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Original Research

Factors limiting and promoting invasion of alien *Impatiens balfourii* in Alpine foothills

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ABSTRACT

Impatiens balfourii is an Asian ornamental plant introduced to Europe in the 20th century from the Himalayas. It is far less invasive than two congeneric species from the same area, *I. glandulifera* and *I. parviflora*. The factors responsible for its limited success are poorly known, though they may be related to low frost tolerance and low popularity as an ornamental plant. Maladaptive habitat preferences, a factor not studied to date, may also play an important role. The aim of this study was to determine those responsible factors and to examine the consequences of habitat selection by *I. balfourii* on the Swiss-Italian border, where the species is assumed to be invasive. After exhaustive mapping of its distribution and measurement of the plants' performance parameters, we checked for signs of disease and pest attack on individual plants growing in different habitats, and analysed the local abiotic characteristics. The distribution pattern differed significantly between the two studied countries. There were four times as many Italian localities of *I. balfourii* and they were clearly concentrated along roadsides, whereas the few Swiss localities were scattered among other habitats. The level of leaf damage along roadsides was lower, suggesting higher release from natural enemies there, which, however, did not translate into investment in plant size or fecundity. Patch area along roadsides correlated positively with the presence of buildings and shading; the plant's ability to spread decreased with elevation. These results confirm that invasion by this shade-tolerant species is driven by propagule pressure and that its dispersal ability is low; that may change with climate warming. Although roads provide suitable conditions and invasion corridors, and despite possibly higher propagule pressure on the Swiss side, in Switzerland the preference for this habitat is maladaptive for *I. balfourii*, due to intensive mowing, which seems to create an ecological trap.

1. Introduction

Impatiens balfourii is an Asian annual introduced to Europe from the western Himalayas as an ornamental. Its cultivation began in the early 20th century in France, Great Britain and Italy. Later it was cultivated in Hungary, Switzerland, Germany and most other European countries. Only in the Mediterranean zone has the species successfully escaped from cultivation and formed numerous stable and expanding populations (Adamowski, 2009). This limited success is rather surprising in view of the fact that two other very closely related Asian species, *I. glandulifera* and *I. parviflora*, are among the most invasive alien plants in large parts of Europe (Jacquemart et al., 2015; Janssens et al., 2009; Schmitz and Dericks, 2010; Ugoletti et al., 2013). *Impatiens balfourii* is reported as invasive from only three European countries (France, Italy, Croatia; Banfi and Galasso, 2010; EPPO Global Database, 2017; Fried et al., 2014) and as potentially invasive from another three (Spain, Switzerland, Germany; EPPO, 2016; Nehring et al., 2013).

In part due to its relatively small range and low invasiveness, studies of *I. balfourii* in Europe began only 15 years ago, and the species still only rarely attracts the attention of researchers. The ISI Web Of Science Database (2017) shows only 10 papers on *I. balfourii*, as against 203 on *I. glandulifera* (full Latin species names were used for this query). Although non-invasive and locally invasive 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 development of invasiveness, important to the theoretical aspects of biological invasions as well as to the development of practical mea-

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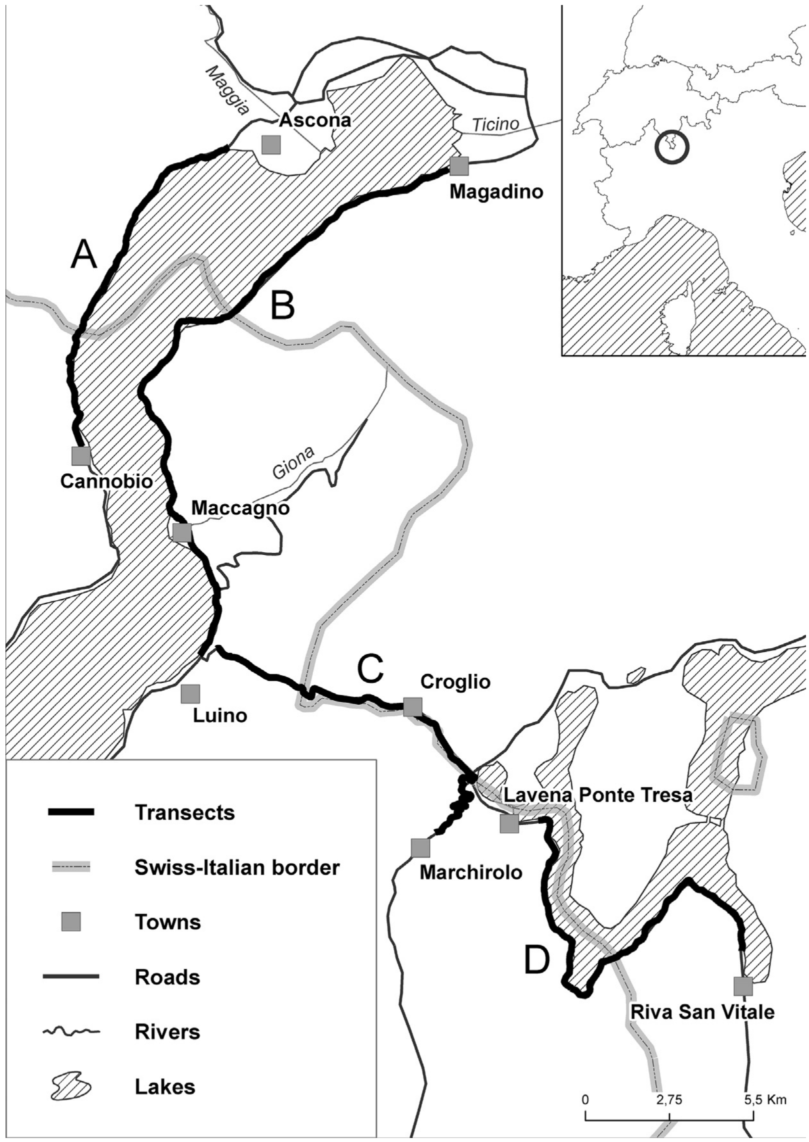

