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International Journal of Pest Management

ISSN: 0967-0874 (Print) 1366-5863 (Online) Journal homepage: http://www.tandfonline.com/loi/ttpm20

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To cite this article: Kamil Najberek, Wojciech Solarz, Damian Chmura, Edward Walusiak & Wiesław Król (2016) An invertebrate harmfulness scale for research on plant pest diversity and impacts, International Journal of Pest Management, 62:3, 185-194, DOI: 10.1080/09670874.2016.1182229

To link to this article: http://dx.doi.org/10.1080/09670874.2016.1182229

INTERNATIONAL JOURNAL OF PEST MANAGEMENT, 2016
VOL. 62, NO. 3, 185–194
http://dx.doi.org/10.1080/09670874.2016.1182229

An invertebrate harmfulness scale for research on plant pest diversity and impacts

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ABSTRACT
Traditional methods of quantifying the harmful effects of invertebrates on plants require time-consuming identification of large numbers of individuals at species level. Collected specimens usually are killed; this may be unacceptable for some strictly protected species and may bias the results of subsequent surveys at the same site.

We developed a "harmfulness scale" for quick, non-invasive assessment of invertebrate impacts on plants, and used the scale to test differences in invertebrate attack on species of *Balsaminaceae*, *Polygonaceae* and *Asteraceae* growing in lowland and mountains in Poland. In 2010–2011, we recorded 9190 invertebrates and identified them *in situ* to family or superfamily level. Among them were 7593 pests, accounting for 82.6% of all recorded organisms. Pests were three times more numerous in the mountains than in the lowland. *Balsaminaceae* were most heavily attacked by pests (92.9% of all organisms detected on them). *Aphidoideae* were the most numerous pests.

This method can help reduce the costs and labour required for this type of research, facilitating progress in theoretical biology and in the development of practical phytosanitary measures.

ARTICLE HISTORY
Received 28 July 2015
Accepted 13 April 2016

KEYWORDS
Plant–pest interaction; pests of plants; pest impact; plant protection; invasive alien plants; Enemy Release Hypothesis

Introduction

Research on the diversity of invertebrate plant pests focuses mainly on crop protection. Consequently, while our knowledge of pests that damage crops is increasing, we have scant information on pests of wild-growing plants, especially those with no commercial value.

Research papers on this type of interaction usually refer to single or a few exceptionally harmful invertebrate species and their impact on a given plant species, or at most on a genus or a plant association (Afidchao et al. 2013). There are no general model methods to quickly quantify the harmful effect of a higher invertebrate taxon on a particular group of plants. Such tools would be useful especially in studies which up to now have required identification of very large numbers of individuals at species level, which is very time consuming and often involving the work of many taxonomists.

Our approach to this problem is to create a "harmfulness scale" for the relevant taxonomic groups, based on previously acquired knowledge: for example, data on their biology and ecology available in fauna monographs on particular areas, regions or countries. This information is often scattered and usually is not detailed, but when compiled it can give a sufficiently clear and reliable picture of the negative or positive impacts of larger taxonomic units of invertebrates on plants. On the basis of these data, the proportion of pests in a given group of organisms can be estimated, and the extent of their negative impact of pests can be calculated without the need to identify each species individually. This method should assist research involving very large numbers and a large variety of invertebrates, which is extremely time consuming if done by traditional methods.

This paper presents the concept of an invertebrate harmfulness scale and describes its application to research done in 2010–2011 in southern Poland. The study investigated differences in the number and diversity of invertebrates, including pests, occurring on the same herbaceous plant species in lowland areas and mountains, and assessed their potential negative impact on these plants.

Materials and methods

The study was done in 2010 and 2011 at sites located in Rów Skawiński (19.78582 E, 49.98014 N) and Rów Podtatrzański, including the Olczyska Valley, in Tatra National Park (19.97976 E, 49.29364 N). Fieldwork in the national park was performed under a permit from its authorities.

Rów Skawiński is a lowland area in the upper reaches of the Vistula River. The average elevation of

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the study sites is 262 m.a.s.l. Rów Podtatrzański and the Tatras are mountainous areas with a severe climate (Kondracki 2013). The average elevation of the studied mountain sites is 900 m.a.s.l.

Seven herbaceous plant species from three families, both indigenous and alien to the flora of Poland, were selected for the study:

- *Balsaminaceae* (balsams): *Impatiens noli-tangere* L., *I. parviflora* DC, *I. glandulifera* Royle,
- *Polygonaceae* (knotweeds): *Polygonum bistorta* L., *Reynoutria japonica* Houtt. (= *Fallopia japonica* (Houtt.) Ronse Decraene),
- *Asteraceae* (asters): *Solidago virgaurea* L. and *S. gigantea* Aiton.

Each species was studied at one site per mesoregion. The 14 study sites selected were typical for the habitat requirements of that species (Zarzycki et al. 2002). The number of invertebrates and the diversity of taxa occurring on the studied plants were determined every fortnight. The earliest survey was on 9 May, and the latest on 1 September. The number of surveys at each individual site depended on the vegetation period of the studied plants, and ranged from 4 to 10 in each study year. The surveys were carried out in comparable weather conditions. A total of 191 surveys were performed: 92 in the mountains and 99 in the lowland. The above-ground parts of 15 randomly selected plants (of the 50 marked at a given site) were examined during each survey, beginning from the top of the plant. If a new invertebrate individual appeared on a plant part that had already been checked it was not included. To further minimise the possibility of multiple counts of the same invertebrate, a problem of particular concern for highly mobile groups (e.g. *Apidae*), care was taken to track their movements.

