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ORIGINAL PAPER

Enemy pressure exerted on alien and native plants may differ between montane and lowland regions

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Abstract

This study analyzed the enemy release hypothesis (ERH) assumptions under different climatic conditions in a lowland region and a mountain region in Poland. A common garden experiment was performed in 2010 and 2011 using 3 native (*Impatiens noli-tangere*, *Solidago virgaurea*, and *Polygonum bistorta*), 2 noninvasive alien (*Impatiens walleriana* and *Impatiens balsamina*), and 4 invasive alien (*Impatiens glandulifera*, *Impatiens parviflora*, *Solidago gigantea*, and *Reynoutria japonica*) species. The species were surveyed for leaf damage and invertebrate pest attacks. In all tests, leaf damage and pests were recorded more frequently in the lowland than in the mountains. The differences were particularly evident in the models for *Impatiens* and in the leaf damage model for *Solidago*. The distinction was irrelevant for some species (Polygonaceae); however, these results should be interpreted with caution because the taxonomic relations between the studied Polygonaceae were lower than those between the other tested species. Considering all the tests, the assumptions of the ERH hypothesis were confirmed in 6 cases (29%), whereas there was no confirmation in 15 cases, including 7 cases of nonsignificance and 8 cases of the opposite results. Moreover, the overall result of the comparison between the noninvasive and invasive alien species was the opposite of that predicted by the ERH hypothesis; in more than 2/3 of the cases, invasive alien species were released from the enemy less effectively than were noninvasive ones. In conclusion, the assumptions of the ERH hypothesis do not always hold true, and the invasion success of alien species may depend on several factors, including specific local conditions.

Keywords Biological invasions · Common garden · Enemy release hypothesis · Invasive alien species · Noninvasive alien species · Lowlands and mountains

Introduction

A number of hypotheses have been proposed to explain the mechanisms determining the invasiveness of alien species (Catford et al. 2009; Holzmueller and Jose 2011). One of the most frequently studied (Najberek et al. 2017b) is the enemy release hypothesis (ERH). The ERH assumes that the success of alien species depends on the release from the pressure of local enemies, such as predators, herbivores or pathogens, after introduction into new areas (Elton 1958; Maron and Vilà 2001; Keane and Crawley 2002). While within their native ranges, species are suppressed by natural enemies, liberation from this limiting factor in new areas may lead to rapid expansion.

To date, the ERH assumptions were either fully supported (e.g., Mitchell and Power 2003; Hartley et al. 2010; Comont et al. 2014), confirmed only partially (e.g., Agrawal et al. 2005; Liu et al. 2007; Cripps et al. 2010), proved negative (e.g., Blaney and Kotanen 2002; Skou et al. 2011; Najberek et al. 2017b), or definitely rejected (e.g., Parker and Hay 2005; van Kleunen and Fischer 2009; Schultheis et al. 2015). Taking into account such diversity of results, one can assume that the invasion success may be determined by natural enemies only for some species or only in specific

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local conditions. The pressure exerted by enemies on alien plant species was tested with respect to many aspects. For instance, ERH tests were conducted at adult individuals (e.g., Vilà et al. 2005) or at seed stage (e.g., Najberek et al. 2018), including many plant species in one type of habitat (e.g., Engelkes et al. 2008) or using a single species in many habitats (Najberek et al. 2017a), as well as taking into account plant size, from trees (e.g., Cincotta et al. 2009), through shrubs (e.g., Memmott et al. 2000) to perennials/annuals (e.g., White et al. 2008). Some of these studies were innovative enough to evolve into new hypotheses (e.g., the enemy reduction hypothesis or the enemy inversion hypothesis; Catford et al. 2009). It is also known that in different regions, biological invasions may proceed in different ways (Hawkes 2007; Sugiura 2010). However, neither the ERH nor its subsequent hypotheses compared the enemy release levels in areas differing in climate, such as lowlands and mountains. At the same time it is known that montane climate is more severe and can reduce the presence of some pests and pathogens (Stohlgren 2011). In this study, we present the results of a common garden ERH experiment conducted in cultivation plots located in lowland and montane areas in southern Poland. The experiment was carried out using the community approach (Colautti et al. 2004) and took into account native and alien species, both noninvasive and invasive. Although noninvasive alien species may not pose an imminent serious threat to native biodiversity or local economies, studying them is particularly important because they may yield insights into the mechanisms of the development of invasiveness, which is important for the theoretical aspects of biological invasions as well as for the development of practical measures to mitigate their effects (van Kleunen et al. 2010; Ugoletti et al. 2011). In this experiment, following the ERH, we assumed that the level of pressure exerted by enemies on noninvasive alien species would be higher than that on the related invasive alien species and, at the same time, lower than that on the related native species. The two noninvasive alien species (*Impatiens walleriana* and *Impatiens balsamina*) included in this study are frequently cultivated in Poland. It cannot be ruled out that in the future, e.g., due to climate warming, these species will establish stable populations in warmer parts of the country, such as cities at lower elevations.

We took into account both pathogen pressure (recording the number of leaves with symptoms of disease or damage) and pest pressure (recording the number of invertebrates on the surveyed plants, including pests, defined as ‘invertebrates which may be harmful for the studied plant species’). Previously, the ERH tests were based either only on the level of leaf damage (e.g., Vilà et al. 2005; Adams et al. 2009) or only on pathogen pressure (e.g., Mitchell and Power 2003; Mitchell et al. 2010). Moreover, the climatic divergences between the lowland and mountains were explicitly tested to show that the climate of the latter region was significantly more severe. Following Stohlgren (2011), we assume that these climatic conditions limit the number of enemies attacking plants in mountains. It can also be hypothesized that under the same level of enemy attack in the lowland and mountains, an alien species invasion would be more limited in the latter region because enemies would magnify the stress exerted by a severe climate.

Methods

Species selected for the study

Nine species were chosen for the study: four species of alien origin that are invasive, two cultivated noninvasive aliens, and three natives (Table 1). The invasive alien species (*Impatiens glandulifera*, *Impatiens parviflora*, *Solidago gigantea*, *Reynoutria japonica*) were chosen because they are among the worst invaders in many European countries, including Poland, and specifically the study area (Tokarska-Guzik et al. 2012). Following the ERH assumptions, we compared them with native,

Table 1 Invasiveness and native range of the species selected for the study

Species	Family	Status	Time of introduction in Poland	Native range
Impatiens noli-tangere	Balsaminaceae	Native	–	Europe, Asia, western North America
I. balsamina	Balsaminaceae	Cultivated alien	–	Southern Asia
I. walleriana	Balsaminaceae	Cultivated alien	–	Eastern Africa
I. parviflora	Balsaminaceae	Invasive alien	1850	Central Asia
I. glandulifera	Balsaminaceae	Invasive alien	ca. 1890	Central Asia
Solidago virgaurea	Asteraceae	Native	–	Europe, Asia
S. gigantea	Asteraceae	Invasive alien	1853	North America
Polygonum bistorta	Polygonaceae	Native	–	Europe, North and West Asia
Reynoutria japonica	Polygonaceae	Invasive alien	1882	East Asia

closely related species that co-occur in the study area in the same habitats (personal observations). Neither of the two noninvasive alien balsams selected for the study (*I. balsamina* and *I. walleriana*) has been recorded in Poland from natural habitats. However, they were included in the experiment because they are frequently cultivated and it cannot be ruled out that they may establish in Poland in future.

