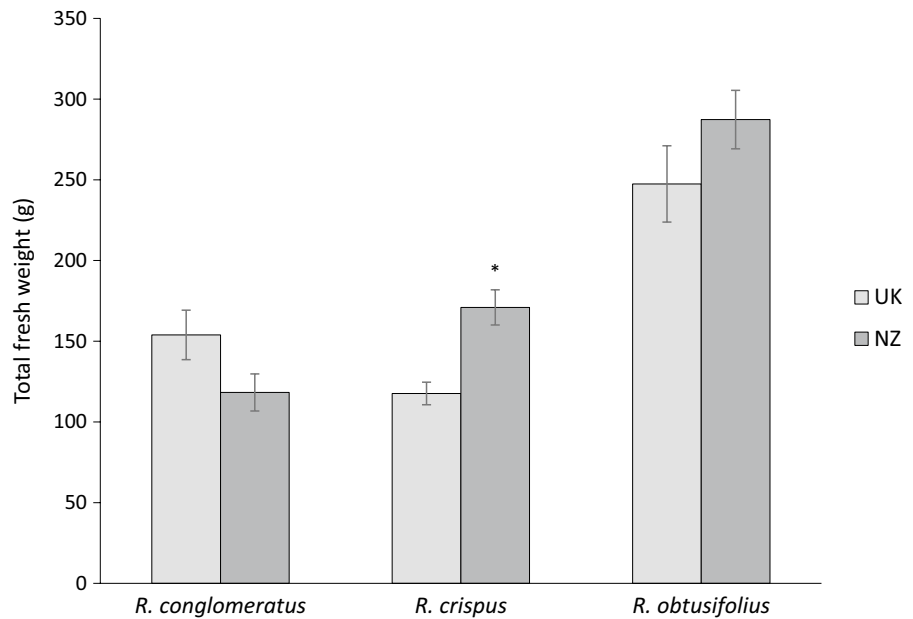
introduced range (0.58 ± 0.05) for all three *Rumex* study species ($p < 0.001$; Fig. 5b).

Plant biomass

In the introduced range, *R. crispus* plants had significantly ($p = 0.04$) higher total fresh weight than in the native range. The other two *Rumex* species showed no significant differences in the total fresh weight between ranges (Fig. 6).

Fig. 6 Mean fresh weight of *Rumex conglomeratus*, *R. crispus* and *R. obtusifolius* plants collected from populations in their native and introduced ranges. *P < 0.05. Error bars ± 1SE

Discussion

We provide evidence of enemy escape as a result of fewer herbivorous insects and indicated by lower damage in the introduced range for all three *Rumex* species. Even though damage was lower in the introduced range (NZ), only *R. crispus* showed evidence for enemy release, having a higher biomass in NZ. Two *Rumex* species (*R. conglomeratus* and *R. obtusifolius*) had a greater diversity of insect morphospecies in the native range (UK), but no difference between ranges was observed for *R. crispus*. All three *Rumex* species had a greater abundance of chewing insect herbivores, as well as greater leaf and root damage in the native range, as opposed to the introduced range. Specialist insect herbivores, although found frequently on plants in the native range, were absent from the introduced range.

At a family level, there was a greater diversity and abundance of chewing insect herbivores on *Rumex* plants in the native range than in the introduced range, which may reflect the fact that the native range hosts a greater variety of chewing insect families than the introduced range. For example, in the UK there are 103 Coleoptera families (UK Natural History Museum 2020), whereas in New Zealand, there are only 82 Coleoptera families (Leschen et al. 2003). However, among sap-sucking insects the same

six Hemiptera families were found on plants from both the native and introduced range and Hemipteran abundance was similar between ranges, despite greater diversity in the UK. Alternatively, lower diversity and abundance in the families of insect herbivores could be a result of the lack of co-evolved herbivores in the introduced range, as predicted for enemy escape (Keane and Crawley 2002).

For all three *Rumex* study species, specialist herbivores like *Gastrophysa viridula* and *Pyropteron chrysidiforme*, although fairly common in the native range, were absent from the introduced range. Thus, it appears that introduced *Rumex* populations have indeed escaped from specialist herbivores, as have other species (Kwon 2008; Kwon et al. 2006; Park et al. 2008), such as tall goldenrod, *Solidago altissima* L. (Asteraceae) (Uesugi and Kessler 2016), and creeping thistle, *Cirsium arvense* (L.) Scop. (Cripps et al. 2011, 2010). Instead, insect herbivores feeding on the three *Rumex* species in the introduced range have been recorded as generalist feeders in the native range (Cavers and Harper 1964), consistent with the predictions for arthropods colonizing introduced plants (Fraser and Lawton 1994) and other comparative studies (Goeden 1974; Jobin et al. 1996; Memmott et al. 2000). Introduced plants can also be colonised by native insect species, which can thus act as potential biocontrol agents, as was the case