Fig. 1. Research area with four road transects (A, B, C, D: see Methods) surveyed in 2016.

sures to mitigate their effects (Ugoletti et al., 2011; van Kleunen et al., 2010; Vasquez and Meyer, 2011).

The paucity of studies of *I. balfourii* makes it difficult to pinpoint the reasons for its surprisingly slow expansion in Europe. Some authors suggest that low frost tolerance (Adamowski, 2009; Perrins et al., 1993; Tabak and von Wettberg, 2008) and restricted availability in trade (Adamowski, 2009; Schmitz and Dericks, 2010) may play some role here. Another suggestion is that the invasion of *I. balfourii* may still be in a lag phase, as it was introduced 60 years after the invasive *I. glandulifera* (Adamowski, 2009; Ugoletti et al., 2013). Nevertheless, in its attractiveness to pollinators, high reproductive capacity and growth traits, *I. balfourii* is by no means inferior to *I. glandulifera* (Jacquemart et al., 2015; Ugoletti et al., 2011). The habitat preferences of the species often overlap those of *I. parviflora* (Schmitz and Dericks, 2010), which also suggests that *I. balfourii* has the potential to become invasive. However, habitat selection may be maladaptive (Misenhelter and Rotenberry, 2000): a species may choose a habitat which in fact limits its reproductive success. In both native and invaded areas, *I. balfourii* occurs on stream banks, roadsides, ruderal sites and woodland margins, and in meadows and mesic deciduous forest (Adamowski, 2009; Nasir, 1980; Schmitz and Dericks, 2010), but no data on population parameters in different habitats are available.

The aim of this paper was to determine the factors and consequences of habitat selection of *I. balfourii* on the Swiss-Italian border, where the species is established and expanding (Info Flora, 2017; Schmitz and Dericks, 2010). To identify the factors favouring the spread of *I. balfourii*, we made detailed surveys of its distribution and compared individuals growing in different habitats in terms of their performance and their level of release from the pressure of natural enemies. The latter factor is thought to influence the invasion success of alien species (Enemy Release Hypothesis, ERH; Keane and Crawley, 2002; Maron and Vilà, 2001). We also analysed abiotic characteristics of the habitats in order to discover those of key significance to the occurrence of *I. balfourii*.

2. Methods

2.1. Research area

Data were collected between September and October of 2015 and 2016 on the Swiss-Italian border in southern Ticino, northern Lombardy and Piemont (Fig. 1). The study area is in a lake region in the foothills of the Southern Alps. The local climate is mild, with significant differences in annual precipitation between the western part (Lago Maggiore lake, approx. 2000 mm) and eastern part (Lago di Garda lake, approx. 1000 mm) (Berger, 2009). The habitat favours thermophilous alien plants (Dainese et al., 2014), including *I. balfourii* (Info Flora, 2017; Schmitz and Dericks, 2010).

2.2. Species distribution

The localities of *I. balfourii* were GPS-logged in both years of the study, during the flowering period when the plants are conspicuous and easy to detect. In our study area, *I. balfourii* flowers and sets seeds in September and October (Ugoletti et al., 2013).

During the thorough field survey in 2015 the following areas were surveyed:

- road from Someo (CH) to Lugano (CH) through Locarno (CH), Luino (IT) and Ponte Tresa (CH) – 80 km; road from Colmegna (IT) to Curiglia (IT) – 15 km;
- right bank of Maggia River in Locarno (2.5 km up the river from the lake; CH) and in Someo (1.8 km; CH), left bank of Ticino River in Magadino (2.6 km up the river from the lake; CH), both banks of Giona stream in Maccagno (2 km up the stream from the lake; IT);
- tourist trails in Maccagno (IT), Caslano (CH) and Alpine Monteviasco (IT);
- Swiss towns: Someo, Locarno (Monti Trinita and areas neighbouring the marina), Gordola, Magadino, Vira, Piazzogna, Gambarogno, Ronco, Caviano, Termine, Monteggio, Croglio, Barico and Caslano;
- Italian towns: Pino Sulla Sponda del Lago Maggiore, Maccagno, Colmegna, Monteviasco, Luino, Trebedora, Longhirolo, Cucco, Pianazzo, Longhirolo, Torbera and Fornasette.

The results from 2015 indicated that the species occurred mainly at roadsides, so in 2016 the surveys continued along roads. Those field surveys covered four transects along the main local roads crossing the Swiss-Italian border (Fig. 1):

- A: Ascona (CH) to Cannobio (IT) –13 km,
- B: Magadino (CH) to Luino (IT) –23 km,
- C: Luino (IT) to Marchirolo (IT) through Croglio (CH) and Ponte Tresa (CH) –15 km,
- D: Riva San Vitale (CH) to Lavena Ponte Tresa (IT) –16 km.