The majority of the recorded invertebrates were identified to family/superfamily level (herein referred to as family) directly on the plant, without trapping. Problematic organisms difficult to identify were photographed directly on the plant (Canon EOS 400D camera; lens: Canon EF 100 mm f/2.8 Macro USM) and identified in the laboratory from the images, using identification keys. Large clusters of invertebrates (e.g. aphids) were photographed and then all the individuals in the cluster were precisely counted from the picture.

Harmfulness scale

Based on the Polish literature on invertebrate fauna (Jura 1986; Wiktor 2004; Bogdanowicz et al. 2004, 2007, 2008; Błaszak 2009, 2011; Wilkaniec 2009, 2011) containing assessments of the impact of each invertebrate group on herbaceous plants, an index reflecting the degree of their harmfulness to herbaceous plants (H_i) was assigned. Harmfulness ranged from 0 to 1, covering three intermediate values: 0.25, 0.5 and 0.75. The H_i values were established according to the following scheme (expressions used in the literature are numbered):

$H_i = 0$ – groups that inflict no or marginal harm on the studied plants (e.g. *Formicidae*). All species within these groups are (1) predators, (2) parasites of animals, (3) saprophagous organisms, (4) beneficial organisms or (5) natural enemies of pests;

$H_i = 0.25$ – groups that very rarely feed on herbaceous plant tissues (e.g. *Mecoptera*). Most species within these groups are (1) predators but there also are some phytophagous species, (2) they rarely feed on sap, (3) they rarely are phytophagous and (4) they are pests of trees and bushes but few of them are pests of herbaceous plants;

$H_i = 0.5$ – groups for which herbaceous plant tissues are a permanent but not predominant source of food (e.g. *Cecidomyiidae*). They are (1) predators and phytophagous species, (2) predatory, phytophagous and omnivorous species, and (3) saprophagous species, some of them damaging roots;

$H_i = 0.75$ – groups in which most species are obligatory phytophages, parasites and pathogen carriers, but with a considerable share of species inflicting no or marginal harm on the studied plants (e.g. *Hemiptera*, which include predatory and hematophagous species as well as phytophages). They are (1) species feeding on living or dead plant tissues, many considered to be serious pests, (2) most species feeding on sap, with few predators and parasites, and (3) mainly phytophagous, with few predators;

$H_i = 1$ – groups in which all species are obligatory phytophages (e.g. *Coreidae*), parasites (e.g. *Tetranychidae*), or carriers of pathogens with a documented impact on herbaceous plants (e.g. *Aphidoidea*). These are (1) serious pests, (2) exclusively phytophagous species, (3) phytophagous species, often with massive occurrence, and (4) sap feeders.

The H_i values, multiplied by the number of records of individuals from a particular taxonomic group, give a proxy of the number of pests in that group (N pests $= N$ records $\times H_i$; Table 1). According to this scale, the damage caused by 4 individuals belonging to the $H_i = 0.25$ group (e.g. *Mecoptera*) is the same as the damage caused by 2 individuals from the $H_i = 0.5$ group (e.g. *Cecidomyiidae*) and by 1.33 individuals from the $H_i = 0.75$ group (e.g. *Hemiptera*). For all these, the damage is 1 and is equal to the negative

Table 1. List of organisms recorded, their harmfulness indexes (H_i) according to the harmfulness scale, numbers of their records and pests for the Rów Skawiński lowland and the mountainous Rów Podtatrzański (with the Tatras); groups of organisms given at the level of precision allowed by individual identification (e.g. aphids *Aphidoidea* and true bugs *Hemiptera*).

Mountains				Lowland			
Group of organisms	*N* records	Harmfulness (H_i)	*N* pests (= *N* records × H_i)	Group of organisms	*N* records	Harmfulness (H_i)	*N* pests (= *N* records × H_i)
Aphidoidea	4967	1.00	4967.00	*Aphidoidea*	862	1.00	862.00
Stylommatophora	303	0.75	227.25	*Stylommatophora*	836	0.75	627.00
Muscidae	173	0.00	0.00	*Araneae*	606	0.00	0.00
Diptera	113	0.50	56.50	*Formicidae*	302	0.00	0.00
Araneae	97	0.00	0.00	*Muscidae*	154	0.00	0.00
Hymenoptera	83	0.25	20.75	*Apidae*	68	0.00	0.00
Apidae	59	0.00	0.00	*Diptera*	63	0.50	31.50
Auchenorrhyncha	40	1.00	40.00	*Hymenoptera*	41	0.25	10.25
Formicidae	32	0.00	0.00	*Collembola*	27	0.00	0.00
Drosophilidae	22	0.25	5.50	*Coleoptera*	27	0.50	13.50
Hemiptera	19	0.75	14.25	*Culicidae*	27	0.00	0.00
Collembola	15	0.00	0.00	*Hemiptera*	20	0.75	15.00
Plecoptera	13	0.25	3.25	*Drosophilidae*	12	0.25	3.00
Coleoptera	13	0.50	6.50	*Auchenorrhyncha*	10	1.00	10.00
Coccinellidae	13	0.25	3.25	*Curculionidae*	10	1.00	10.00
Symphyta (caterpillar)	13	1.00	13.00	*Lepidoptera* (caterpillar)	8	1.00	8.00
Psylloidea	11	0.50	5.50	*Acari*	8	0.25	2.00
Acari	10	0.25	2.50	*Vespidae*	5	0.25	1.25
Chironomidae	9	0.00	0.00	*Syrphidae*	4	0.25	1.00
Culicidae	8	0.00	0.00	*Chrysopidae*	4	0.00	0.00
Cercopidae	8	1.00	8.00	*Psocoptera*	3	0.50	1.50
Psocoptera	6	0.50	3.00	*Chironomidae*	3	0.00	0.00
Lepidoptera (caterpillar)	5	1.00	5.00	*Psychodidae*	3	0.25	0.75
Curculionidae	5	1.00	5.00	*Symphyta* (caterpillar)	3	1.00	3.00
Syrphidae	4	0.25	1.00	*Tipulidae*	3	0.50	1.50
Pentatomidae	2	0.75	1.50	*Mecoptera*	2	0.25	0.50
Aleyrodidae	2	1.00	2.00	*Neuroptera*	2	0.25	0.50
Chloroperlidae	2	0.25	0.50	*Orthoptera*	2	0.25	0.50
Neuroptera	1	0.25	0.25	*Ixodidae*	2	0.00	0.00
Orthoptera	1	0.25	0.25	*Opiliones*	2	0.00	0.00
Arionidae	1	1.00	1.00	*Sminthuridae*	2	0.00	0.00
Cecidomyiidae	1	0.50	0.50	*Porcellionidae*	2	0.00	0.00
Panorpidae	1	0.00	0.00	*Coccinellidae*	2	0.25	0.50
Sciaridae	1	0.00	0.00	*Plecoptera*	1	0.25	0.25
Psychodidae	1	0.25	0.25	*Ceratopogonidae*	1	0.00	0.00
Vespidae	1	0.25	0.25	*Trombidiidae*	1	0.00	0.00
Trichoceridae	1	0.00	0.00	*Pentatomidae*	1	0.75	0.75
				Aleyrodidae	1	1.00	1.00
				Cantharidae	1	0.25	0.25
				Cicadellidae	1	1.00	1.00
				Arionidae	1	1.00	1.00
				Coreidae	1	1.00	1.00

