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ORIGINAL RESEARCH PAPER

Do local enemies attack alien and native *Impatiens* alike?

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Abstract

The enemy release hypothesis (ERH) attributes the invasive behavior of some alien species to decreased pressure from natural enemies, as they have been left behind in the hosts' native range. The majority of research supports this idea, but some studies confirm it only partially or even contradict it. Here, we present the results of ERH tests of three *Impatiens* species studied in southern Poland in 2010–2011. Two of them are alien and invasive in Europe (*Impatiens glandulifera*, *I. parviflora*) and one is native (*I. noli-tangere*). We compared the three species in terms of the percentage of all leaves showing symptoms of disease and/or damage, and also the number of pests recorded on the monitored plants.

In 1071 individual plant controls, we assessed 17 180 leaves, 7552 of which showed symptoms of disease/damage, and we recorded 5721 invertebrates, 5220 of them were pests. Rusts and spots were the predominant symptoms and Aphidoidea were the dominant group of pests. Comparisons of the two alien and one native *Impatiens* did not confirm the ERH in 90% of the performed tests. Most of the differences between the species were not significant, and most of the significant ones contradicted the ERH. The only results confirming the ERH were found in comparisons between *I. parviflora* and *I. noli-tangere*. The tests between two alien species showed that *I. parviflora* was under higher pest pressure, while *I. glandulifera* had more disease and damage symptoms, thus, plant–enemy relations differed between the two balsams. In summary, the presented results add evidence that the success of some alien species may depend on factors related to biotic and/or abiotic conditions in ways that are not explained by the enemy release hypothesis.

Keywords

biological invasions; enemy release hypothesis; invasiveness; congeneric pairs; harmfulness scale; leaf damage; pest attack; plant–enemy relations

Introduction

One of the main goals in biological invasion studies is to determine the drivers of the invasive behavior of some alien species [1,2]. According to the latest data, as many as 5–20% of the alien species that manage to establish become invasive [3]. A number of hypotheses have been proposed to explain invasiveness [4], including the diversity invasibility hypothesis [5], empty niche hypothesis [5,6], enemy release hypothesis [5,7,8], biotic resistance hypothesis [5,8], propagule pressure hypothesis [9], invasional meltdown hypothesis [10] and novel weapons hypothesis [11,12].

Among these, the one most frequently tested is the enemy release hypothesis (ERH) (hits for the phrases: 731 for "enemy release hypothesis", 190 for "diversity invasibility hypothesis", 177 for "propagule pressure hypothesis", 42 for "empty niche hypothesis", 33 for "invasional meltdown hypothesis") [13]. It posits that invasive alien species are successful because they leave behind their natural enemies (e.g., herbivores, pathogens, and parasites) in the native range [5,7,8]. Moreover, the evolution of increased competitive ability hypothesis (EICA), which was derived from the ERH, states that the energy and/or biomass that had to be spent for defense against enemies in the native range can be invested in more effective reproduction in the new areas taken over after introduction [14]. This leads to an increase in the population numbers of the alien species, its spread, and consequently invasiveness, manifested in negative impacts on native biodiversity, ecosystem services, the economy, and human wellbeing (e.g., [15,16]).

A considerable number of ERH tests have supported these assumptions (e.g., [17–21]), but the hypothesis and associated testing methods have also been criticized [22–24]. Some tests have confirmed it only partially [25–27], have proved negative (e.g., [28–30]), or have led to conclusions contradicting it [31–33]. A review of the results of ERH tests [34] indicated that for alien plant species the hypothesis was confirmed in about 57% of experimental studies. This means that the importance of (the absence of) natural enemies to the success of invasive alien species is unclear. It may play a crucial role for only some species, or only in specific local conditions (e.g., [35]).

In this work, we tested the ERH in native and alien plant species of the flora of southern Poland, using the community approach [36]. The hypothesis would be confirmed if the level of enemy attack on the alien species is lower than on co-occurring native species. Since the level of release of alien species from their enemies may differ between the areas where they were introduced [37], we included two mesoregions significantly differing in physiography: lowland – Skawiński Trench (Rów Skawiński in Polish) and montane – Podtatrzański Trench (Rów Podtatrzański in Polish) at the foot of the Tatras. In this way, we could test whether differences in enemy release partially account for the lower susceptibility of mountains to biological invasions as compared to lowlands [38–40]. For the tests, we used the alien *Impatiens glandulifera* and *I. parviflora*, and the native *I. noli-tangere*. Despite the very high invasiveness of both alien species [41], they have not been subjected to such tests in Poland at all, and rarely elsewhere in Europe [42–44]; this is surprising in view of the efforts made to develop biological control methods against these plants [45,46].