2.3. Statistical analysis

All statistical analyses employed SPSS ver. 24.0 (IBM Corp, 2016). The data were analysed with the use of generalized linear mixed models (GLMM). Linear models were used for interval target variables, negative binomial regression for numerical data, and binary logistic regression for binary data. All GLMM models used post-estimation, Satterthwaite approximation and robust covariances. We applied pairwise contrasts for comparisons between the studied habitats.

To reduce the dimensions of the data on plant size we carried out principal component analyses (PCA) based on a correlation matrix incorporating three related variables: leaf length, leaf width and height of stem (Kaiser-Meyer-Olkin measure of sampling adequacy was 0.57; Bartlett's test, $p < 0.001$). The correlations between variables were significant (at $p < 0.001$): the leaf length correlated with leaf width ($r = 0.84$), leaf width with stem height ($r = 0.49$) and leaf length with stem height ($r = 0.37$). The percent of variance accounted for by the respective variables were: 72% for leaf length, 23% for leaf width, and 5% for stem height. The respective component matrix values for the same variables were: 0.90, 0.94 and 0.68. As a result the variables were combined to calculate a single variable representing plant size (termed 'size' here).

Details of statistical procedures for particular analyses are described below in the relevant sections.

Table 1
Localities and corresponding habitats chosen for plant performance and enemy release tests; 50 plants were examined at each locality.

Study site	Elevation [m a.s.l.]	*I. balfourii* area [m^2]	Habitat description
Ruderal area (B)	201	3	Ruderal area near buildings
Stream (S)	256	4	Bank of Giona Stream, on scarp covered with forest, near tourist trail
Forest (F)	332	3	Verge of forest, near forest path
Roadside (R)	352	4	Roadside

2.4. Plant condition and enemy release in different habitats

To determine the optimum habitat for *I. balfourii*, in 2015 we assessed the size and fecundity of individual *I. balfourii* plants growing in different habitats, as well as the level of natural enemy pressure. Plant size, fecundity components and levels of enemy pressure were assessed for four study sites representing different habitats (Table 1, Fig. 2). The roadside locality (R) was picked randomly from all recorded *I. balfourii* localities. The same selection procedure could not be applied for the remaining habitats (B, S, F) because only one locality of the species was found in each of them in 2015; those three localities were included in the assessment.

At each of the selected sites, 50 *I. balfourii* plants were randomly selected from the pool of plants in the same development phase (flowering and seed set) and individually marked for tracking in subsequent surveys. Temperature data-loggers (DS1923-F5, iButton) were installed at each locality at a level corresponding to the average height of the studied plants. Temperature was recorded every hour.

Each study site was surveyed four times between 21.09.2015 and 02.10.2015, every three days between 09:00 and 15:00, by the same researcher. The survey days were sunny and windless, with air temperature ranging from 13 °C to 29 °C. Air temperature and light intensity were measured during each survey with a hand-held environmental meter (Extech 45170CM).

During each control mature seeds were collected from the surveyed plants (total seeds $N = 284$). They were weighed on the same day to 0.001 g accuracy in controlled conditions (Radwag PS 360.R2 scale). The number of flowers (including buds) on each plant was counted during the second control (total 2070 flowers recorded). In the last survey the 200 marked plants were measured for stem height as well as the width and length of each fully developed leaf.

Of the 50 plants marked at each locality, 15 were randomly designated for counts of the number of leaves showing signs of disease and/or damage (e.g. rusts and spots, deformation or mining by insects; collectively termed 'leaf damage' here; Appendix A). Also, all invertebrates observed on the surveyed plants were recorded, photographed and identified (Appendix B). To estimate the numbers of harmful pests among these invertebrates we applied the harmfulness scale of Najberek et al. (2016), obtaining values on a pest index (H_i; Appendix B).

In three models with habitat type as fixed effect we compared the condition of *I. balfourii* at each locality. Size (variable obtained from PCA), total weight of seeds and number of flowers were the respective target variables in these models. Calculations were made at the level of an individual plant ($N = 50$ per habitat).

In the model examining leaf damage as the target variable, the fixed effects were number of leaves, habitat, plant size and daily average temperature, the latter calculated from the 24-hourly