effect of one individual belonging to the most harmful $H_i = 1$ class, such as *Coreidae*, *Tetranychidae* or *Aphidoidea*.

In order to statistically compare the frequencies of invertebrate records from plants surveyed in the two study regions, the difference between the two proportions (herein referred to as the proportion test) and contingency tables (*G* test) were analysed using Statistica (STATSOFT INC 2011) and R software (R Core Team 2012).

Results

General patterns

In total, we recorded 9190 invertebrates (Table 1), 66 % of which ($N = 6056$) were found in the mountains and 34% ($N = 3134$) in lowland; the difference was statistically significant (proportion test, $p < 0.001$). We were able to identify 71.3% of the invertebrates to family level, and the most difficult cases were identified to order level; 17 orders and 33 families were identified. Eight of these groups were significantly more numerous in the mountains and 7 in the lowland. Seven groups were found only in mountains, and 12 were restricted to lowland.

True bugs *Hemiptera* predominated ($N = 5945$; 64.7 %) in both regions. The mountains, with 5049 individuals, hosted significantly more true bugs than the lowland with only 896 individuals recorded (proportion test, $p < 0.001$). This group accounted for as many as 83.4% of the records in the mountains and for only 28.6% in the lowland. Other dominant groups (*Diptera*, *Stylommatophora*, *Hymenoptera*, *Araneae*) had markedly larger shares in the lowland than in the mountains.

Among the recorded organisms, there were 7593 pests (82.6 % of all records), and they were three times more numerous in the mountains than in the lowland (proportion test, $p < 0.001$; Table 1). As was the case

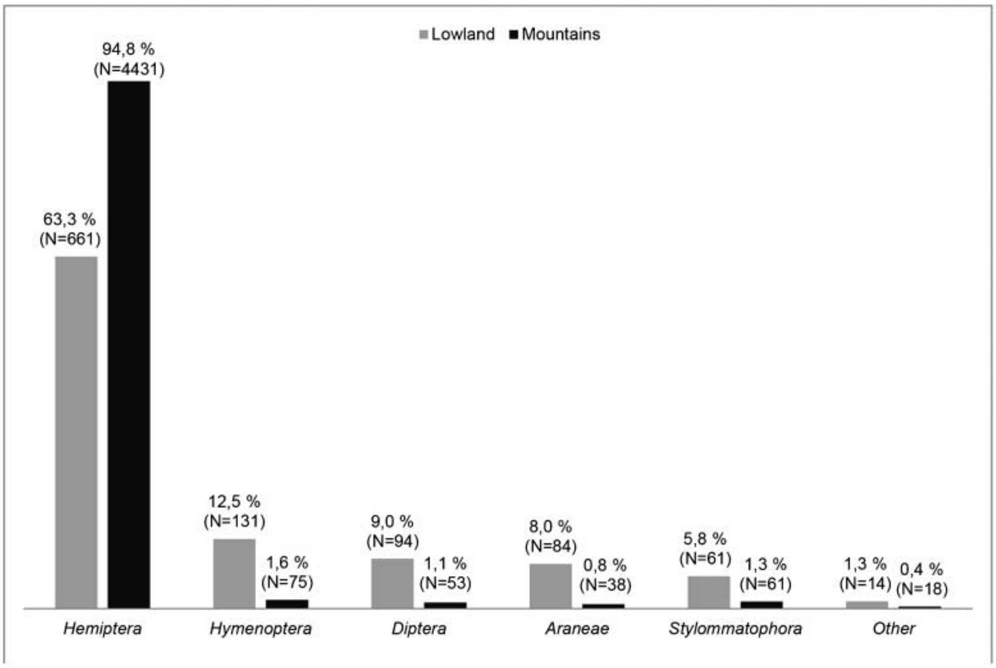

Figure 1. Proportions of invertebrates most frequently recorded on *Balsaminaceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

for total records of invertebrates, *Hemiptera* predominated among the recorded pests (proportion test, $p <$ 0.001), reaching higher numbers in the mountains. The percentage shares of other dominants among the pests (*Stylommatophora*, *Diptera*, *Hymenoptera*, *Coleoptera*) were identical in the two regions.