for *R. obtusifolius* in Korea, where it encountered *Gastrophysa atrocyanea* (Motschulsky) (Coleoptera, Chrysomelidae), *Ostrinia palustralis memnialis* (Walker) (Lepidoptera: Crambidae) and *Allantus luctifer* (Smith) (Hymenoptera: Tenthredinidae). Alternatively, specialist herbivores can sometimes be introduced either at the same time as the host (Canavan et al. 2019) or at a later date and the longer the residence time, the more likely this is to happen by chance (Hawkes 2007; Schultheis et al. 2015). For example, the parsnip webworm (*Depressaria pastinacella* Goeze (Depressariidae)) re-associated with wild parsnip (*Pastinaca sativa* L. (Apiaceae)) roughly 150 years after the introduction of wild parsnip to New Zealand (Zangerl et al. 2008). Although no specialist *Rumex* herbivores have been introduced from their native range, two generalist sap-sucking insect herbivores native to the UK, *Philaenus spumarius* L. (Hemiptera, Aphrophoridae) and *Closterotomus norwegicus* (Gmelin) (Hemiptera, Miridae), were frequently present on *Rumex* plants in both ranges. As they were found on 18–24% of surveyed plants and have been present in NZ since at least the 1960s (Archibald et al. 1979; Myers and China 1928), it is possible that these two species could have limited enemy release for *R. conglomeratus* and *R. obtusifolius*. Of note is the fact that New Zealand has two native *Rumex* species (*R. flexuosus* Sol. and *R. neglectus* Kirk), both of which are endemic and of cultural importance for the Māori people. This would make it unlikely that specialists will be introduced to New Zealand for the biocontrol of invasive *Rumex* species, as there would be a high chance that the native species will also be affected.

Rumex plants in the native range had significantly higher herbivore damage on both roots and leaves than plants in the introduced range, as predicted by the ERH and found in other studies (Adams et al. 2009; Castells et al. 2013; Cripps et al. 2006; DeWalt et al. 2004; Memmott et al. 2000; Veselkin et al. 2019; Vilà et al. 2005 but see Williams et al. 2010), including in New Zealand (Fenner and Lee 2001; Lieurance and Cipollini 2012, but see Cripps et al. 2010). Leaf herbivory in our system was low in both ranges, which could mean herbivory had only a modest effect on plant performance. Other studies that found low levels of leaf damage (<10%), similarly did not find support for enemy release in the introduced range (Adams et al. 2009; Kater 2016; Lieurance and Cipollini 2012).

Gastrophysa viridula has been shown to significantly reduce the performance of *Rumex* (Moore et al. 2003), although this only occurs at experimental densities of at least two adult beetles and their offspring per plant (Bentley and Whittaker 1979), whereas under natural conditions we found an average of 0.83 individuals (adult and larvae) per plant. This suggests that most of the leaf damage was not caused by chewing insects, but possibly by snails and slugs, which can be found frequently on *Rumex* plants in both the native and introduced ranges (Costan C. A., pers. obs.). Mammalian herbivores or anthropogenic disturbances can also greatly affect the development and growth of *Rumex* plants, but in this study, we excluded highly disturbed or heavily grazed sites. Thus, it is likely that for the plants that we surveyed, insect herbivory played a prominent role.

Together these results suggest enemy escape in the introduced range, but there is little evidence of a performance increase, and therefore enemy release, as a result of this loss of natural enemies. Since fecundity is likely highly corelated to biomass in *Rumex* (Pino et al. 2002; Bufford and Hulme 2021), an increase in biomass would be a good indication of success. In the introduced range, *R. crispus* had a significantly greater fresh weight than in the native range, possibly as a result of lower root herbivory compared to *R. crispus* plants in the native range. Both *Rumex conglomeratus* and *R. obtusifolius* had lower root herbivory than *R. crispus* and tend to have multiple tap roots, while *R. crispus* plants generally have one main tap root with a larger diameter (Cavers and Harper 1964). This makes *R. crispus* a more favourable target for attack by larvae of the specialist clearwing moth, *Pyropteron chrysidiforme*, which needs a sufficiently large root diameter to survive (Spafford et al. 2008). Consistent with this, a closely related insect species *Pyropteron doryliformis* (Ochsenheimer), which was introduced as a biocontrol agent in Australia, established on *R. crispus* plants but not on *R. obtusifolius* and *R. conglomeratus* (Morley et al. 2008). Plant biomass was similar for *R. conglomeratus* and *R. obtusifolius* between ranges, suggesting that the differences in herbivory had modest effects on performance and that escape from specialist herbivores does not always result in an increased plant performance (Chun et al. 2010). This provides at best mixed evidence for the ERH and that evidence is primarily for effects of below-ground herbivores, which are less often examined in ERH studies.

Conclusion

This work provides multi-species evidence that invasive plant species can escape from specialist insect herbivores in their introduced range and, although hosting a different insect herbivore community, experience greatly reduced herbivory compared to their counterparts in their native range. Herbivore damage in both ranges was low, however, and no significant difference in plant biomass was observed between the native and introduced ranges for *R. conglomeratus* and *R. obtusifolius*, suggesting that enemy escape is not a main driver of the success of these two *Rumex* species in New Zealand. For *R. crispus,* however, release from root herbivory in the native range may explain the significantly greater fresh weight of *R. crispus* plants in the introduced range, which could indicate support for the enemy release hypothesis for this species in New Zealand and emphasizes the importance of considering below-ground interactions.

Data availability If the manuscript is accepted for publication, the data will be archived in Figshare.

Code availability The code generated during the study is available upon reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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