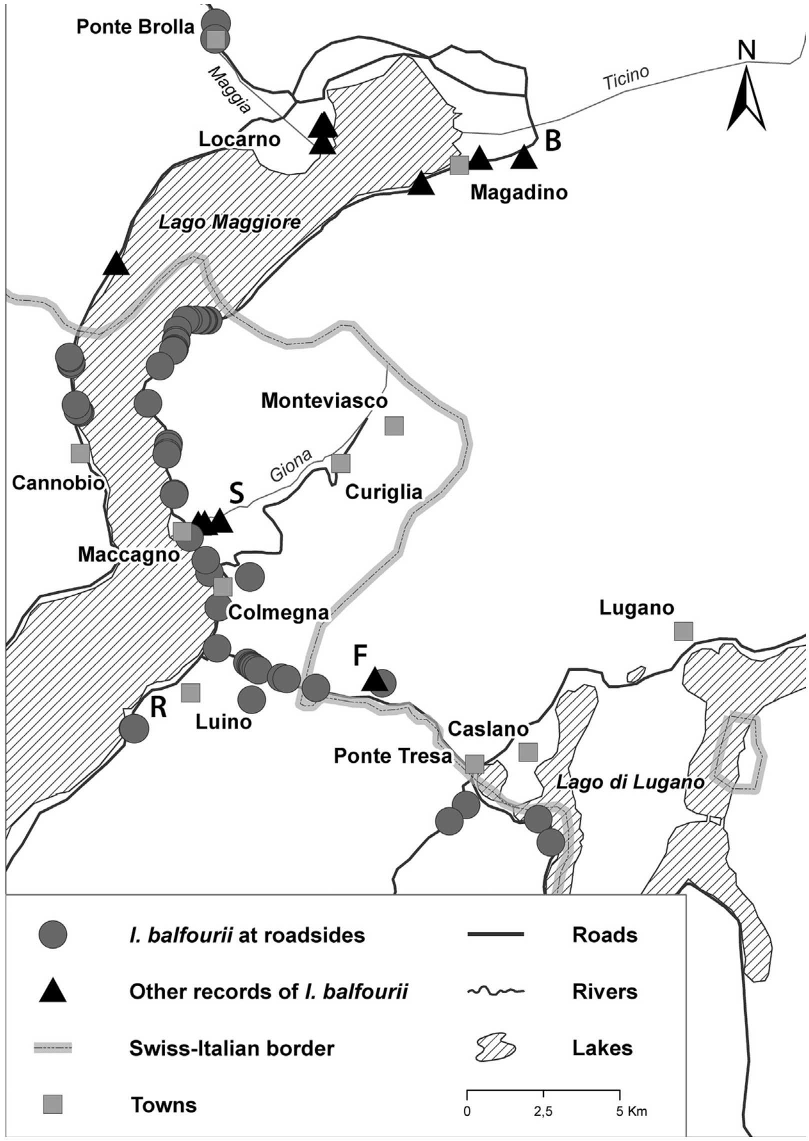

Fig. 2. Northeast part of the Lago Maggiore region with *Impatiens balfourii* records. Records selected to compare plant condition and enemy release ability between different habitats: B – Ruderal area, F – Forest, R – Roadside, S – Stream.

temperature measurements logged each survey day. The analysed values were estimated separately for each survey of each controlled plant (N = 60 for B, F and R, N = 59 for S). Individual ID was taken as random effect (covariance type: first-order autoregressive AR1). This was derived from the random selection of plants before each survey, which generated different numbers of surveys for each of them.

In the model for number of recorded pests, the pest index obtained using the harmfulness scale was multiplied by 100 to convert decimal values to integers required for negative binomial regression. The pest index was the target variable and the fixed effects were habitat, size, temperature and light intensity recorded during the surveys. As in the leaf damage model, Individual ID was random effect (covariance type: first-order autoregressive AR1). The analysed values were estimated separately for each survey of each controlled plant.

2.5. Occurrence along roads

To determine the habitat characteristics most important for *I. balfourii* we measured the following for each one of the 47 *I. balfourii* patches surveyed: area (m^2, the target variable), elevation as recorded with a GPS receiver (m a.s.l.), zero-one presence of scarps, and distance from road (m). Additionally, the zero-one presence of buildings and streams were obtained from ArcGis data layers (Imagery and Topographic ArcGIS Basemaps; ESRI, 2017) within a 25 m radius around each study point. Data for patch area were log-transformed prior to the analyses. Aspects of slopes were calculated in ArcGIS (‘Aspect’ function) with the use of the European Digital Elevation Model (DEM) (25 m resolution raster; European Environment Agency, 2017). The original values of aspect were converted to obtain a sun exposure index (termed ‘SEI’ here) denoting the angle (0–180°) measured between north and the direction the slope faces. The maximum value of 180° was assigned to south-facing slopes, indicating the highest level of sun exposure given the latitude of the study area. The minimum value of 0° indicates north-facing slopes which experience the least insolation. An SEI equal to 90° was assigned to DEM raster cells in which flat, horizontal surfaces prevailed.

To check whether *I. balfourii* localities had any specific characteristics favouring the species, they were compared with virtual points generated by GIS along transects B and C (24 and 13 ‘true’ localities, respectively). Along the Italian sections of these transects, a total of 434 virtual points were generated by GIS every 50 m. For further analyses, 37 localities (corresponding to the total number of true localities) were randomly selected from this pool.

The following data from true and virtual localities were included in the model: zero-one species presence (the target variable), DEM elevation (the European DEM, 25 m accuracy grid; European Environment Agency, 2017), SEI, buildings and streams. To account for differences between the two distinguished transects, we took transect ID as random effect (covariance type: variance component).

Between-country differences along roadsides were tested by comparing abiotic characteristics on both sides of the border. A total of 1333 virtual points were generated in ArcGIS every 50 m along 4 transects. Each point included data on DEM elevation, SEI and buildings. To calculate the distance at which the effect of spatial autocorrelation was nonsignificant, each point was correlated with the next-adjacent point until the correlation reached nonsignificance, using DEM elevation. That threshold distance turned out to be 500 m, which allowed 134 points to be chosen. In all models transect ID was taken as random effect (covariance type: variance component), which additionally weakened the possible influence of spatial autocorrelation.