Pests were classified to 12 orders and 20 families. The mountains harboured four groups of pests that were absent from the lowland, and eight pest groups that were significantly more numerous than in the lowland. Five pest groups were restricted to the lowland and three groups were significantly more numerous there than in the mountains (Table 1).

Balsaminaceae (balsam family)

As many as 5721 invertebrates were found on *Impatiens* plants, with significantly more (82%, $N = 4676$) occurring at mountain sites (proportion test, p <0.001). *Hemiptera* dominated in both mesoregions, reaching 94.8% in the mountains (proportion test, $p < 0.001$) and 63.3% in the lowland (proportion test, $p < 0.001$). *Hymenoptera*, *Diptera*, *Araneae* and *Stylommatophora* were also recorded in large numbers, but in different proportions in each region. For example, equal numbers of *Stylommatophora* were found in the two areas but their share was more than three times smaller in the lowland than in the mountains (Figure 1).

Thirty-six groups of organisms were recorded in the two areas: 29 in the lowland and 25 in the mountains. Four of the groups common to both regions had significantly more records in the lowland, and two had more records in the mountains. Eleven invertebrate taxa were specific to the lowland, and five were specific to the mountains.

Nearly all invertebrates found on *Impatiens* plants were pests: 5315 or 92.9% of the total recorded on *Impatiens* (4548 in mountains, and significantly fewer in lowland – 767; proportion test, $p < 0.001$). The percentage of pests was higher in the mountains (97%) and lower in the lowland (73%). As in the general count of invertebrates on *Impatiens*, *Hemiptera* significantly predominated among the pests in both regions (proportion tests for both regions, $p < 0.001$). They represented 97.4% of the pests in the mountains, and 86.2% of the pests in the lowland (which is 22.9% more than in the general count). *Stylommatophora* and *Diptera* also figured among the dominants, together forming 12.1% in the lowland and 2% in the mountains. There were significant differences between regions for them as well (Figure 2).

We found 25 groups of pests on *Impatiens* species, 19 in each region. Thirteen groups were common to both mesoregions; two groups had more records in the mountains and one had more records in the lowland. There were six region-specific groups in each area.

To summarise, the two mesoregions showed statistically significant differences in both the frequency of all invertebrates ($G = 486.5$, $df = 13$, $p < 0.001$) and the frequency of pests ($G = 106.6$, $df = 9$, $p < 0.001$) found on *Balsaminaceae*.

Polygonaceae (knotweed family)

We found 2182 invertebrates on *Polygonaceae*, 71% ($N = 1552$) of them in the lowland (proportion test, $p <$

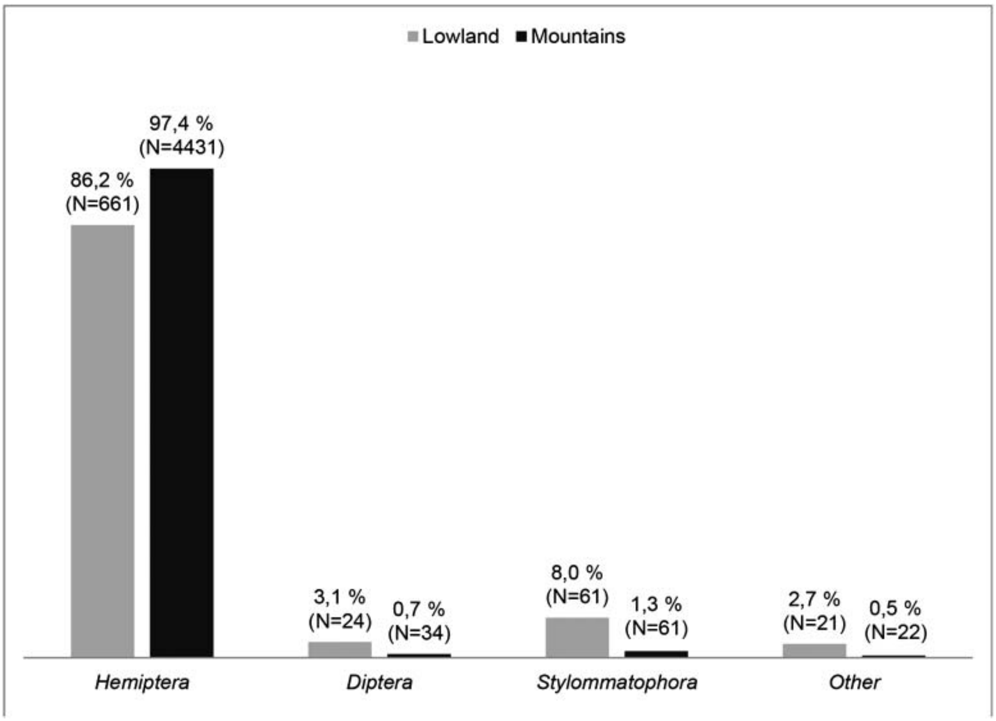

Figure 2. Proportions of pests most frequently recorded on *Balsaminaceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

0.001). *Stylommatophora* were dominant in the total (42.3%; proportion test, $p < 0.001$) and in the lowland (48.4%; proportion test, $p < 0.001$). In the mountains the dominant taxon was *Diptera* (39.5%; proportion test, $p < 0.001$), found in much smaller numbers in the lowland. An opposite trend regarding the two regions was observed for *Stylommatophora*. Other dominants of both areas were *Hymenoptera*, *Hemiptera* and *Araneae* (Figure 3).