Material and methods

Species selected for study

The selected alien balsams, *Impatiens parviflora* DC and *I. glandulifera* Royle, occupy diverse habitats in their native and introduced ranges. These species colonize temperate broadleaved and mixed forests, and altered ruderal habitats such as built-up areas, fallow land in cities, abandoned fields, ditches, and roadsides [47]. Both species are invasive in areas where the climate matches that of the native range. *Impatiens noli-tangere* is native and common throughout Poland [48]. All three balsams are annuals and reproduce only by seeds [49,50].

Impatiens parviflora and *I. glandulifera* are native to Central and East Asia [41,47] and were first recorded in Europe around 1830 and 1839, respectively [51,52]. In Poland, *I. parviflora* was first observed around 1850, and *I. glandulifera* in 1890 [41,47]. The former probably was introduced accidentally [53], and the latter was brought in intentionally as an ornamental and medicinal plant [41]. Both Asian species have spread across Poland and their numbers have been increasing steadily [41]. Despite some opinions negating the harmful impact of alien *Impatiens* species [53,54], on the national scale they are classified as highly invasive [41]. *Impatiens glandulifera* is officially listed as an alien species whose importation, possession, and trade are restricted both in Poland and Europe [55]. The main mechanism of the negative impact of alien balsams is displacement of native flora in the habitats they invade [56,57]. This is particularly significant in the case of *I. glandulifera*, as the species competes successfully with native plants thanks to its high attractiveness for pollinators, high reproductive capacity [58,59], and antimicrobial, antioxidant, and allelopathic potential [60,61]. Allelopathic compounds, for example, may change soil properties and decrease the arbuscular mycorrhiza colonization on tree saplings, which may in turn negatively affect the performance of a tree (e.g., *Acer pseudoplatanus*) [62]. Changes in soil properties in forest ecosystems may also result in changes in the number and diversity of invertebrates such as gastropods [63]. Although *I. parviflora* has lower allelopathic potential [60], this species occurs in forests much more frequently than *I. glandulifera*; thus, its overall negative impact may be even more substantial. Moreover, there are some indications that the native *I. noli-tangere* may also be undergoing displacement by *I. parviflora*, as both species occupy similar habitats [64].

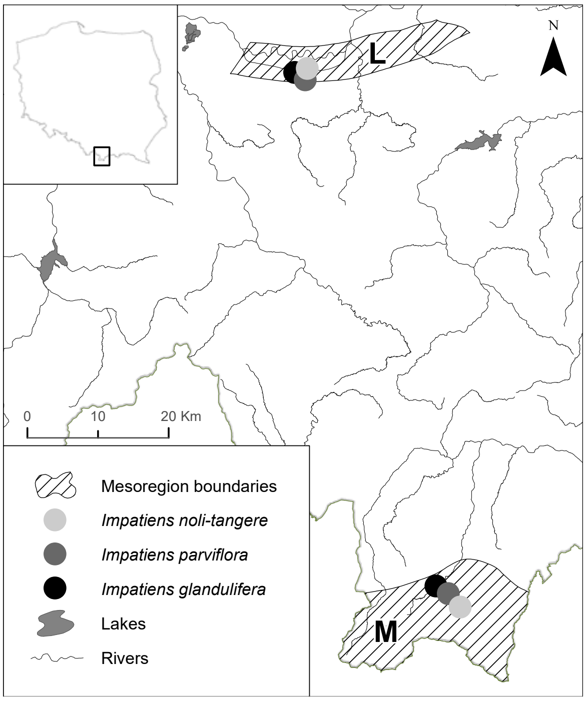

Fig. 1 Balsam species studied in the Skawiński Trench (lowland, L) and Podtatrzański Trench at the foot of the Tatra Mountains (M) in southern Poland. Map was created using ArcGIS software by Esri.

Study sites

The study was performed in southern Poland in two mesoregions: the lowland Skawiński Trench and the montane Podtatrzański Trench at the foot of the Tatras (Fig. 1). These two areas are about 70 km apart and differ in elevation by more than 600 m; the mean elevation of the study sites is 290 m above sea level in the lowland and 909 m above sea level in the mountains.

The Skawiński Trench (labeled "lowland" or "L" here) is situated along the upper course of the Vistula river. It is sparsely forested, with considerable cover of meadows, fallows, and other human-altered vegetation. It abuts the Carpathian foothills in the south and forms the border between continental and alpine biogeographic mesoregions [65]. Pollution in this area can be attributed to heavy industry, high population density, and the dense transport network.