Comparisons of enemy pressure between the native and alien species were performed in congeners: *Impatiens* spp. and *Solidago* spp. Another pair, namely *R. japonica* and *Polygonum bistorta*, included representatives of the same family (Table 1); such comparisons are suitable in the absence of close relatives in the study area (e.g., Agrawal and Kotanen 2003). Therefore, we decided to also include these species in the experiment. Each of the invasive alien species was introduced to Poland in the nineteenth century; thus, their residence times are similar.

Study sites

The study was conducted in two regions in southern Poland: the lowland Rów Skawiński (L) and the montane Rów Podtatrzański (M). One cultivation plot was set up in each region: in the lowland, in Wielkie Drogi Village on a private property (215 m a.s.l.; 49.961 N, 19.704 E), and in the mountains, at the Center for Research and Conservation of Mountain Plants of the Institute of Nature Conservation, Polish Academy of Sciences in Zakopane (917 m a.s.l.; 49.292 N, 19.976 E). Both regions were described in detail by Najberek et al. (2017b).

The land preparation, sowing, and planting were similar for both plots and were always supervised by the same person. Each plant species was cultivated in conditions compatible with its habitat preferences; however, in both plots, the area surrounding the plants was frequently mowed and raked, and the cuttings were removed.

In 2009, seedlings of all the native and invasive alien species were transplanted to each plot from neighboring localities in the particular regions. The plants developed and reproduced successfully in 2009, 2010, and 2011 with no need for supplementary sowing. In contrast, the noninvasive alien plants (*I. walleriana* and *I. balsamina*) were sown in each study year using seeds purchased from the same producer. These species are not capable of establishing stable populations in Poland and occur only in cultivation.

The number of surveyed plants was equal for all the species; there were always 50 tagged individuals (per species and per plot), and redundant individuals were removed each year.

Data collection

The plots were surveyed every 2 weeks between June and September in 2010 and 2011. These surveys began with the onset of the vegetative phase of the plants and continued to the subsenile phase. Surveys were always conducted by the same researcher to strictly maintain the standard scheme for the classification of natural enemies. The plot in the lowland was visited first, while the plot in the mountains was visited within two subsequent days. The surveys started at 9 a.m. and continued until 3 p.m. They were conducted in favorable weather conditions, which were comparable between particular surveys in both regions. A total of 240 surveys were conducted at the study sites: 23 for *Impatiens noli-tangere* (14 in L, 9 in M), 24 for *I. balsamina* (19 in L, 5 in M), 24 for *I. walleriana* (12 in L, 12 in M), 28 for *I. parviflora* (15 in L, 13 in M), 30 for *I. glandulifera* (16 in L, 14 in M), 24 for *Solidago virgaurea* (14 in L, 10 in M), 28 for *S. gigantea* (13 in L, 15 in M), 25 for *P. bistorta* (13 in L, 12 in M), and 34 for *R. japonica* (17 in L, 17 in M). The differences in the numbers of surveys were due to differences in the vegetation period between the species and regions (it was shorter in the mountains).

Before each survey, 15 of the 50 plants were randomly selected. During the survey, the number of leaves showing symptoms of disease or damage (collectively termed 'leaf damage' here; Online Resources, Appendices 1A–D) was recorded. Sick-to-healthy leaf ratio was calculated. The leaf damage was classified into 8 categories: rusts and spots, browning, discolorations, necrosis, wilting, mines, and deformations and mildews. Invertebrates observed on the surveyed plants were also recorded, photographed, and identified (Online Resources, Appendices 1A–D). We identified 64% of the invertebrates to the family or superfamily level. The invertebrates that were difficult to identify were classified to infraorder (1%) or order (14.3%). All the snails (20.7%) were categorized as belonging to clade Stylommatophora. To estimate the number of pests among the recorded invertebrates, the harmfulness scale (Najberek et al. 2016) was applied. The H_{i} values assigned to each taxon (Online Resources, Appendices 1A–D) were multiplied by the number of individuals within that taxon recorded on each plant, which provided a proxy for the number of pests attacking a given plant. The scale can help to reduce the costs and labor required for identification and quantifying the harmful effects of invertebrates on plants, particularly for comparisons in which the identification of large numbers of invertebrates to the species level is not necessary (Najberek et al. 2016).

To account for significant differences in size of the selected plant species, dry weight of the plants was measured each study year using scale Radwag PS 360.R2

(0.001 g accuracy). The weight was then used in models of enemy release.

Statistical analysis

The statistical analyses were carried out using R and RStudio (R Development Core Team 2015).

Climatic differences between the regions

Because extreme temperatures may increase plant phenological development (Hatfield and Prueger 2015), we included climatic data for May and August in our analyses of differences between the two studied areas. These months are crucial because in May, plants germinate and may be exposed to late spring frosts (which is particularly important for annual plants, such as *Impatiens*; Perrins et al. 1993; Tabak and von Wettberg 2008), whereas in August, all of the studied plants are in the reproduction phase. The minimum temperatures in May and the maximum temperatures in August were analyzed. The results confirmed that both study areas significantly differ in terms of climate conditions. The August temperatures were 4.8 °C higher in the lowland than in the mountains, and the respective difference in the May was 4.1 °C. The differences in precipitation were opposite, with the average value for both months ~ 1.7 times higher in the mountains than in the lowland (Online Resources, Appendix 2). It is worth to stress that the combination of high temperatures and precipitation may delay plant phenological development (Hatfield and Prueger 2015).

The ERH tests

The ERH statistical calculations were made at the level of each survey of each controlled plant. Spearman rank correlations were used to assess the level of dependence between leaf and the number of pests. The correlations were made for each studied plant separately.

The leaf damage recorded from the studied plants was analyzed using linear mixed-effects models (LMM) with the *glmer* function and Poisson distributions (Lme4 package; Bates et al. 2016). Generalized linear mixed models using AD Model Builder with a zero inflation parameter and a Poisson distribution (glmmADMB package; Bolker et al. 2012; Fournier et al. 2012; Skaug et al. 2013) were used to analyze the number of pests. The overdispersion effect was also checked in all of the models. The number of pests was rounded to convert decimal values to integers, except for values of 0.25 and 0.5, which were always rounded to 1 so that no records of pests were excluded.

In the base models for leaf damage, the response variable was the number of damaged leaves (‘Leaf damage’; Online Resources, Appendix 3). The covariates were the total number of leaves (‘N leaves’), the plant species (‘Species’), the study region (lowland or mountains; ‘Region’), the study year (2010 or 2011; ‘Year’), and the average dry weight of particular plants (‘Weight’). In the base models for the pest analysis, the response variable was the number of recorded pests (‘N pests’; Online Resources, Appendix 3). The covariates were ‘Species,’ ‘Region,’ ‘Year,’ and ‘Weight.’ In both types of models, the following interactions were assessed: species with study region (Species * Region) and species with study year (Species * Year). The number of surveys of each controlled plant individual varied, which was an effect of (1) random selection of 15 out of the 50 tagged individuals before each survey in a particular locality and (2) differences in the vegetation period between the species and between the regions. Therefore, the ‘individual ID’ variable was taken into account as a random effect. This also accounted for the possible dependence of the recorded data on the leaf damage/number of pests in subsequent surveys.