We identified 34 invertebrate groups on *Polygonaceae*, including 30 in the lowland and 29 in the mountains; 22 groups were common to both mesoregions. Eight groups were more abundant in the lowland, and eight in the mountains; five groups were specific to the mountains or the lowland.

The number of pests on *Polygonaceae* was 1509 (significantly more in lowland: 1091; proportion test, $p < 0.001$). Pests accounted for 69% of all organisms

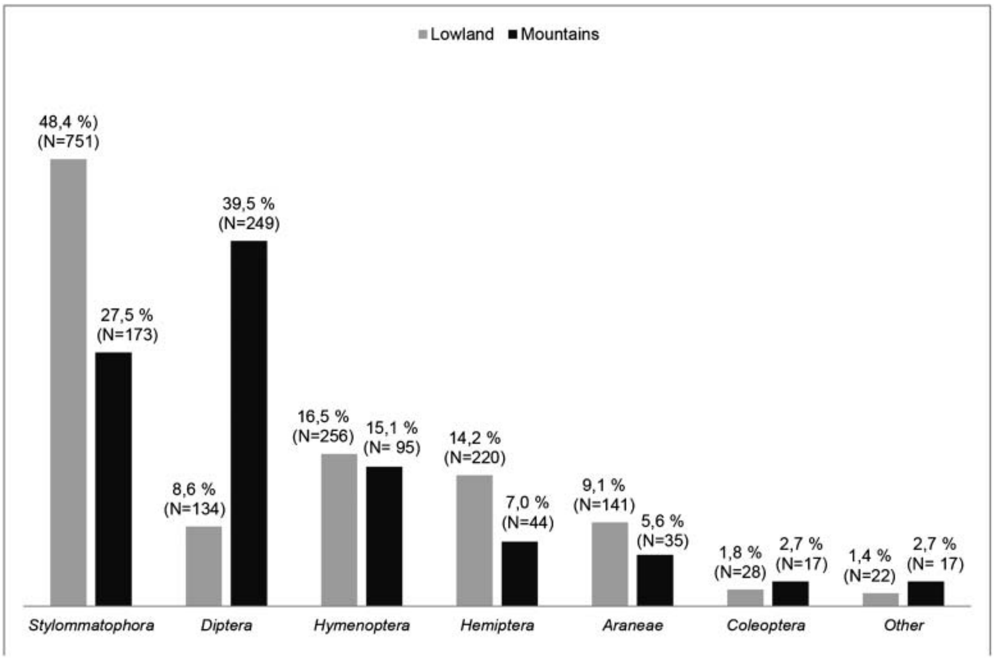

Figure 3. Proportions of invertebrates most frequently recorded on *Polygonaceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

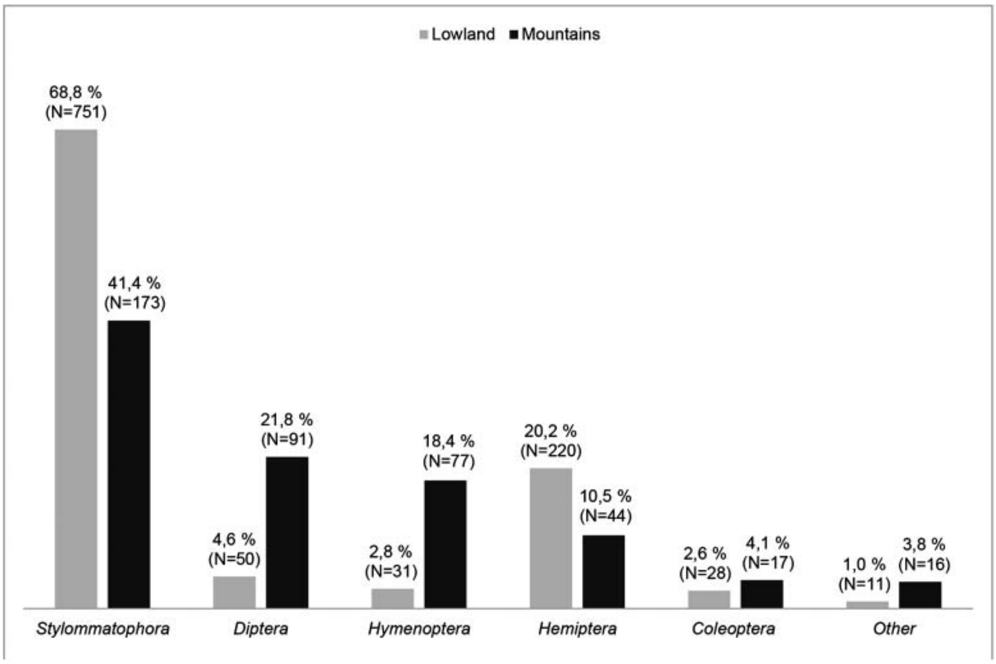

Figure 4. Proportions of pests most frequently recorded on *Polygonaceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

recorded in this family. They occurred in similar proportions in the two study areas: 66% in the mountains and 70% in the lowland. *Stylommatophora* were dominant pests in both regions but nearly 70% of all their records were from lowland (proportion tests for both regions, $p < 0.001$). The share of *Stylommatophora* was smaller in the mountains, where the number of pests of other groups (*Diptera*, *Hymenoptera*, *Hemiptera*) was also high (Figure 4).

Pests of the knotweed family represented 24 taxonomic groups: 20 in lowland areas and 22 in the mountains. Six of the groups occurring in both mesoregions were more abundant in the mountains, and five were more abundant in the lowland. Two groups were specific to the lowland, and four to the mountains.