The Podtatrzański Trench and the neighboring Tatra Mountains (labeled "mountains" or "M" here) is an alpine area with a harsh high-mountain climate and short vegetation period [65]. Despite the lack of heavy industry, this area receives pollutants due to the presence of 2.5 million tourists who visit the main city of Zakopane and the Tatra Mountains every year [66].

For each of the three studied balsam species, in habitats typical for each of them, we selected one lowland and one montane study site in 2009 (Fig. 1, Tab. 1). To minimize the effect of abiotic site-specific characteristics on enemy release [67], the study sites within the regions were situated close to each other (within 0.5 km in lowland and within 1.8 km in mountains; Fig. 1).

At each site, we individually tagged 50 plants with a numbered plastic band in each of two successive study seasons (2010 and 2011). We selected plants in the same development phase to avoid the need for stratified-random sampling, and excluded plants growing at patch edges and patch centers. In each of the two study years, the surveys began with the onset of the vegetative phase and continued to the subsenile phase [68,69], whereupon the dry weight of aboveground parts of the plants was measured to 0.01 g accuracy (plants were dried in room temperature).

Data collection

Each of the six study sites was visited every 2 weeks between June and September in 2010 and 2011. These surveys were always conducted by the same researcher in order to strictly maintain the standard scheme for classification of natural enemies. Surveys started at 9 a.m. and continued until 3 p.m. They were carried out in favorable weather conditions, comparable between the surveys. A total of 79 visits were made at the study sites: 23 for *I. noli-tangere* (10 in L and 13 in M), 26 for *I. parviflora* (14 in L and 12 in M), and 30 for *I. glandulifera* (16 in L and 14 in M).

For each site survey, we randomly selected 15 of the 50 plants tagged previously and recorded the percentage of all leaves showing symptoms of disease and/or damage on

Tab. 1 Abiotic characteristics of the localities chosen for the enemy release tests.

Species	Region	Locality	Altitude (m a.s.l.)	Exposition	Shading (%)	Habitat description
I. noli-tangere	Skawiński Trench	Kopytówka village	280	Northern	75	Small wetland in mixed forest
I. parviflora	Skawiński Trench	Kopytówka village	290	Flat	75	Mixed forest, near footpath
I. glandulifera	Skawiński Trench	Kopytówka village	299	Southern	25	Edge of mixed forest, near footpath and buildings
I. noli-tangere	Podtatrzański Trench	Tatra Mts, Dolina Olczyska valley	928	Southern	75	Bank of stream, forest
I. parviflora	Podtatrzański Trench	Zakopane, Antałówka	913	Southern	75	Hilltop covered with a group of trees, near tourist trail
I. glandulifera	Podtatrzański Trench	Zakopane, Jaszczurówka	886	Flat	25	Bank of stream, near buildings

each controlled plant (total 1071 plants and 17 180 leaves checked; Appendix S1). Also recorded were the number and diversity of all invertebrates on the leaves, flowers, and stem of each controlled plant. In most cases, the invertebrates were identified in situ without capture. We made digital images (Canon EOS 400D, Canon EF 100 mm f/2.8 Macro USM lens) of invertebrates that could not be identified in situ, and identified them later with the help of zoologists from the Institute of Nature Conservation and the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, and the Institute of Zoology of the Jagiellonian University. We also used digital images to identify and precisely count invertebrates occurring en masse (e.g., Aphidoidea). We identified 70.5% of all invertebrates to family or superfamily level. Invertebrates that were difficult to identify were classified to infraorder or order.

Harmfulness of invertebrates

We used a harmfulness scale to analyze the data on the number and diversity of true pests among all the invertebrates recorded on the plants [70]. Use of the scale enabled us to estimate the negative impact of those pests on the plants (Appendix S2). The scale was developed using literature data on the harmfulness of invertebrates (H_i). It assigns H_i values to the recorded taxonomic groups (families, superfamilies, orders, suborders) on a scale from 0 to 1, with three intermediate values (0.25, 0.5, 0.75): 0 for taxa that do little or no harm to the studied plants; 0.25 for taxa that very rarely feed on herbaceous plant tissues; 0.5 for taxa having herbaceous plant tissues as a permanent but not the predominant source of food; 0.75 for taxa in which most species are obligatory phytophages, parasites, and pathogen carriers but for which a considerable share of the species in that group do little or no harm to the studied plants; and 1 for taxa in which all species are obligatory phytophages. The H_i values assigned to the taxa, multiplied by the number of individuals within these taxa recorded on each plant, give a proxy assumed to represent the number of pests attacking a given plant; this is a method of dealing with a large sample of pests, enabling the extent of their negative impact on plants to be estimated quickly and simply [70]. Earlier work has indicated the need for harmfulness estimation when more harmful and less harmful pests are being studied [71].