The base models were used to generate best-fit models (Online Resources, Appendix 3) with low corrected Akaike information criterion (AIC_c) and delta (Δ) values < 2 (Burnham and Anderson 2002). This operation was performed with the use of the MuMIn package and *dredge* function (Bartoń 2016). Moreover, to test for differences between the studied species growing in the two regions, the data were reduced to the particular region, and then the best-fit model without the ‘Region’ covariate and the Species × Region interaction was prepared. Differences between the 2 years of the study were analyzed in the same way: the data were reduced to the particular year, and then the best-fit model without the ‘Year’ covariate and Species × Year interaction was prepared.

Wald χ^2 statistics were used to test for fixed effects (car package; Fox and Weisberg 2011). Subsequently, the significance of the differences among the levels by changing the reference level of the ‘Species’ variable was assessed; however, it was necessary only in the models for the *Impatiens* genus, where the five species were compared with one model.

Results

Recorded enemies

In total, we checked 52,208 leaves, of which 43.3% ($N = 22{,}586$) had leaf damage (Online Resources, Appendix 1A). The damage was recorded from 3329 plant individuals (94.7% of all the surveyed individuals). The predominant damage symptoms were ‘rusts and spots’: 17,122 leaves (32.8% of all the surveyed leaves) recorded from 2982 plants (84.8% of all the surveyed plants). The minor damage symptom was ‘mildews’: 14 leaves (0.03% of all the surveyed leaves) recorded from 4 plants (0.11% of all the surveyed plants; Online Resources, Appendix 1A).

In total, we recorded 4664 invertebrates, of which 68.2% ($N = 3182$) were classified as pests (Online Resources, Appendix 1A) and were included in further ERH analysis. The overall dominant group of pests was Aphidoidea ($N = 2128$; 66.9% of all the recorded pests), although they dominated only in five species: *I. parviflora*, *I. noli-tangere*, *I. glandulifera*, *S. virgaurea*, and *P. bistorta*. For the noninvasive alien plants, *I. walleriana* and *I. balsamina*, the most frequently recorded pests were Stylommatophora ($N = 727$; 22.8% of all the recorded pests). The least recorded pest groups were Rhopalidae, Staphylinidae, and Tetranychidae. Each of these groups was recorded once during the studies (Online Resources, Appendix 1A).

The ERH analyses were carried out using data on local enemies recorded from the particular plant species. All the results of leaf damage and recorded invertebrates/pests were added as Electronic Supplemental Material (Online Resources, Appendices: 1B for *Impatiens*, 1C for *Solidago* and 1D for *Polygonum* and *Reynoutria*).

ERH analysis

The correlations between the two response variables, namely the extent of leaf damage and the number of pests, were nonsignificant for the noninvasive alien species *I. balsamina* and *I. walleriana*. For the native species *I. noli-tangere*, *P. bistorta*, and *S. virgaurea* as well as for the invasive alien species *I. glandulifera*, *S. gigantea*, and *R. japonica*, the results were significant and, in almost all cases, weak ($0.1 < r_S \le 0.3$). The exception was the invasive alien species *I. parviflora*, for which the correlation strength was moderate ($r_S = 0.37$). Because of the weak correlations, further analyses were conducted separately for leaf damage and the number of pests.

Impatiens

In the leaf damage model for the *Impatiens* species (Table 2), two interactions had the greatest impact on the obtained results: 'Species * Region' and 'Species * Year.' The first interaction showed that the level of leaf damage for each *Impatiens* species depended on the study region (Fig. 1a), whereas the second confirmed that the level of leaf damage varied between years (Fig. 1b).

The overall level of leaf damage in the lowland was higher than that in the mountains (contrast: estimate = 0.42, SE = 0.079, $z = 5.35$, $p < 0.001$). In the lowland, the highest damage was noted for *I. noli-tangere*, *I. balsamina*, and *I. glandulifera* (Fig. 1a). A moderate level of leaf damage was detected for *I. parviflora*, and the lowest level was detected for *I. walleriana* (Fig. 1a). Thus, the assumption of the ERH, which presumes that native species should be under higher enemy pressure than related alien species, was confirmed in the two comparisons: *I. noli-tangere* with *I. parviflora* (contrast: $z = -2.41$, $p = 0.015$) and *I. noli-tangere* with *I. walleriana* (contrast: $z = -5.93$, $p < 001$). The results of the comparisons between *I. noli-tangere* with *I. balsamina* and between *I. noli-tangere* with *I. glandulifera* were nonsignificant (Fig. 1a), which is not consistent with the ERH assumptions. The results also revealed strong differences among the alien species, of which *I. balsamina* and *I. glandulifera* were under higher enemy pressure than *I. walleriana* and *I. parviflora* (Fig. 1a).

Table 2 Results of the best-fit model for leaf damage (response variable) in *Impatiens* species (sample size = 1841)

Covariates	χ^2	d.f.	p value
N leaves	861.00	1	< 0.001
Species	422.43	4	< 0.001
Region	422.43	1	< 0.001
Year	0.05	1	0.8
Weight	3.92	1	0.047
Species * Region	42.77	4	< 0.001
Species * Year	121.31	4	< 0.001

In the mountains, *I. glandulifera* still had the highest level of leaf damage, while the damage in *I. balsamina* and *I. noli-tangere* decreased (Fig. 1a). The native *I. noli-tangere* was the least attacked species (Fig. 1a), which means that in all the comparisons, the results were contrary to the ERH hypothesis (at $p < 0.001$ in all cases). A comparison between *I. balsamina* and *I. walleriana* was similar to the results in the lowland: the latter was less attacked in both regions (Fig. 1a); however, in the mountains, the differences between the species, although significant, were less pronounced than in the lowland (Fig. 1a). As a result, the differences in leaf damage for both noninvasive balsams and *I. parviflora* were nonsignificant (Fig. 1a).

The overall level of leaf damage differed in both years of the study, with more damage in 2011 (estimate = 0.41, SE = 0.075, $z = 5.49$, $p < 0.001$). The differences were prominent mainly for *I. noli-tangere*, for which the level of damage in 2010 was the lowest (Fig. 1b), while in 2011, it sharply increased, exceeding the damage recorded for *I. balsamina*, *I. walleriana*, and *I. parviflora* (Fig. 1b). The differences between *I. parviflora*, *I. balsamina,* and *I. walleriana* were also significant. In 2010, the results for *I. parviflora* were similar to those for *I. balsamina* and *I. walleriana* (Fig. 1b), while in 2011, the three species differed significantly (Fig. 1b). This was a result of the concurrent decrease in the pressure noted for both noninvasive alien species in 2011.