There was a significant difference between lowland and mountain areas in the frequency of all invertebrates ($G = 284.3$, $df = 13$, $p < 0.001$) and pests ($G = 223.3$, $df = 10$, $p < 0.000$) on *Polygonaceae*.

Asteraceae (aster family)

We recorded 1287 invertebrates on the two *Solidago* species, significantly more (58%, $N = 750$) in the mountain area (proportion test, $p < 0.001$). The distribution of dominants differed markedly between the two mesoregions. The mountains were dominated by *Hemiptera* (76.5%; proportion test, $p < 0.001$), while *Araneae* dominated the lowland (70.9%; proportion test, $p < 0.001$). Groups dominant in one area occurred surprisingly rarely in the other area; for example, *Hemiptera* were 38 times rarer in the lowland. *Stylommatophora*, *Diptera* and *Hymenoptera* were abundant in both regions (Figure 5).

We found 35 invertebrate taxa on *Asteraceae*, including 27 in the lowland and 24 in the mountains. Sixteen groups were common to both areas, four of them more abundant in the mountains and four in the lowland. Nineteen groups were unique to a given region: 11 to the lowland and 8 to the mountains.

Nearly 60% ($N = 769$) of all invertebrates found on *Asteraceae* were pests, but their shares differed between the two regions: 92.5% in the mountains and only 14% in the lowland (proportion test, $p < 0.001$). The dominant groups in the mountains were *Hemiptera* (82.7%) and *Stylommatophora* (10.1%), and in the lowland *Stylommatophora* (33.3%), *Hemiptera* (20.0%) and *Diptera* (14.7%; Figure 6).

Pests were classified into 23 taxonomic groups: 18 in the lowland and 16 in the mountains. Eleven groups were common to both mesoregions; four of them more abundant in the mountains and one in the lowland. Twelve groups were unique to one region: seven to the lowland and five to the mountains.

As in the case of *Balsaminaceae* and *Polygonaceae*, there were significant differences between the two regions in the frequency of all recorded invertebrates ($G = 910.2$, $df = 14$, $p < 0.001$) and pests ($G = 106.4$, $df = 9$, $p < 0.001$) occurring on *Asteraceae*.

Discussion

The harmfulness scale presented in this paper produces an estimate of the number and diversity of pests among a group of recorded invertebrates. It can serve

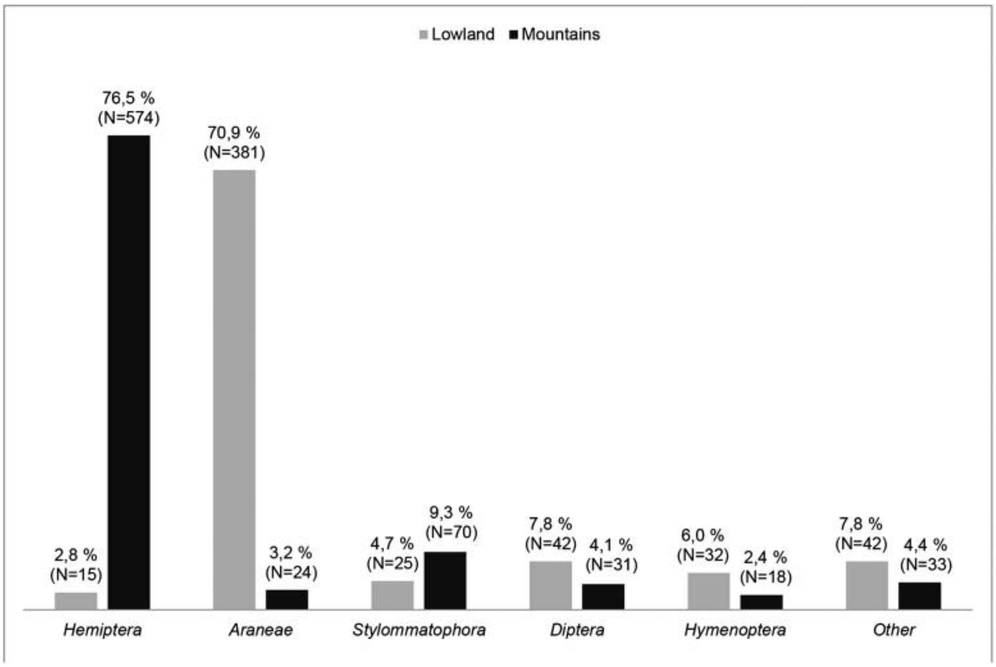

Figure 5. Proportions of invertebrates most frequently recorded on *Asteraceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

as a proxy for the extent of the negative impact they have on plants. The need for such an assessment has been suggested in earlier works, for example, a study focused on biological invasions (Vasquez & Meyer 2010). Much effort has recently been put into developing scientifically sound risk-assessment protocols for different taxa and environments, formalising the process of distinguishing harmful organisms, including pests of plants of economic importance (Brunel et al. 2010, Kenis et al. 2012, CABI 2016). Such a process must be rigorous and transparent, since listing a species as a pest may be legally binding and may have significant economic consequences, including import bans or high management costs. In most cases it would be impractical to apply equally comprehensive protocols to uncultivated plants, due to budget and staffing limitations. At the same time, the need to address environmental issues in plant pest research is stressed in