Three models were tested, with country as the fixed effect. The target variables were DEM elevation in the first model, SEI in the second, and buildings in the third. The target variables were calculated as in the analysis of occurrence along roads.

3. Results

3.1. *Species distribution*

During both years of the study, 70 localities of *I. balfourii* were recorded (Fig. 2), most of them on roadsides (N = 57; 81%) and some in urban green areas (N = 6; 9%) and along streams (N = 5; 7%). There were single localities on a forest verge (N = 1; 1%) and in a ruderal area near an abandoned building (N = 1; 1%). The species distribution pattern differed significantly between Italy and Switzerland, with more than three fourths of all localities recorded on the Italian side (N = 56; 80%). In Italy, all but three Giona stream localities were recorded along roads. The continuous distribution of the species along Italian roads extended to the Swiss border and sharply disappeared after crossing it; only four localities were noted along all Swiss roads. The remaining Swiss records were distributed among all distinguished habitat types.

3.2. *Plant condition and enemy release in different habitats*

Plant size differed significantly between all studied habitat types (Fig. 3A; $F_{3,235} = 94.22$, $p < 0.001$). Individuals from roadsides were largest, and those from the locality along the stream were smallest (all pairwise differences significant at $p < 0.001$).

Plant fecundity was approximated by two variables: seed weight and N flowers. Seed weight was highest in ruderal areas, significantly higher than for plants growing in forests and next to the stream (Fig. 3B; B-F contrast: t = 2.42, df = 45, p = 0.02, B-S contrast: t = 3.48, df = 45, p = 0.001). Plants in forests had the fewest flowers, significantly fewer than for the plants in all other habitats (Fig. 3C; $F_{3,196} = 52.39$, $p < 0.001$; pairwise differences significant at $p < 0.001$).

Thirty-nine percent of the 8517 controlled leaves showed leaf damage. Rusts and spots were the predominant symptoms (57% of leaves with symptoms; Appendix A). Only 16% of the total 226 invertebrates we recorded were pests (average 0.19 pests per plant per survey; Appendix B). The most abundant invertebrate taxa were

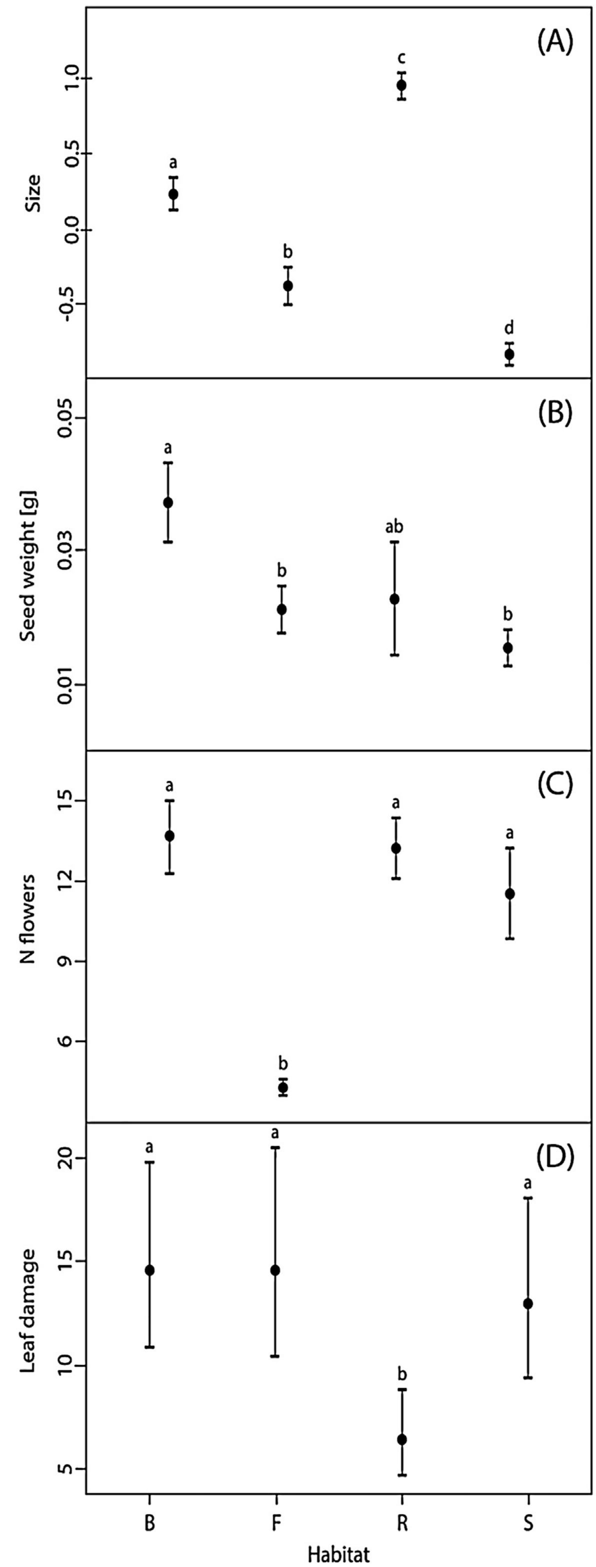

Fig. 3. Mean size (±SE; plot A), mean seed weight (±SE; plot B), mean number of flowers (±SE; plot C) and estimated means of leaf damage (± confidence intervals; plot D) of *Impatiens balfourii* in different habitats. Dissimilar letters above error bars indicate significant differences between habitats. The size variable (plot A) represents plant size and was calculated by PCA based on three variables: leaf length, leaf width and stem height (the percentages of variance accounting for those variables were 72%, 23% and 5%, respectively). B – Ruderal area, F – Forest, R – Roadside, S – Stream.

ants (Formicidae, 41%) and spiders (Araneae 18%). Snails (Stylommatophora) were the most frequent pests (23% of pests).