The model calculated for the number of pests (Table 3) was influenced by all included variables; however, the

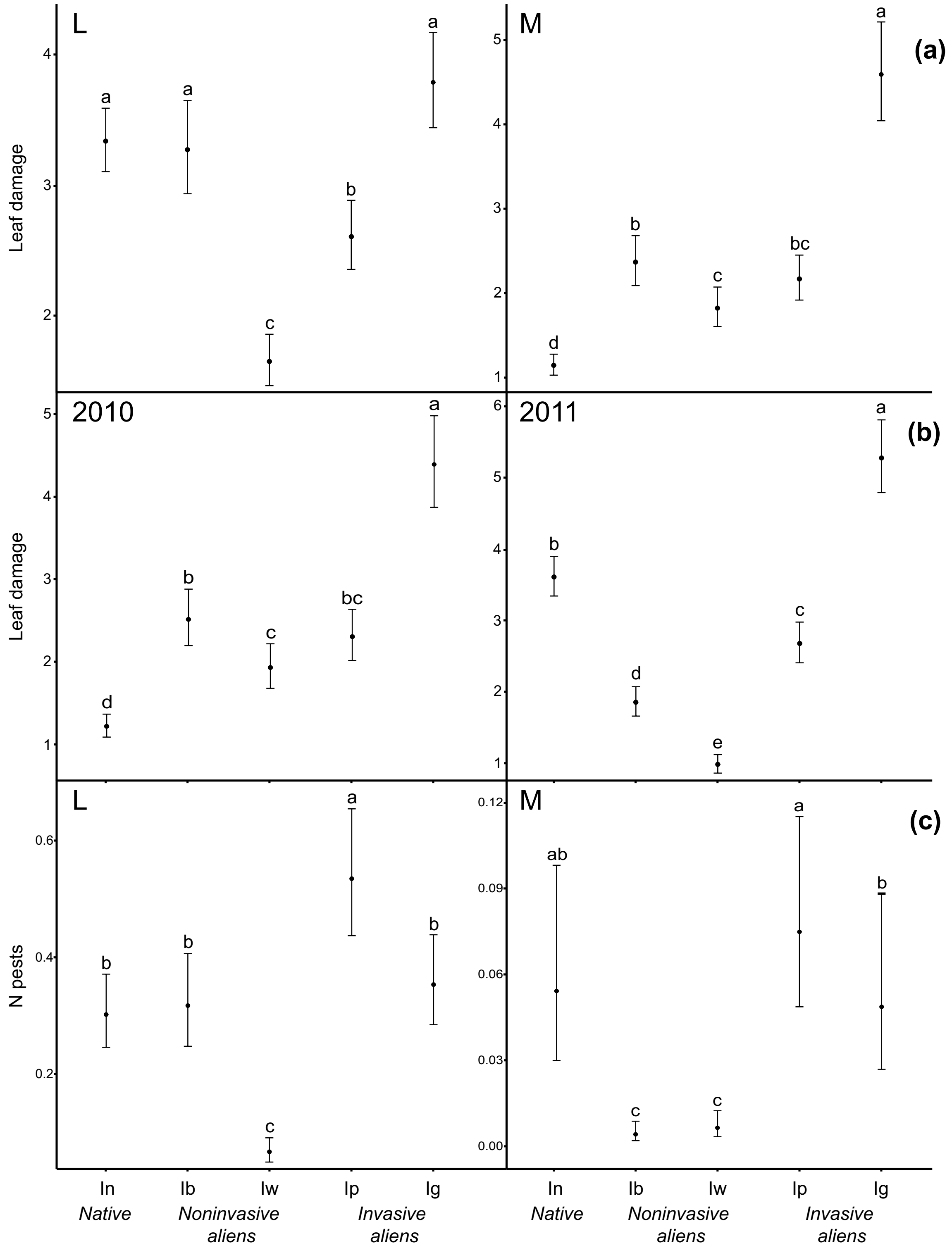

Fig. 1 Enemy release in native, noninvasive alien, and invasive alien *Impatiens* species. Estimated means for **a** the leaf damage in the lowland (L) and mountain (M) regions, **b** the leaf damage in each study year, and **c** the number of pests in the lowland (L) and mountain (M) regions. Dissimilar letters above the error bars indicate significant differences between species. *In Impatiens noli-tangere*, *Ib Impatiens balsamina*, *Iw Impatiens walleriana*, *Ip Impatiens parviflora*, *Ig Impatiens glandulifera*

Table 3 Results of the best-fit model for the number of pests (response variable) in *Impatiens* species (sample size = 1841)

Covariates	χ^2	d.f.	p value
Species	47.35	4	< 0.001
Region	6.96	1	0.008
Year	41.21	1	< 0.001
Weight	6.12	1	0.013
Species * Region	19.89	4	< 0.001

significant interaction between ‘Species’ and ‘Region’ was the most important variable (Fig. 1c).

In the lowland region, the overall number of pests was higher than that in the mountains (contrast: estimate = 0.96, SE = 0.32, $z = 3.04$, $p = 0.002$), which is consistent with the results obtained for the leaf damage. In the lowland, the pest pressure was highest on *I. parviflora*, moderate on *I. noli-tangere*, *I. balsamina*, and *I. glandulifera*, and lowest on *I. walleriana* (Fig. 1c). Thus, the results confirmed the ERH in one case: the comparison between *I. noli-tangere* and *I. walleriana*, with the native species attacked by pests more than the alien species (Fig. 1c; contrast: $z = -5.93$, $p < 0.001$). However, there was also a result opposite to the hypothesis, with *I. parviflora* under higher pressure than *I. noli-tangere* (Fig. 1c; contrast: $z = 2.84$, $p = 0.005$). The result for *I. noli-tangere* and *I. balsamina* was also not consistent with the ERH assumptions, similarly for *I. noli-tangere* and *I. glandulifera* (Fig. 1c).

In the analysis of pest pressure in the mountains, the hypothesis was confirmed in two cases: *I. noli-tangere* compared with *I. balsamina* (Fig. 1c; contrast: $z = -3.48$, $p < 0.001$) and *I. noli-tangere* compared with *I. walleriana* (Fig. 1c; contrast: $z = -3.26$, $p = 0.001$). Both noninvasive alien species were under lower pressure than the native species; moreover, the pressure exerted on these species was considerably lower in comparison with the two invasive alien species: *I. parviflora* and *I. glandulifera* (Fig. 1c). The highest number of pests was noted for *I. parviflora* and *I. noli-tangere* (Fig. 1c). *Impatiens glandulifera* was attacked by pests to a lesser degree than *I. parviflora* (Fig. 1c; contrast: $z = 2.22$, $p = 0.03$); however, the results for *I. glandulifera* were comparable to those obtained for *I. noli-tangere* (Fig. 1c).

Solidago

The leaf damage model for the *Solidago* species (Table 4) was most influenced by the two included interactions. The first (‘Species * Region’) indicated a difference in the level of leaf damage between the regions (Fig. 2a), while the second (‘Species * Year’) indicated a difference between the study years (Fig. 2b).

Table 4 Results of the best-fit model for leaf damage (response variable) in *Solidago* species (sample size = 814)

Covariates	χ^2	d.f.	p value
N leaves	619.67	1	< 0.001
Species	12.86	1	< 0.001
Region	1.90	1	0.17
Year	0.21	1	0.65
Weight	11.13	1	< 0.001
Species * Region	34.80	1	< 0.001
Species * Year	19.40	1	< 0.001

In the lowland, more leaf damage was recorded than in the mountains (contrast: estimate = 0.31, SE = 0.09, $z = 3.42$, $p < 0.001$). In the former region, there were no differences in damage between *S. virgaurea* and *S. gigantea* (Fig. 2a; contrast: $z = 0.52$, $p = 0.61$), while in the latter, the differences were significant, with more damage in *S. gigantea* (Fig. 2a; contrast: $z = 6.70$, $p < 0.001$). Thus, the assumption that native species should be attacked more than invasive alien species was not confirmed. Moreover, the result obtained for the mountain data was contrary to the assumption. The differences in both study years were significant (at $p < 0.001$ for 2010; at $p = 0.03$ for 2011); however, in both years, the trend was the same: *S. virgaurea* always had less leaf damage than *S. gigantea* (Fig. 2b).