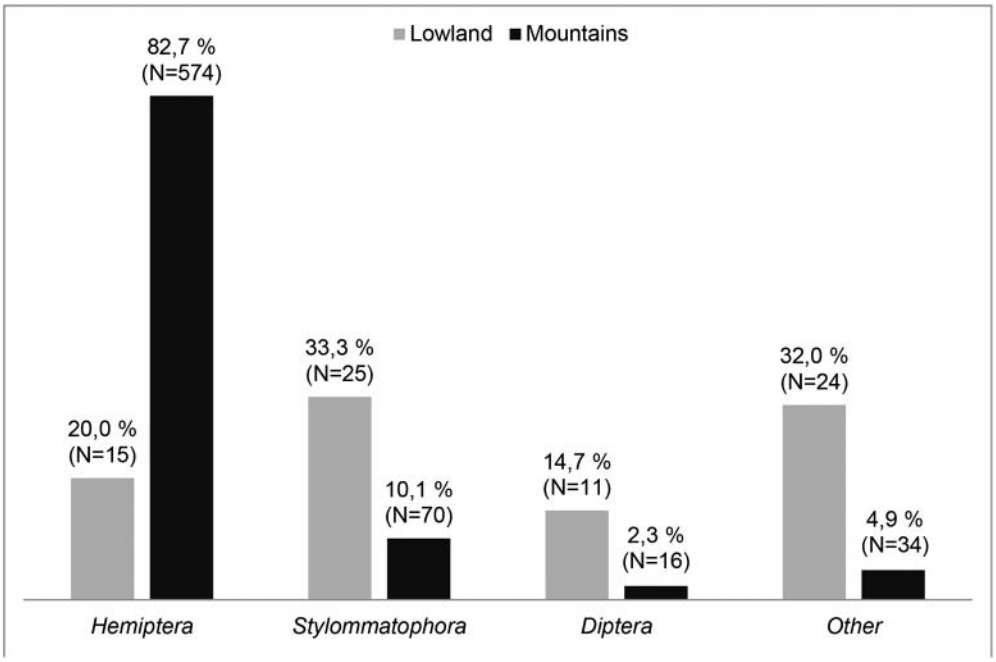

Figure 6. Proportions of pests most frequently recorded on *Asteraceae* in lowland (Rów Skawiński) and mountains (Rów Podtatrzański, with the Tatras).

international protocols on nature conservation, such as the Convention on Biological Diversity, and also in those mainly concerned with plant production, such as the International Plant Protection Convention (ISPM 2013).

Initially, it takes some effort to collect the literature data required to construct the presented scale, but then it can serve a variety of studies which otherwise would be very time consuming, requiring collection of specimens and species-level identification by teams of taxonomy experts. When such expertise and/or funds are limited, the proposed scale may be the best option available. This scale might also prove useful in a variety of experimental designs, such as assessments of pest pressure on single plants within the same study site or comparisons at higher spatial scales (between study sites or regions).

Another advantage of the presented method over existing alternatives is that it is intravital: the field data can be collected in photographic form, obviating the need to kill invertebrates for subsequent identification. This is a particular benefit when it is important to keep the studied organisms alive, as when they are strictly protected, or when reduction of their numbers by traditional trapping would bias subsequent qualitative/ quantitative surveys at the same study site.

For an inexperienced user it may be difficult to employ photography to document invertebrates, particularly those capable of flight. However, pictures can be taken from a distance of up to 1.5 m, reducing the researcher‘s disturbance of the invertebrates' behaviour to a minimum. This allows a more accurate estimate of their diversity and abundance than with traditional trapping, where some of the sampled individuals may avoid the trap or escape. Moreover, counts of individuals on photographed clusters of invertebrates (e.g. aphids) will be more accurate than field estimates. A potential source of inaccuracy is that highly mobile invertebrates may be counted more than once, giving an overestimate of the absolute number. This, however, should not affect comparisons of the relative frequency of invertebrates, or pests, between species or regions. In our study, this potential bias was minimised by top-down counting and by taking care to keep track of their positions.

The level of family, used in this study, adequately captures species diversity, and generally the identification of an organism to a family poses no difficulty even for novice researchers and does not require collecting specimens or disturbing their behaviour. Ranking individual invertebrates according to a harmfulness scale for higher taxonomic units may be good enough for broader studies, where dozens of invertebrate groups and thousands of individuals are considered, but that level of resolution may be too low for use in detailed studies of a small number of invertebrate groups. The taxonomic level notwithstanding, it should be borne in mind that pest numbers calculated using this method are proxies rather than absolute values, particularly since this method does not directly measure the absolute impact of the pests on plants. This, however, does not negate the utility of these proxies as a measure of pest pressure for comparisons between plant species and regions.

The presented results add to the body of data on altitudinal differences in invertebrate abundance and diversity presented in other studies (Driessen et al. 2013; Hodkinson 2005; Stohlgren 2011). The proportion of pests in relation to all invertebrates differed both between the regions and between the studied plant families. Their share on *Asteraceae*, where pests represented 60% of the records, was more than 6.5 times larger in the mountains than in the lowland. The difference in shares of pests was smaller for *Balsaminaceae*: 97% in mountains and 73% in lowland. The shares of pests on *Polygonaceae* were nearly equal (66% in mountains and 70% in lowland). The differences between the shares of pests arise chiefly from large variation of the numbers of records in the taxonomic groups common to both regions. In the case of *Asteraceae*, they result from the significantly higher index of harmful *Hemiptera* ($H_i = 0.75$) in the mountains, with *Araneae* ($H_i = 0$) dominant in the lowland. One mechanism that may contribute to such a pattern is the reduction of pest pressure in the lowland by the locally abundant *Araneae*. In the mountains, this group was six times less numerous, which may explain the high numbers of pests there.