Enemy release coefficients

Field data were used to calculate two coefficients of enemy release (ER). They were estimated for each survey of each controlled plant ($N = 1071$). Data on leaf disease and damage were used to calculate the disease and damage coefficient (ER_D):

$$ER_D = \frac{N\ leaves\ with\ disease\ or\ damage \times 100}{N\ leaves}$$

The pest coefficient (ER_P) was calculated with use of number of recorded invertebrates and their harmfulness (H_i). The coefficient reflects the total number of recorded pests:

$$ER_P = N\ pests = N\ invertebrates \times H_i$$

Statistical analyses

Spearman rank correlations were used to assess the level of dependence between the two ER coefficients for the three studied plants.

Linear mixed-effects models (LMM) with the lmer function (Lme4 package) [72] and generalized linear mixed models using AD Model Builder with zero inflation parameter (package glmmADMB) [73–75] were used. The first allow analysis of interval data (ER_D) with a Gaussian distribution. The second were used for numerical data with a negative binomial distribution (ER_P). ER_P coefficients were rounded to convert decimal values to integers, except for values 0.25 and 0.5, which were always rounded to 1 so that no records of pests were excluded.

In base models (Appendix S3), the response variables were the enemy release coefficients ER_D and ER_P. Covariates were: the plant species ("species"), the study mesoregion (lowland or mountains; "region"), the study year (2010 or 2011; "year") and the average dry weight of plants at each study site ("weight"). In both models we also assessed the following interactions: species with study mesoregion (Species × Region) and species with study year (Species × Year). The number of surveys of each controlled plant varied (it was the effect of randomly selecting 15 of the 50 individuals before each survey of particular locality), so "individual ID" was taken into account as a random effect. This also accounted for the possible dependence of leaf damage or the number of pests recorded in subsequent surveys.

Each of the two base models was used to generate best-fit models (Appendix S3) with the lowest corrected Akaike information (AICc) and delta (Δ) values. In order to indicate strong evidence for the model, the criterion with $\Delta < 2$ was included [76]. It was achieved with the use of the "dredge" function from the MuMIn package [77]. Moreover, to test differences between the studied species growing in the two mesoregions, the data was reduced to the particular mesoregion and then the best-fit model without "region" covariate and Species × Region interaction was tested. All data were analyzed using R v. 3.3.2 and RStudio v. 1.0.136 [78].

Results

We recorded 7552 leaves with disease and damage symptoms. Rusts and spots were the predominant symptoms, recorded on 90.6% of the leaves showing symptoms (Appendix S1). The vast majority of the 5721 recorded invertebrates were pests (5220; 91.2%). Aphidoidea were the dominant group, accounting for 95.2% of all recorded pests (Appendix S2).

ERH analysis

The results of correlations among ERH coefficients were significant only for *I. parviflora* and *I. glandulifera*, and these correlations were weak ($r_s = 0.23$, $p < 0.001$ and $r_s = -0.10$, $p = 0.05$, respectively).

Tab. 2 GLMM comparing enemy pressure levels in two sets of tests: ERH – between invasive alien species (Ip – *Impatiens parviflora*, Ig – *I. glandulifera*) and native species (In – *I. noli-tangere*); IAS – between invasive alien species (Ig vs. Ip).

Comparison type	ER coefficient (response variables)	Enemy pressure					Model result
		all	lowland	mountains	2010	2011	
ERH	ER$_D$	**Ip < In *****	**Ip < In****	ns	ns	ns	χ^2 *df* *p* Species 18.67 2 <0.001 Region 12.51 1 <0.001 Year 0.006 1 0.94 Weight 10.10 1 0.001 Sp × Re 20.04 2 <0.001 Sp × Ye 1.32 2 0.52
ERH		ns	Ig > In**	ns	ns	ns	
IAS		Ig > Ip ***	Ig > Ip***	ns	ns	ns	
ERH	ER$_P$	Ip > In **	ns	Ip > In***	ns	ns	χ^2 *df* *p* Species 166.70 2 <0.001 Region 2.75 1 0.096 Year 9.74 1 0.002 Weight 2.43 1 0.11 Sp × Re 98.88 2 <0.001
ERH		Ig > In **	Ig > In***	Ig > In***	ns	ns	
IAS		Ig < Ip ***	Ig > Ip***	Ig < Ip***	ns	ns	