The model for the number of pests was influenced only by the ‘Species’ and ‘Weight’ variables (Table 5). There were differences between the species (native species were attacked more frequently by pests than were alien species; Fig. 2c) but not between the regions or study years (Fig. 2c).

Reynoutria and *Polygonum*

The leaf damage model for the *Reynoutria* and *Polygonum* species (Table 6) was influenced by all the variables and one interaction: between ‘Species’ and ‘Year’ (Fig. 3a). The interaction between ‘Species’ and ‘Region’ was nonsignificant.

The damage was recorded more frequently for *R. japonica* than *P. bistorta* (Fig. 3a); thus, the result was contrary to the ERH hypothesis. A similar trend was noted when the damage was considered after including the study years (Fig. 3a; at $p < 0.001$). The differences between plant species were not driven by region; however, in general, the level of leaf damage was higher in the lowland than in the mountains (contrast: estimate = 0.40, SE = 0.08, $z = 4.9$, $p < 0.001$).

The model for the number of pests (Table 7) was influenced by all the covariates and one interaction: between ‘Species’ and ‘Year’ (Fig. 3b). As in the model for leaf damage, the differences between the species were not driven by region.

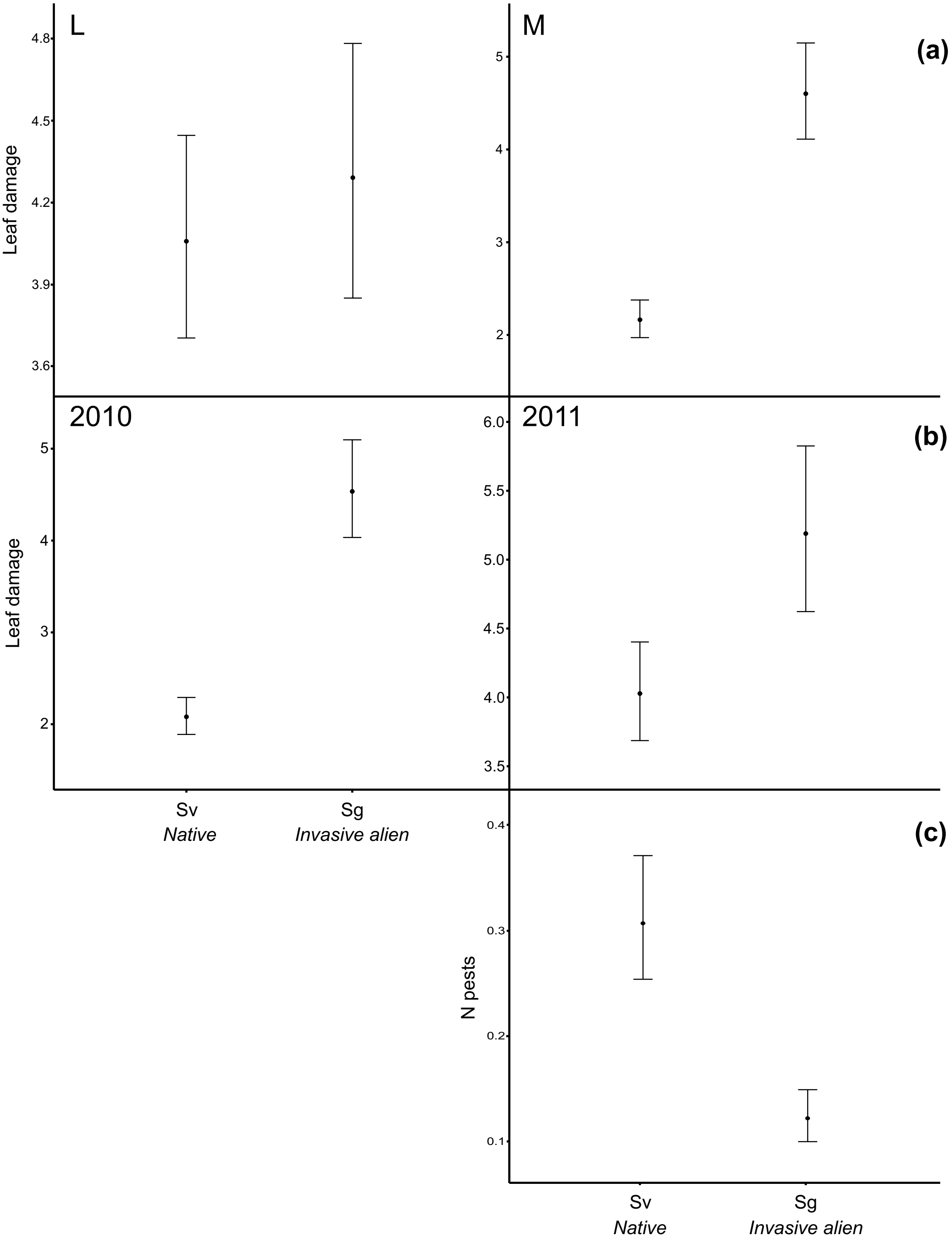

Fig. 2 Enemy release in native and invasive alien *Solidago* species. Estimated means for **a** the leaf damage in the lowland (L) and mountain (M) regions, **b** the leaf damage in each study year, and **c** the number of pests recorded throughout the study. *Sv Solidago virgaurea*, *Sg Solidago gigantea*

Table 5 Results of the best-fit model for the number of pests (response variable) in *Solidago* species (sample size = 814)

Covariates	χ^2	d.f.	*p* value
Species	23.62	1	< 0.001
Weight	17.45	1	< 0.001

Table 6 Results of the best-fit model for leaf damage (response variable) in *Reynoutria* and *Polygonum* species (sample size = 861)

Covariates	χ^2	d.f.	*p* value
N leaves	291.48	1	< 0.001
Species	101.17	1	< 0.001
Region	28.28	1	< 0.001
Year	54.77	1	< 0.001
Weight	4.06	1	0.044
Species * Region	2.73	1	0.1
Species * Year	3.70	1	0.054

Study year had an impact on the level of damage; however, the trend in damage was similar for the two species (Fig. 3b). Moreover, as in the model for leaf damage, more pests were recorded in the lowland region than in the montane region (contrast: estimate = 1.51, SE = 0.16, $z = 9.41$, $p < 0.001$). Similarly, the native species (*P. bistorta*) was under lower pest pressure than the alien species (*R. japonica*; Fig. 3b). Thus, in both analyses, the results were contrary to the ERH hypothesis.

Discussion

In all the ERH tests, leaf damage and pests were recorded more frequently in the lowland than in the mountains. This finding is consistent with the concept that a severe montane climate limits enemies (Stohlgren 2011). This pattern was also preliminarily tested in our earlier study on enemy release (Najberek et al. 2017b). In that study, leaf damage was more frequently recorded in the lowland than in the mountains, while the levels of pest pressure were similar between the regions. The earlier study was conducted on the two invasive alien species, namely *I. parviflora* and *I. glandulifera*, and the native species *I. noli-tangere*; however, the study was conducted under natural conditions without the inclusion of cultivation plots.