Leaf damage was lowest for plants at roadsides (Fig. 3D; $F_{6,17} = 7.99$, $p = 0.006$; pairwise differences significant at $p < 0.01$). There were no significant differences in pest pressure between the three other habitats. Daily average temperature significantly influenced the number of diseased/damaged leaves ($F_{1,232} = 10.65$, $p = 0.001$) and had a negative impact on the target variable. In habitat comparisons there were differences in temperature between the following: ruderal area and stream (temp. B > temp. S; $p < 0.001$), forest and ruderal area (temp. F < temp. B; $p < 0.001$), and roadside and stream (temp. R > temp. S; $p < 0.001$). Plant size had a significant positive impact on the target variable ($F_{1,143} = 8.65$, $p = 0.004$).

Unlike leaf damage, number of recorded pests did not differ significantly between the studied habitats ($F_{3,232} = 0.50$, $p = 0.7$). Plant size, temperature and light intensity had no significant impact on this parameter.

3.3. Occurrence along roads

The abiotic characteristics of the 47 *I. balfourii* patches surveyed are presented in Appendix C. Patch area did not depend on elevation, SEI, or distance from road. Nor was patch size limited by the presence of scarps along the roads. Even in sections with no scarps the patches ran parallel to the road rather than perpendicular to it. The presence of buildings had a significantly positive effect on patch size ($F_{1,39} = 7.93$, $p = 0.008$) but the result for the presence of streams was only close to significance ($F_{1,39} = 3.41$, $p = 0.073$).

Our comparison of 37 true and 37 virtual localities of *I. balfourii* revealed that even though the maximum elevation was only 477 m a.s.l. (see Appendix D for the parameters characterising these localities), the likelihood of occurrence of the species was negatively correlated with elevation ($F_{1,26} = 4.52$, $p = 0.043$). The other parameter influencing the occurrence of *I. balfourii* was SEI; plants were significantly more likely to occur in areas less exposed to sunlight ($F_{1,69} = 5.2$, $p = 0.026$). The presence of buildings, shown to positively affect patch area, was not significant for species occurrence. The presence of streams also had no significant effect on its occurrence.

Between-country differences along roadsides were also studied. The differences in elevation and sun exposure between Switzerland and Italy were non-significant (DEM elevation: $F_{1,132} = 2.19$, $p = 0.1$; SEI: $F_{1,130} < 0.001$, $p = 0.99$). The difference in the presence of buildings was significant ($F_{1,132} = 7.81$, $p = 0.006$), with more buildings on the Swiss side.

4. Discussion

4.1. Species distribution

The distribution of *I. balfourii* on the Swiss-Italian border is concentrated along roadsides. More than 80% of its records were in this habitat type. The pattern was particularly evident in Italy, where *I. balfourii* was recorded away from the roads at only three of the 56 localities visited there. The situation was strikingly different on the Swiss side: immediately after crossing the border the species was almost non-existent along roads, with only four records. Together with two more records near the stream, in Switzerland there were only six records along typical linear invasion corridors (Schupp, 2011). The remaining Swiss records seemed to reflect random human-mediated ephemeral occurrence rather than self-propelled directional expansion of well-established populations. Taking into consideration all found localities, the occurrence of this species was very restricted in Switzerland, with only a quarter of the records in comparison with Italy.

4.2. Plant condition and enemy release in different habitats

The conspicuous association of *I. balfourii* with roads cannot be explained solely on the grounds of the better performance of plants growing in this habitat. Indeed, the plants occurring there stood out for their large size and low pressure from enemies, but the roadside habitat apparently did not boost seed weight or number of flowers as compared with the three other habitats. On the other hand, the roadside habitat did not handicap the plants in any respect.

Plants growing along roadsides face some trade-offs. The drawbacks may include stress (Mattson and Haack, 1987) caused by traffic and/or road maintenance (e.g. the use of salt in winter; Munns, 2002). Traffic-induced mortality of pollinators may be another disadvantage (Mckenna et al., 2001; Seibert and Conover, 1991). At the same time, though, traffic may reduce the number of natural enemies attacking plants. Dai et al. (2014) showed that leaf miners and leaf gallers on *Castanopsis carlesii* seedlings had different responses to distance from road: leaf miners were recorded less frequently than leaf gallers along roadsides.

The level of pest attack may also depend on plant vigour, with the strongest pressure being on plants that perform exceptionally well (Price, 1991). The lower level of disease and damage recorded on *I. balfourii* growing along roadsides may result in part from the fact that the quality of plants growing there (expressed as fecundity) was not significantly higher than elsewhere. This dependence was confirmed by the overall positive effect of plant size on recorded leaf damage. However, while this relation held true for the whole dataset, for roadsides alone the situation was the reverse: although the plants growing there were largest, they were at the same time significantly less attacked by enemies. The thermal regime may have played some role here, as the level of leaf damage in each habitat was negatively related to the temperatures measured there. However, the temperature on roadsides differed only from that measured on the bank of the stream, and by only 0.35 °C.