Enemy pressure was measured as coefficients of leaf disease and damage (ER$_D$) and attack by pests (ER$_P$). Results are presented for the whole dataset (all) and separately for the two studied mesoregions (lowland and mountains) and two study years (2010 and 2011). Results that confirmed the enemy release hypothesis are set in boldface. Model results are also presented. Weight – weight of plants at study site, Sp × Re – Species × Region interaction; Sp × Ye – Species × Year interaction; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Base model is given in Appendix S3.

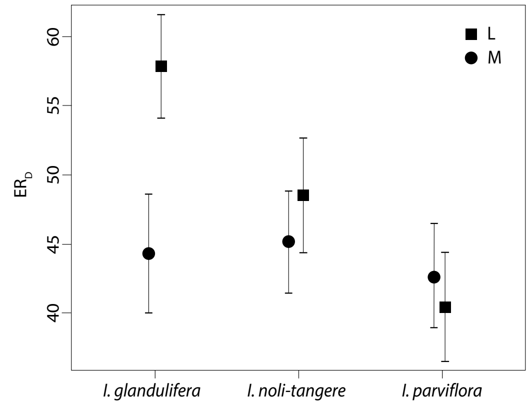

Fig. 2 Estimated means for disease and damage coefficient ER$_D$ (± confidence intervals) of *Impatiens* species in the lowland (L) and mountain (M) mesoregion.

In the model for the ER$_D$ coefficient (Tab. 2, Appendix S3), for the whole dataset (“all”) there were significant differences between *I. parviflora* and *I. noli-tangere* ($t = 2.97$, $p = 0.003$) and between *I. glandulifera* and *I. parviflora* ($t = 4.07$, $p < 0.001$). The first result confirms the ERH, and the second shows that *I. glandulifera* was under stronger pest attack than *I. parviflora*. The remaining analyses between species (for study mesoregion and study year) produced significant results only for interaction between species and mesoregions (Fig. 2, Tab. 2). Significant differences were noted for all three combinations in lowland: *I. parviflora* with *I. noli-tangere* ($t = 3.10$, $p = 0.002$), *I. glandulifera* with *I. noli-tangere* ($t = 3.19$, $p = 0.001$), and *I. glandulifera* with *I. parviflora* ($t = 6.11$, $p < 0.001$). The result for *I. parviflora* and *I. noli-tangere* confirms the ERH (enemy pressure was higher on native species), while the result for the second pair was contrary to the hypothesis. Comparison between the two alien plants revealed that *I. parviflora* was under lower enemy pressure than *I. glandulifera* (Fig. 2, Tab. 2). Moreover, mesoregion exerted effect with more leaf disease and damage in lowland than in mountains (Tab. 2) and the model was influenced by plant weight (Tab. 2).

In the model for the ER$_P$ coefficient (Tab. 2, Appendix S3), comparisons for the whole dataset (“all”) produced results contrary to the ERH: *I. glandulifera* and *I. parviflora* were under higher pressure than *I. noli-tangere* ($z = 2.93$, $p = 0.003$ and $z = 11.25$, $p < 0.001$, respectively). In contrast to the results for the ER$_D$ coefficient, *I. parviflora* was under higher pest pressure than *I. glandulifera* ($z = 7.12$, $p < 0.001$). Results for Species × Region interaction (Fig. 3, Tab. 2) were driven mainly by high differences in pest pressure level between *I. parviflora* and the two other species in mountains. These two comparisons had the most significant impact on the obtained results. In the *I. parviflora* – *I. noli-tangere* pair, the alien species escaped enemies much less effectively than the native one ($z = 14.25$, $p < 0.001$), while the result obtained for the pair of alien *I. parviflora* and *I. glandulifera* indicated significantly higher pressure on the former species ($z = 9.22$, $p < 0.001$). There were two other results that were non-consistent with the ERH assumptions, with *I. glandulifera* escaping enemies less effectively than *I. noli-tangere* ($z = 2.58$, $p = 0.009$ in mountains and $z = 2.79$, $p = 0.005$ in lowland). Moreover, the relation between the two alien species in lowland was opposite to that of the whole dataset (and to the mountains) – *I. glandulifera* was under higher pest attack than *I. parviflora* ($z = -4.39$, $p < 0.001$; Fig. 3, Tab. 2).