The present study revealed that the ability to be released from enemy attack under different climatic regimes depends on both the plant species and enemy type. The effect of region was particularly evident for the *Impatiens* genus, where four out of five species differed between the regions regardless of enemy type. Only the noninvasive alien *I. walleriana* was exposed to similar levels of pest pressure in the two regions. In contrast, leaf damage in *I. walleriana* differed between the regions, whereas similar levels of damage (in the two regions) were noted for *I. glandulifera*. Differences in plant species were also driven by region in *Solidago*, where the interaction between species and region was significant in the model for leaf damage. However, the number of pests recorded from *Solidago* did not differ between the regions. Similarly, in both pest and leaf damage models for the native species *P. bistorta* and the invasive alien species *R. japonica*, the results were not driven by region. Notably, the taxonomic relations between the Polygonaceae species were lower (family level) than those between the remaining species (genus level), which may have influenced the results.

The differences between the lowland and the mountains were most pronounced for the *Impatiens* genus, where native, noninvasive, and alien species were compared. The differences between these species were mainly driven by the level of pressure recorded in the native species *I. noli-tangere*. Regarding the recorded pests, the results for *I. noli-tangere* were consistent and average in the two regions; however, the level of leaf damage for this species was low in the mountains and very high in the lowland. The reason for this result may be that *I. noli-tangere* in the mountains is more resistant than the other tested *Impatiens* to local pathogens. This may be the result of a longer period of adaptation to the montane European climate, which may be more severe for the tested alien *Impatiens* species than, for instance, the Himalayan climate (Adamowski 2009).

The results for the noninvasive species *I. walleriana* were consistent for the two types of enemies, and in both regions, this species was almost always under the lowest enemy pressure. The results for the leaf damage in the other noninvasive alien species, *I. balsamina*, were more similar to those obtained for the invasive alien species *I. parvilora* and *I. glandulifera*. The pest level of *I. balsamina* was significantly lower and more similar to that of *I. walleriana* in the mountains than in the lowland. In *Impatiens*, contrary to the ERH assumptions, the highest enemy pressure was recorded for one of the two invasive alien species. Irrespective of the region, *I. parviflora* was under the highest pest pressure, while *I. glandulifera* had the highest level of leaf damage. The same results were obtained for the two invasive *Impatiens* species by Najberek et al. (2017b), which confirmed a significant difference in the enemy–plant relationship between those species.

In general, the overall results of the comparison between the noninvasive and invasive alien species demonstrated that noninvasive alien species were attacked to a lesser degree than invasive alien species. According to the ERH assumptions adopted for noninvasive and invasive alien counterparts (Najberek et al. 2018), the invasive alien species should be

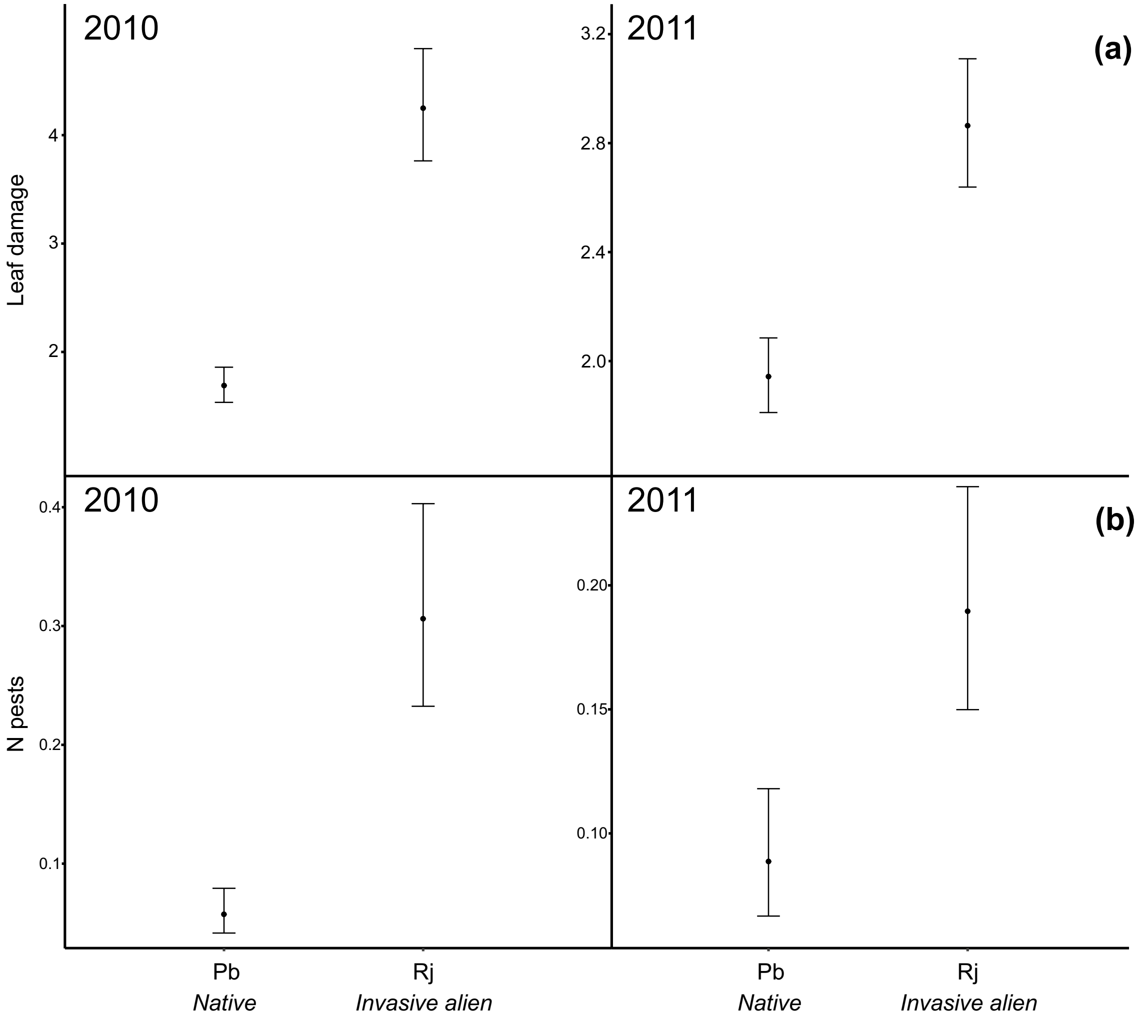

Fig. 3 Enemy release in invasive alien *Reynoutria* and native *Polygonum* species. Estimated means for **a** the leaf damage in each study year, and **b** the number of pests in each study year. *Pb Polygonum bistorta*, *Rj Reynoutria japonica*

attacked by enemies at a lower intensity than the noninvasive ones. A possible explanation for such a difference may come from Gruntman et al. (2017), who suggested that individuals from younger populations of *I. glandulifera* were capable of being released from natural enemies more effectively than those from older populations. Such a trend was also revealed in studies conducted with seedlings of alien tallow tree (*Sapium sebiferum*) and two native trees, namely sweetgum (*Liquidambar styraciflua*) and hackberry (*Celtis laevigata*) (Siemann et al. 2006), where the accumulation of pests and rodents increased with population age and correlated negatively with the tree growth rate. Notably, the noninvasive alien species *I. walleriana* and *I. balsamina* do not occur in the wild in Poland. Therefore, they may be less recognized by local enemies than the established and widely distributed invasive alien species *I. parviflora* and *I. glandulifera*. The noninvasive alien species may, therefore, correspond to the ‘younger population’ concept, while the invasive alien species may be treated as the ‘older population.’ It is also known that the diversity and density of soil pathogens increase with time since invasion, which leads to a corresponding decrease in plant survival (Siemann et al.