Very few pests were recorded in any of the studied habitats. Their diversity was low as well, with only one species per plant per control as the most frequent value, which prevented the use of that parameter in these analyses; the Shannon Wiener index differed from zero in only 2% of the surveys. In a study of *I. noli-tangere, I. parviflora* and *I. glandulifera* in southern Poland, Najberek et al. (in press) recorded an average of 3.9 pest individuals per plant per survey, but in the present work that value was only 0.15 pests per *I. balfourii* plant. One possible explanation of the difference is the longer period covered by the study done in Poland, extending over the whole vegetation season. Nevertheless, the result obtained for *I. balfourii* on the Swiss-Italian border was strikingly low. The main reason for the low level of pest impact recorded in the present study is the absence of very harmful aphids (Aphidoidea), the dominant taxon attacking *Impatiens* species in Poland. In Switzerland and Italy only three aphids were recorded on *I. balfourii*. Here we note that the main aphid outbreak in Poland was late in the vegetation period, the same time span covered by the *I. balfourii* surveys; in view of this, the results from the Swiss-Italian border indeed suggest that this species is effectively released from enemies (cf. Burkhart and Nentwig, 2008).

4.3. Occurrence along roads

Linear landforms, both natural and manmade, provide dispersal corridors for plant and animal species (Hulme et al., 2008). Facilitated dispersal may in fact be one of the main advantages of growing along roadsides; it is known that vehicle traffic can foster short-distance spread, lengthening the distance via passive dispersal (Randall, 2017; Taylor et al., 2012; von der Lippe and Kowarik, 2007). In our study the area of *I. balfourii* patches along roads increased with proximity to buildings, a finding which probably reflects the temporal pattern of its spread, starting with escapes from cultivation in gardens. *I. balfourii* is grown as an ornamental in both Italy and Switzerland (Adamowski, 2009). Unfortunately, the local gardens were practically inaccessible to us for surveying, so we could not verify the degree of popularity of this species in cultivation (the one location found is certainly an underestimation). Ornamental plants with ballistic seed projection, such as *I. balfourii*, are particularly capable of escape by projecting of seeds directly from gardens to nearby roadsides. The near-significantly positive correlation between patch area and the presence of streams also suggests that its seeds can be projected to streams that pass by gardens at higher elevations, and then are brought down to roadsides by the current.

Surprisingly, scarps along roads did not limit the area of the 47 *I. balfourii* patches we surveyed, and had no impact on their shape. Such limitation is particularly common in montane areas, where roadsides run along rocky cliffs or else along steep slopes stabilised with concrete. Almost 4/5 of the records were from localities below scarps, and in some cases the available strip of land was only two metres wide. The association of *I. balfourii* with roads was a strict one: in wider sections not limited by scarps, the patches tended to expand along the road rather than away from it.

Neither the level of sun exposure nor elevation influenced patch area in any locality of *I. balfourii*, but a comparison of true and virtual records indicated that on a broader spatial scale both parameters were significant to its occurrence. Our analysis indicated that the species does not tolerate extended periods of exposure to direct sunlight; this is typical for most *Impatiens* (Janssens et al., 2009). Although the preference of *I. balfourii* for exposure to sunlight is higher than that of *I. parviflora* (Schmitz and Dericks, 2010), it is at the same time considered to be more adapted to shading than *I. glandulifera* (Ugoletti et al., 2011). Shading should therefore not be regarded as a major factor limiting the spread of *I. balfourii*.

The influence of elevation seems much more important in this respect. The study area was not at high elevation, but in Alpine foothills the interplay between elevation and temperature can become very dynamic, and introduced species are progressively eliminated by the increasingly severe climatic conditions along the elevational gradient. These could be significant factors especially for thermophilous species such as *I. balfourii* (Dainese et al., 2014). For *I. balfourii*, which is known to have low frost tolerance (Adamowski, 2009; Tabak and von Wettberg, 2008), the consequences of seemingly small differences in elevation may be very substantial. Nevertheless, it is interesting that *I. balfourii* has also been recorded in cold areas like Tartu in Estonia, where the average January temperature is about −7 °C (Adamowski, 2009). There the species successfully escaped from the botanical garden. Thus we cannot rule out the possibility that the altitudinal range of the species will increase in the future, but it is more likely that further invasions of this species will be more successful at lower elevations. It is also likely that some other factors (not necessarily climatic) may limit the spread of *I. balfourii* at higher altitudes. For example, the decrease of human settlements with altitude may result in lower propagule pressure.

In montane areas, alien plants are known to first colonise low elevations, where propagule pressure is higher and conditions are milder; next they spread to higher elevations (Alexander et al., 2011). This is the likely scenario for the best dispersers, which are predisposed to adapt to novel conditions. The low tolerance of *I. balfourii* to even small changes in elevation suggests that it is a poor disperser. In the future this species might undergo post-introduction evolution of traits allowing better success. Its future expansion might also be facilitated by changing climatic conditions (Adamowski, 2009; Ugoletti et al., 2011; Walther et al., 2009). We note, however, that the phenotypic plasticity of the extremely invasive and closely related *Impatiens glandulifera* differs little between plants from invaded (Norway) and native areas (India; Elst et al., 2016); this species, at least, needed neither post-introduction evolution nor climate change to achieve its invasion success.