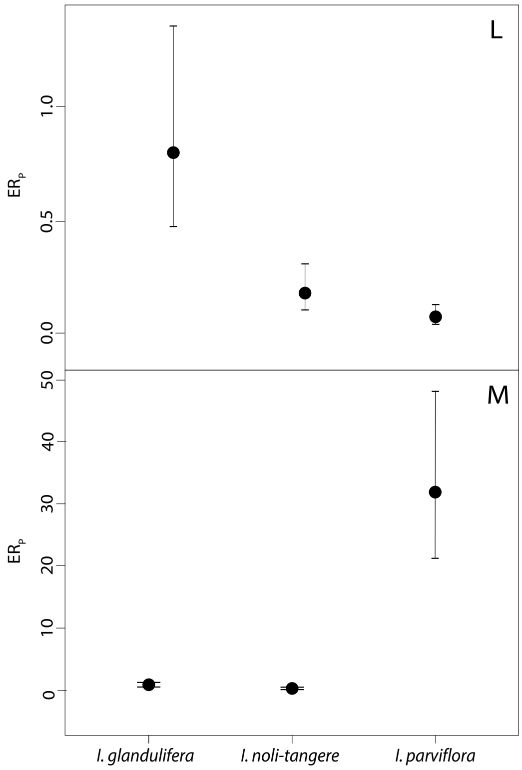

Fig. 3 Estimated means for pest coefficient ER_P (± confidence intervals) of *Impatiens* species in lowland (plot L) and mountain (plot M) mesoregion

The models testing differences between the two alien and one native species confirmed the ERH in two cases (Tab. 2). More than half of the results were non-significant (60%), and enemy attack was heavier on the alien than on the native species in six of 20 cases (30%). This means that significantly fewer tests (10%; proportion test, $\chi^2 = 38.4$, $df = 1$, $p < 0.001$) produced results consistent with the ERH hypothesis.

In comparisons of pest attack on the two invasive alien balsams (*I. glandulifera* and *I. parviflora*; Tab. 2), half of the results (50%) were non-significant. Significant results (50%) seemed to be related with the studied region – enemy pressure was higher on *I. glandulifera* in lowland and higher on *I. parviflora* in mountains.

Discussion

We found very little confirmation of the enemy release hypothesis in comparisons of enemy attack on alien and native *Impatiens*. The only two confirming results (10%) were found – for *I. parviflora* and *I. noli-tangere* in disease and damage symptoms analysis (ER_D). Nevertheless, more than a half of the results showed non-significant differences, and six tests (30%) produced results contrary to those predicted by the ERH, indicating that both alien species were under stronger enemy pressure than the native one. Moreover, half of the tests showed no differences in enemy release level between *I. parviflora* and *I. glandulifera*. The significant results for the whole dataset showed that *I. parviflora* was under higher pest pressure, while *I. glandulifera* had more disease and damage symptoms, thus plant–enemy relations differed between the two balsams. Moreover, *I. parviflora* showed significantly higher enemy release in lowland, and *I. glandulifera* in mountains.

The studied balsam species were tested by the community method, which is considered to be a more rigorous way of testing the ERH [36]. This method confirms the ERH when the obtained results show that an alien species is attacked less than a co-occurring native congener. The pair *I. parviflora* – *I. noli-tangere* was tested by this method in the Czech Republic [43]. In that study, the compared plants showed similar damage caused by natural enemies, which is consistent with 60% of the results presented here. In two other works, *I. glandulifera* was tested by the biogeographical method [36], in which enemy pressure on a particular species is compared in two regions: native and introduced. The first study suggested that, in Switzerland, the species had no enemies harming it [42]. Taking into account our results and those from Switzerland, we can speculate that, since *I. glandulifera* had become acclimated to higher pressure in its primary area of occurrence, its success was driven not only by release from enemies but also by higher tolerance of the negative effects of their presence, which would be consistent with the assumptions by Schierenbeck et al. [79] and the enemy tolerance hypothesis [80]. In line with this, Gruntman et al. [44] found that herbivore pressure on *I. glandulifera* in the introduced range increased with age of populations, with the highest levels noted for those 45–65 years old. However, herbivore pressure for the oldest populations (65–85 years) sharply fell to the lowest level, equal to the level noted for native populations. This provides evidence of an evolutionary response of *I. glandulifera* to rising enemy pressure over time, resulting in herbivore resistance. Moreover, Elst et al. [81] showed that the herbivore defense of *I. glandulifera* rose with habitat productivity, and suggested that the productivity of European habitats could be higher than in its native range in the Himalayas, which in turn could be critical to the success of *I. glandulifera* after introduction.