Table 7 Results of the best-fit model for the number of pests (response variable) in *Reynoutria* and *Polygonum* species (sample size = 861)

Covariates	χ^2	d.f.	*p* value
Species	37.36	1	< 0.001
Region	88.47	1	< 0.001
Year	15.97	1	< 0.001
Weight	6.68	1	0.0097
Species * Year	8.77	1	0.003

2016; Cunard and Lankau 2017). Meanwhile, the seedlings of *I. walleriana* and *I. balsamina* (in contrast to those of the remaining tested plants) were germinated in pots and transplanted to the garden only after the last spring frost. Thus, the noninvasive species *I. walleriana* and *I. balsamina* were exposed to soil pathogens for a shorter period of time than were the invasive alien species *I. parviflora* and *I. glandulifera*. Therefore, an alternative explanation is that seedlings of the noninvasive *Impatiens* species reduced investment in defense against soil pathogens and reallocated the saved resources to the improvement of other abilities, such as increased accumulation of allelopathic compounds, which may increase enemy resistance (Mitchell et al. 2007).

In the comparison between the invasive alien species *S. gigantea* and the native species *S. virgaurea*, the level of leaf damage differed between the lowland and mountains. In the lowland, the species did not differ in this respect, while in the mountains, the level of leaf damage was significantly higher for the alien species *S. gigantea* than for its native counterpart. As in the comparison between the native species *I. noli-tangere* and alien species of *Impatiens*, this may be the result of a longer period of adaptation of the native *Solidago* to the montane European climate. The success of a particular species may depend on one or more of its traits, the importance of which changes according to the biotic and/or abiotic conditions of the site where the species was introduced (Najberek et al. 2017b). In the presented results, this relationship was clearly pronounced in the Polygonaceae. Although *R. japonica* is a highly invasive alien species in Europe, it was under higher enemy pressure (regardless of the enemy type) than was the native *P. bistorta*. Therefore, other factors likely determine its invasion success.

Knowledge of the differences in resistance against different types of enemies may be useful in the development of methods for the biological control of invasive alien species. For this reason, we compared enemy release abilities between only the invasive alien species (Online Resource, Appendix 4). For leaf damage, we found that *I. parviflora* had the lowest level of attack in both regions, while none of the remaining species were notable in this respect. There were also differences in the number of recorded pests. Regardless of region, the highest pressure exerted by pests was recorded for *R. japonica*, while the lowest pressure was recorded for *S. gigantea*.

We assume that, similar to enemy type, the elevation of the study area could be an additional factor masking the relevance of the ERH. In the present study, we obtained five results that were opposite to the predictions of the ERH in the mountains, whereas only one result was opposite in the lowland. At the same time, analyses in the lowland provided three more nonsignificant results and one more confirmation of the hypothesis than did analyses in the mountains. Thus, in general, it seems that the ERH hypothesis may be more applicable in the lowland than under montane conditions. However, more general conclusions should be drawn with caution because of the small sample size (nine species) used in our study.

It should be noted that prior to this study the knowledge of enemies attacking the particular plant species was poor. The lists of the leaf damage types and invertebrates (including pests) recorded from the studied plants are included as electronic supplemental material. It is worth mentioning that for the noninvasive alien plants, the most frequently recorded pests were Stylommatophora. This may suggest that these generalists may be considered the most dangerous pests for alien plant species at the onset of invasion.

Aphidoidea were the most frequently recorded pest group in invasive *Impatiens* species, while Stylommatophora were the predominant pests for *S. gigantea* and *R. japonica*. Thus, Aphidoidea and Stylommatophora, generalist pests, could be considered the most effective pests against invasive alien species that are establishing in new areas. However, further studies on such plant–enemy relationships are needed.

The number of recorded pests exceeded 4600 individuals; therefore, the harmfulness scale (Najberek et al. 2016) was used instead of classifying the organisms to the species level. This method was used in our previous studies (Najberek et al. 2016, 2017a, b) and proved to be effective in studies where the sample size is large. Moreover, in addition to the quick and noninvasive assessment of invertebrate impacts, this method allows for the identification of pests without capturing them, as we took digital photographs. Therefore, the method did not affect the level of enemy pressure during subsequent surveys and allowed for the inclusion of legally protected invertebrate species. However, it must be stressed that the pest pressure calculated using the harmfulness scale should be treated as a proxy rather than an absolute measure of pest impact on plants. It should be also noted that we used one study plot per region; however, in common garden ERH experiments, such an approach is widely accepted not only in studies that use multiple species like we did in our experiment (e.g., Dawson et al. 2014) but also for tests of a single species (e.g., Zou et al. 2008; Hornoy et al. 2011; Joshi and Tielbörger 2012).

Conclusion

In the current study, we found that the level of enemy pressure on native and alien plants may significantly differ between lowland and montane areas, which was clearly pronounced at the genus level (*Impatiens* and, to a lesser degree, *Solidago*). We found that leaf damage and pests were recorded more frequently in the lowland than in the mountains, which was most likely because a severe montane climate is limiting for the enemies. This distinction was irrelevant for some species (Polygonaceae); however, this result should be interpreted with caution because the relations between the studied Polygonaceae species were lower (family level) than those between the remaining species (genus level).

Numerous studies have confirmed that the release from enemies is an important factor that may determine alien species success after introduction to new areas (Mitchell and Power 2003; DeWalt et al. 2004; Vilà et al. 2005; Cincotta et al. 2009; Comont et al. 2014). However, in our study, the level of confirmation was nearly twice as low, with only 29% of the results concordant with the ERH assumptions. We also found that the noninvasive alien species were attacked to a lesser degree than were the invasive alien species, whereas following the ERH assumptions, the result should have been the opposite. It can therefore be concluded that these assumptions do not always hold true and that the invasion success of alien species depends on several factors, including life history traits, population age, propagule pressure, invasibility of habitats, and specific local climatic conditions.