4.4. Differences between Swiss and Italian roadsides and their populations

While the distribution pattern of roadside *I. balfourii* differed completely between Switzerland and Italy, there were no significant differences in elevation or sun exposure between those countries. The only difference was that there were more buildings on the Swiss side. This makes the near absence of *I. balfourii* along roads in Switzerland particularly surprising; on the Italian side the presence of buildings was shown to favour the species due to garden escapes. The same introduction pathway certainly should operate in Switzerland, and new propagules are also likely to be actively spread or passively brought from the Italian populations just across the border.

The most likely explanation for the absence of the species along Swiss roads involves differences in the road maintenance regimes of the studied countries. These differences were evident in both years of study (Najberek, pers. observ.). In Switzerland the roadsides were thoroughly mown along entire road sections, while on the Italian side they were mown only within towns. Regular mowing of roadsides is recommended for eradication of invasive alien species such as goldenrods *Solidago* spp. (Szymura et al., 2016).

Although *I. balfourii* propagule pressure (inferred from the number of buildings) is likely to be higher in Switzerland than in Italy, road maintenance creates an ecological trap for it on the Swiss side, effectively preventing its invasion on a larger scale. Applying the same method could limit its invasion in Italy as well, particularly since the spread of *I. balfourii* has clearly been curbed by climate rather than by factors such as pressure from enemies (present study), low attractiveness to pollinators or low reproductive capacity (Jacquemart et al., 2015; Ugoletti et al., 2011). In view of ongoing climate change, however, the time frame in which road maintenance will remain an effective weapon against *I. balfourii* is shrinking.

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Appendix A. Number of individuals and leaves of *I. balfourii* with disease and/or damage symptoms (leaf damage)

Symptom	N plants with diseased/damaged leaves	N diseased/damaged leaves
All symptoms	239	3360
Rusts and spots	233	2237
Browsing	148	873
Deformation	138	640
Necrosis	40	68
Discoloration	24	74
Mechanical damage	24	28
Mining	15	25

Appendix B. Abundance of invertebrates recorded on *I. balfourii*. Harmfulness values follow Najberek et al. (2016)

Taxon	Taxonomic rank	N records	Harmfulness (H_i)	Pest index (=N records * H_i)
Formicidae	family	92	0	0
Araneae	order	41	0	0
Stylommatophora	order	11	0.75	8.25
Psocoptera	order	10	0.5	5
Apidae	family	9	0	0
Collembola	order	6	0	0
Apocrita	suborder	5	0.25	1.25
Curculionidae	family	5	1	5
Dicyphus	genus	4	0.25	1
Trombidiidae	family	4	0	0
Drosophilidae	family	4	0.25	1
Coleoptera	order	3	0.5	1.5
Aphidoidea	superfamily	3	1	3
Boreidae	family	3	0	0
Protapion fulvipes	species	3	0	0
Lepidoptera (larvae)	order	2	1	2
Diptera	order	2	0.5	1
Muscidae	family	2	0	0
Psylloidea	superfamily	2	0.5	1
Vespoidea	superfamily	2	0	0
Auchenorrhyncha	suborder	2	1	2
Cecidomyiidae	family	2	0.25	0.5
Sphingidae	family	2	0	0
Opiliones	order	1	0	0
Hemiptera	suborder	2	0.75	1.5
Sphecidae	family	1	0	0
Aleyrodidae	family	1	1	1
Pompilidae	family	1	0	0
Symphyta	suborder	1	0.25	0.25
SUM		226	–	35.25

The scale uses literature data to rank the impact of invertebrates on herbaceous plants, from 0 for harmless organisms to 1 for obligatory pests, with intermediate values of 0.25, 0.50 and 0.75. 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.

Appendix C. Parameters characterising the 47 *I. balfourii* patches recorded along roads.

Variable	Min	Max	Mean	Unit
Patch area	0.2	30	5.07	m^2
GPS elevation	202	453	250	m a.s.l.
SEI	0	154	65	°
Distance from road	1	10	1.5	m

Minimum, maximum and mean values for patch area, elevation, SEI and distance obtained for 47 studied points.

Variable	N and% of records
Buildings	21 (45%)
Streams	8 (17%)
Scarps	36 (77%)

Presence of buildings, streams and scarps recorded at the 47 studied points.

Appendix D. Parameters characterising 37 true and 37 virtual localities of *I. balfourii* along the roads.

Variable	True/Virtual	Min	Max	Mean	Unit
DEM elevation	True	190	448	244	m a.s.l.
DEM elevation	Virtual	190	477	256	m a.s.l.
SEI	True	0	154	62	°
SEI	Virtual	4	180	83	°

Minimum, maximum and mean values and units of elevation and sun exposure index calculated for 74 studied points.

Variable	True/Virtual	N and% of records
Buildings	True	11 (15%)
Buildings	Virtual	17 (23%)
Streams	True	7 (9%)
Streams	Virtual	4 (5%)

Presence of buildings and streams recorded at 74 studied points.

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