In this study, we compared enemy pressure between two areas differing in physiognomy: lowland and montane mesoregions. Pathogen pressure (ER_D) was significantly higher in lowland for all of the tested plants. Our results may be related to climate, which, in mountains, is more severe and can reduce the presence of some pathogens. In the case of pests, mesoregion affected the ERH test results but the difference in number of pests was not significant. In this connection we note that, again, montane climate should affect invertebrates (including pests) in a limiting way [82]. Two comparisons of ERH for number of pests [tests for ER_P: (***i***) *I. parviflora* with *I. noli-tangere*, (***ii***) *I. glandulifera* with *I. noli-tangere*] showed that, in mountains, the invasive alien species tended to be under higher pressure from pests than the native species. It was particularly well-pronounced in comparison between *I. parviflora* and *I. noli-tangere*, for which differences were the most significant and had strong influence on the overall ER_P results. Mountains are thought to be less vulnerable to biological invasions [39]. The factors considered responsible for that are severe climate, high cover by forest, and low human population [83]. Our results may indicate that stronger pest pressure can also limit biological invasions at higher altitudes. Nevertheless, the obtained differences between mountains and lowland are preliminary and should be interpreted with due caution.

In view of our results and those of others, do natural enemies really have an impact on invasive alien plants after their introduction to a new area? A review by Prior and Hellmann [34] found that the ERH has only been confirmed in 57% of the cases they studied. Furthermore, as the ERH was first formulated, it was pointed out that the role of pests in plant invasions had not been examined adequately [8]. Vasquez and Meyer [71] tested the condition of *Pastinaca sativa* in two parallel groups of plants. The first was subjected to pressure from natural enemies and the second was isolated. In that study, pest pressure had no significant effect on the condition of the plants. In a similar study, Cripps et al. [26] found that *Cirsium arvense* was under less pressure from natural enemies after its introduction to New Zealand, but that did not increase the plant's performance. Two studies of *Senecio jacobaea* produced opposite results. One study found no increase of vigor in plants released from enemies [84], and the other confirmed such an improvement [85].

Previously, tests of the ERH have been based only on the degree of leaf damage (e.g., [86–88]) or pathogen pressure [18,89]. Joint analysis of the results of tests for pests and symptoms, applied in the present study, seems to be the best way to verify the ERH [90]. Moreover, in this study we applied a novel protocol for collecting data on natural enemies. Some studies have determined pests to species level (e.g., [25]), and others have used a classification species as specialists and generalists [91]. The number of recorded pests in this study exceeds 5000 individuals, belonging to diverse taxonomic groups; it is a huge task, therefore, to examine their food preferences in detail.

Apart from the taxonomic difficulties, which required the involvement of experts in entomology, botany, and microbiology, we had to obtain permission to do research in Tatra National Park. Collecting samples would have required killing some insects (including protected species), which is forbidden in the national parks. Moreover, removing invertebrates from the plants would have affected the level of enemy pressure on them, skewing the data on pest attack. These aspects have not been adequately addressed in discussions of the methods used to test the ERH. Removal is not the only action that has such an effect. The researchers' intrusion can scare away invertebrates, especially flying insects, affecting the data and even leading to the complete absence of a given pest in a sample. In the case of a large plant such as *I. glandulifera*, it is impossible to collect all the invertebrates at one time. To keep our intrusiveness to a minimum, we took digital photographs to document the presence of pests, which helped ensure that the invertebrates were not removed from the host plants and their behavior was not disturbed. A potential source of inaccuracy was that invertebrates that are highly mobile could have escaped before being recorded, or they could have been counted more than once, giving an overestimate of their absolute number. However, this should not affect comparisons of the relative frequencies of pests between the studied plants or regions [70].

Another advantage of using digital photography was that it allowed us to make reliable estimates of the numbers of massively occurring pests such as aphids. A massive occurrence may completely mask the effect of other, less abundant taxa. Despite that danger, some earlier studies excluded massively occurring pests from the analyzed datasets due to methodological problems. Such an omission can significantly affect the conclusions drawn [25]. Digital photography was also employed by Kirichenko et al. [92] as an auxiliary tool for further determination of leaf damage that was hard to identify in ERH tests.