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References

Adamowski W (2009) *Impatiens balfourii* as an emerging invader in Europe. Neobiota 8:183–194

Adams JM, Fang W, Callaway RM et al (2009) A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. Biol Invasions 11:1005–1016. https://doi.org/10.1007/s10530-008-9312-4

Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecol Lett 6:712–715. https://doi.org/10.1046/j.1461-0248.2003.00498.x

Agrawal AA, Kotanen PM, Mitchell CE et al (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989

Bartoń K (2016) MuMIn: multi-model inference. R package, version 1.16.4

Bates D, Maechler M, Bolker B et al (2016) Package 'lme4.' CRAN Repos

Blaney CS, Kotanen PM (2002) Persistence in the seed bank: an experimental comparison of native and alien plants. Écoscience 9:509–517

Bolker B, Skaug H, Magnusson A, Nielsen A (2012) Getting started with the glmmADMB package

Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Divers Distrib 15:22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Cincotta CL, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). Biol Invasions 11:379–388. https://doi.org/10.1007/s10530-008-9255-9

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Comont RF, Purse BV, Phillips W et al (2014) Escape from parasitism by the invasive alien ladybird, *Harmonia axyridis*. Insect Conserv Divers 7:334–342. https://doi.org/10.1111/icad.12060

Cripps MG, Edwards GR, Bourdôt GW et al (2010) Enemy release does not increase performance of *Cirsium arvense* in New Zealand. Plant Ecol 209:123–134. https://doi.org/10.1007/s11258-010-9728-7

Cunard CE, Lankau RA (2017) Declining survival across invasion history for *Microstegium vimineum*. PLoS ONE 12:e0183107. https://doi.org/10.1371/journal.pone.0183107

Dawson W, Bottini A, Fischer M et al (2014) Little evidence for release from herbivores as a driver of plant invasiveness from a multi-species herbivore-removal experiment. Oikos 123:1509–1518. https://doi.org/10.1111/oik.01485

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

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Engelkes T, Morriën E, Verhoeven KJF et al (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. Nature 456:946–948. https://doi.org/10.1038/nature07474

Fournier DA, Skaug HJ, Ancheta J et al (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim Methods Softw 27:233–249

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage Publishers, Thousand Oaks

Gruntman M, Segev U, Glauser G, Tielbörger K (2017) Evolution of plant defences along an invasion chronosequence: defence is lost due to enemy release—but not forever. J Ecol 105:255–264. https://doi.org/10.1111/1365-2745.12660

Hartley MK, Rogers WE, Siemann E (2010) Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. Arthropod-Plant Interact 4:237–245. https://doi.org/10.1007/s11829-010-9105-4

Hatfield JL, Prueger JH (2015) Temperature extremes: effect on plant growth and development. Weather Clim Extrem 10:4–10. https://doi.org/10.1016/j.wace.2015.08.001

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

Holzmueller EJ, Jose S (2011) Invasion success of cogongrass, an alien C4 perennial grass, in the southeastern United States: exploration of the ecological basis. Biol Invasions 13:435–442. https://doi.org/10.1007/s10530-010-9837-1

Hornoy B, Tarayre M, Hervé M et al (2011) Invasive plants and enemy release: evolution of trait means and trait correlations in *Ulex europaeus*. PLoS ONE 6:e26275. https://doi.org/10.1371/journal.pone.0026275

Joshi S, Tielbörger K (2012) Response to enemies in the invasive plant *Lythrum salicaria* is genetically determined. Ann Bot 110:1403–1410. https://doi.org/10.1093/aob/mcs076

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Liu H, Stiling P, Pemberton RW (2007) Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. Biol Invasions 9:773–781. https://doi.org/10.1007/s10530-006-9074-9

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

Memmott J, Fowler SV, Paynter Q et al (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. Acta Oecol 21:213–222

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Mitchell MJ, Brescia AI, Smith SL, Morgan ED (2007) Effects of the compounds 2-methoxynaphthoquinone, 2-propoxynaphthoquinone, and 2-isopropoxynaphthoquinone on ecdysone 20-monooxygenase activity. Arch Insect Biochem Physiol 66:45–52. https://doi.org/10.1002/arch.20196

Mitchell CE, Blumenthal D, Jarošík V et al (2010) Controls on pathogen species richness in plants' introduced and native ranges: roles of residence time, range size and host traits. Ecol Lett 13:1525–1535. https://doi.org/10.1111/j.1461-0248.2010.01543.x

Najberek K, Solarz W, Chmura D et al (2016) An invertebrate harmfulness scale for research on plant pest diversity and impacts. Int J Pest Manag 62:185–194

Najberek K, Nentwig W, Olejniczak P et al (2017a) Factors limiting and promoting invasion of alien *Impatiens balfourii* in Alpine foothills. Flora Morphol Distrib Funct Ecol Plants 234:224–232

Najberek K, Solarz W, Chmura D (2017b) Do local enemies attack alien and native *Impatiens* alike? Acta Soc Bot Pol 86(4):3562. https://doi.org/10.5586/asbp.3562

Najberek K, Pusz W, Solarz W, Olejniczak P (2018) The seeds of success: release from fungal attack on seeds may influence the invasiveness of alien *Impatiens*. Plant Ecol 219:1197–1207

Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecol Lett 8:959–967. https://doi.org/10.1111/j.1461-0248.2005.00799.x

Perrins J, Fitter A, Williamson M (1993) Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. J Biogeogr 20(1):33–44

R Development Core Team (2015) R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna

Schultheis EH, Berardi AE, Lau JA (2015) No release for the wicked: enemy release is dynamic and not associated with invasiveness. Ecology 96:2446–2457

Siemann E, Rogers WE, Dewalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. Proc R Soc B 273:2763–2769. https://doi.org/10.1098/rspb.2006.3644

Siemann E, DeWalt SJ, Zou J, Rogers WE (2016) An experimental test of the EICA Hypothesis in multiple ranges: invasive populations outperform those from the native range independent of insect herbivore suppression. AoB Plants. https://doi.org/10.1093/aobpla/plw087

Skaug H, Fournier D, Nielsen A et al (2013) Generalized linear mixed models using AD Model Builder. R Package Version 081

Skou A-MT, Markussen B, Sigsgaard L, Kollmann J (2011) No evidence for enemy release during range expansion of an evergreen tree in Northern Europe. Environ Entomol 40:1183–1191. https://doi.org/10.1603/EN11063

Stohlgren T (2011) Landscape patterns of plant invasion. Native species richness patterns. In: Encyclopedia of biological invasions. University of California Press, Berkeley, p 422–425

Sugiura S (2010) Associations of leaf miners and leaf gallers with island plants of different residency histories. J Biogeogr 37:237–244. https://doi.org/10.1111/j.1365-2699.2009.02199.x

Tabak NM, von Wettberg E (2008) Native and introduced jewelweeds of the Northeast. Northeast Nat 15:159–176

Tokarska-Guzik B, Dajdok Z, Zając M et al (2012) Rośliny obcego pochodzenia w Polsce. Generalna Dyrekcja Ochrony Środowiska, Warszawa

Ugoletti P, Stout JC, Jones MB (2011) Ecophysiological traits of invasive and non-invasive introduced *Impatiens* species. Biol Environ Proc R Ir Acad 111B:143–156

van Kleunen M, Fischer M (2009) Release from foliar and floral fungal pathogen species does not explain the geographic spread of naturalized North American plants in Europe. J Ecol 97:385–392. https://doi.org/10.1111/j.1365-2745.2009.01483.x

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vilà M, Maron JL, Marco L (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. Oecologia 142:474–479. https://doi.org/10.1007/s00442-004-1731-z

White EM, Sims NM, Clarke AR (2008) Test of the enemy release hypothesis: the native magpie moth prefers a native fireweed (*Senecio pinnatifolius*) to its introduced congener (*S. madagascariensis*). Austral Ecol 33:110–116. https://doi.org/10.1111/j.1442-9993.2007.01795.x

Zou J, Rogers WE, Siemann E (2008) Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. Biol Invasions 10:291–302. https://doi.org/10.1007/s10530-007-9130-0