The degree of attractiveness of the studied plants to pests may help explain the differences in pest shares between the three plant families and between the regions. *Balsaminaceae* were under the strongest pressure, suggesting that this family was most attractive (e.g. most palatable) and/or most accessible (e.g. least repellent). These differences may also result from differences in the shares of generalists and specialists among the recorded pests. According to Keane and Crawley (2002), the impact on plants from generalists is more severe than that from specialists. Our study would confirm this result if we had shown that *Balsaminaceae* were most severely attacked by generalists, but the taxonomic resolution of our protocol was too low to test it.

Nearly twice as many invertebrates and three times as many pests were found in the mountains than in the lowland, while the results differed between the three plant families. The largest number of records in the mountain area was from *Impatiens*, for which the mountain/lowland ratio of records was about 5:1 for all invertebrates and about 6:1 for pests, due mostly to the high abundance and significant dominance of *Aphidoidea* taxa in the mountains. Only slightly more *Asteraceae* invertebrates were found in the mountains, but when only pests are considered, the mountain/

lowland ratio is as high as 9:1, mainly because the invertebrates found in the mountains were mostly pests (*Hemiptera* and *Stylommatophora*), while harmless *Araneae* predominated in the lowland. Unlike on the other plants, on *Polygonaceae* both invertebrates and pests were more numerous in the lowland than in the mountains, nearly 2.5 times so.

As already mentioned, the prevalence of *Aphidoidea* records in the mountains may result from the reduced numbers of their natural enemies, mainly *Araneae* (Schmidt et al. 2004). *Aphidoidea* can nearly double their numbers by escaping from their enemies, a phenomenon studied since the 1950s (Elton 1958) and later formalised as the *Enemy Release Hypothesis* (Keane & Crawley 2002; Maron &Vilà 2001). It states that escape from natural enemies allows a species to accumulate and reallocate resources. After escaping, resources that would otherwise have to be used for a defence against these enemies can be used for faster and/or longer growth and increased fecundity. This in turn leads to population increase and spread, most pronounced in alien species invasions after their introduction to new areas. The same mechanism may be responsible for the increase in the index value of *Aphidoidea* in the mountains.

Although *Hemiptera* were generally most abundant, occasionally that role was taken by other invertebrates within the same plant family. For example, *Hemiptera* dominated on *Solidago* in the mountains, with about 80% of the records, while the dominant position in the lowland was held by *Araneae* (among all invertebrates) and *Stylommatophora* (among pests), with the proportion of *Hemiptera* in the overall number of records dropping below 3%. Another example is the share of *Stylommatophora* among pests of both regions on the genus *Impatiens*. The number of pests in the lowland and the mountains was the same, but their share in the mountains was more than six times smaller. Such differences were noted in all groups, not only the dominant ones. This shows how the diversity of taxonomic groups in the lowland and mountains affects the overall differences between these regions. The major source of dissimilarity, however, seems to be the large differences in numbers of records per taxon common to both areas.

In comparisons of lowland and mountains, climate is usually considered the major factor limiting invertebrate diversity and number at high elevations (Stohlgren 2011). As in the case of enemy release, however, our results do not allow us to draw unequivocal conclusions about the role of climate, as we found nearly twice as many invertebrates and nearly three times as many pests in the mountains. By family, this predominance obtains for *Balsaminaceae* and *Asteraceae*, and shifts to lowland for *Polygonaceae*. As the two areas were surveyed almost simultaneously, this result cannot be due to bad scheduling of checks, hitting the invertebrate abundance peak only in the mountains and missing it in the lowland; however, it may have been affected by temperature, precipitation, oxygen availability and wind turbulence, additionally complicated by differences between species responses to fluctuations in these variables (Hodkinson 2005; Diehl et al. 2013). The influence of such factors has been demonstrated by Hart and Gotelli (2011), who studied the influence of climate on the number of aquatic invertebrates from the *Culicidae* and *Chironomidae* families, as well as by researchers examining the impact of climate change on crop pests (James 2009; Ramamurthy et al. 2009). It is, therefore, possible for untypical results to be caused by progressive changes in global weather, which may affect insects more severely in sensitive mountain areas (Larsen et al. 2011; Deutsch et al. 2008). Climate change may also affect them indirectly, for example, through a negative influence on vegetation that the insects feed on (Pauli et al. 2012). It is also known that the number and diversity of invertebrates may depend on light conditions (Whitham et al. 1991; Louda and Rodman 1996). Light, in turn, depends on factors including relief and foliage cover. Also, in mountains the level of dispersed light is lower and the level of potentially harmful direct light is higher, which may affect invertebrates. We did not measure light level at the study sites, but Salmon et al. (2008) suggested that it can positively affect the number of invertebrates.

Practical application and versatility of harmfulness scales in a variety of studies should verify the utility of our method. For conservation of threatened plant species, it is a way of assessing whether pest damage poses a serious *in situ* threat, and of rapidly assessing the potential damage from pests at *ex situ* conservation sites. It can be used in selecting plants planned for new green areas, to avoid species susceptible to pest damage at a given locality. The robustness of the harmfulness scale can be judged by comparing it with traditional methods of trapping invertebrates and identifying them to species level. In woody plants, the damage done by invertebrate taxa can differ from that done to herbaceous plants (Hodkinson 2005), so it may be necessary to reassess the literature data used to tailor the scale for trees.

Acknowledgments

We thank Dorota Lachowska-Cierlik, Lukasz Przybyłowicz, Paweł Adamski and Andrzej Kosior for their help in developing the harmfulness scale and for identifying problematic invertebrates, and Magdalena Lenda for very useful remarks on the manuscript. Michael Jacobs line-edited the paper for submission.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Science Centre [grants number N N304 326036, 2011/03/B/NZ9/04042]; Doctus, the Małopolska Province Stipend Fund for Doctoral Candidates, under application ZS.4112-125/11.

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