Pathogen identification often requires complex molecular methods [93], which is more of a problem than determining pests to species level. Instead of identifying the causative organisms, we identified symptoms, a method used successfully by others [27]. In testing the ERH, it is sufficient to identify symptoms because it serves the main goal – to compare enemy pressure between native and alien species. We did not estimate leaf damage percentages [88,92]. For such a large sample size (17 180 leaves controlled), it was sufficient to record the sick-to-healthy leaf ratio to produce a reliable dataset.

It should be noted that pest attack calculated using a harmfulness scale is a proxy rather than an absolute value, particularly as it does not measure the direct impact of the pests on the plants [70]. However, some of the recorded invertebrates certainly do harm plants. We observed effects of grazing invertebrates in the present study: one whole *I. noli-tangere* plant was eaten by *Symphyta* larvae. If such grazers dominate in a given area, the condition of their preferred plants will decline. One type of plant response to pest attacks relies on toxic substances that discourage a potential enemy [94]. These substances are secreted when the plant recognizes the enemy. According to Vrchotová et al. [60] and Csiszár et al. [95], the highly invasive alien balsams *I. glandulifera* and *I. parviflora* have the highest allelopathic abilities of all European balsams, including the native *I. noli-tangere*. In our study, however, both species were attacked by enemies as often as or more frequently than *I. noli-tangere*. Possibly the toxins they produce are used rather against other plants than against potential enemies, a case which would suggest the novel weapons hypothesis (NWH) [12]. Such a type of allelopathy would be advantageous in a situation in which enemy pressure from even the most harmful pests had no effects on plant performance. Pavela et al. [96] demonstrated that evaporated methanolic extracts from *Impatiens* species killed the green peach aphid (*Myzus perssicae*); in this regard the most effective extract was from *I. parviflora*. Szewczyk et al. [61] showed some antimicrobial activity of balsam extracts against Gram-positive bacteria as well. However, our knowledge of how the toxins of balsams affect pests is still limited.

If balsam toxins are only employed against plants, it would indicate that alien balsams may be more resistant to enemy attacks than their native counterparts, which supports the ideas proposed by Schierenbeck et al. [79]. Gruntman et al. [44] showed that the post-introduction herbivore resistance of *I. glandulifera* rises with time, while its allelopathic effects do not. They further stressed the need for more investigation, citing their earlier finding that the allelopathic ability of the species significantly evolved in the invaded range. Future research should also focus on the impact of the same enemy in native and introduced ranges of *Impatiens*, such as that of the cosmopolitan *Plasmopara obducens*, recorded both in Europe and in Pakistan [45,97]. Another example is the alien rust fungus *Puccinia komarowii* Tranzsche, attacking *Impatiens* species both in Europe, where it was first found in 1921, and in the native foothills of the Himalayas [46]. It is also worth studying the aphids, which were massively recorded in the present study. For example, *Impatientinum asiaticum*, introduced into Europe around 1967 from Central Asia, attacks *I. parviflora* and *I. noli-tangere* [98]; however, in Germany and in Hungary it occurs also on *I. glandulifera* [99,100].

Although in our present study the most dominant leaf diseases were "rusts and spots", this type of stress does not seem to significantly affect the overall invasiveness of the studied *Impatiens* plants. It is therefore possible that resistance against pathogen enemies was developed long before these plants were introduced to Europe. However, post-introduction evolution of this trait is also very likely; it would be consistent with results from Kollmann et al. [101], who found that resistance of *I. glandulifera* to virus infection differed between plants from different populations throughout Europe. Interestingly, the populations from two out of nine regions (from the Czech Republic and France) were not infected at all. Populations from Poland were not included in that study.

The enemy release hypothesis is one of the several proposed to explain the invasiveness of alien species in new areas [102], and there are many examples confirming it, but our results and those of others suggest that the assumptions of this hypothesis do not always hold true. The success of a particular species depends on one or more of its traits, the importance of which changes according to the biotic and/or abiotic conditions of the site where it was introduced. Moreover, some traits are difficult to establish, requiring studies that take into account many environmental factors, some of which may not be covered by a given research protocol [4,103].

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3562/0:

Appendix S1 Numbers of plants and leaves with disease or damage symptoms recorded in the lowland Skawiński Trench and in the Podtatrzański Trench at the foot of the Tatra Mountains (southern Poland) in 2010 and 2011.

Appendix S2 List of organisms recorded in the lowland Skawiński Trench and in the Podtatrzański Trench at the foot of the Tatra Mountains (southern Poland) in 2010 and 2011, their harmfulness (H_i), number of records, and pest index.

Appendix S3 Base and best-fit models presented in two groups: (***i***) leaf disease and damage coefficient (ER_D) and (***ii***) pest coefficient (ER_P).

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