Journal of Ecology

British Ecological Society

Journal of Ecology 2009, **97**, 393–403 doi: 10.1111/j.1365-2745.2009.01480.x

Impact of invasive plants on the species richness, diversity and composition of invaded communities

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Summary

1. Much attention has been paid to negative effects of alien species on resident communities but studies that quantify community-level effects of a number of invasive plants are scarce. We address this issue by assessing the impact of 13 species invasive in the Czech Republic on a wide range of plant communities.

2. Vegetation in invaded and uninvaded plots with similar site conditions was sampled. All species of vascular plants were recorded, their covers were estimated and used as importance values for calculating the Shannon diversity index H', evenness J and Sørensen index of similarity between invaded and uninvaded vegetation.

3. With the exception of two invasive species, species richness, diversity and evenness were reduced in invaded plots. Species exhibiting the greatest impact reduced species numbers per plot and the total number of species recorded in the communities sampled by almost 90%. A strong reduction of species number at the plot scale resulted in a marked reduction in the total species number at the landscape scale, and in less similarity between invaded and uninvaded vegetation. The decrease in species richness in invaded compared to uninvaded plots is largely driven by the identity of the invading species, whereas the major determinants of the decrease in Shannon diversity and evenness are the cover and height of invading species, and differences between height and cover of invading and dominant native species, independent of species identity.

4. *Synthesis.* Management decisions based on impact need to distinguish between invasive species, as their effects on diversity and composition of resident vegetation differ largely. Tall invading species capable of forming populations with the cover markedly greater than that of native dominant species exert the most severe effects on species diversity and evenness. Since a strong impact on the community scale is associated with reduction in species diversity at higher scales, invaders with a high impact represent a serious hazard to the landscape.

Key-words: impact, neophyte, plant community, plant cover, plant height, plant invasion, species diversity, species evenness, species richness, temperate zone

Introduction

Biological invasions affect biodiversity worldwide at various scales (Tilman 1999; Mack *et al.* 2000; Manchester & Bullock 2000; Davis 2003). Research in the past decade improved our knowledge of the patterns of invasion and substantial progress in understanding the mechanisms of invasion has been achieved (Rejmánek *et al.* 2005). Recently, much attention has been paid to negative effects of alien species on resident communities and functioning of invaded ecosystems (Williamson 1998, 2001; Parker *et al.* 1999; Byers *et al.* 2002; Simberloff *et al.* 2003) and to the mechanisms underlying these impacts (Levine *et al.* 2003). Ecosystem impacts are best documented for invasions by woody species and include, for example, nutrient enrichment (Vitousek & Walker 1989), water loss (Zavaleta 2000) and changed fire regimes (Brooks *et al.* 2004). Large-scale effects of plant invasions include the homogenization of floras, when originally different phytogeographical units become similar thanks to massive plant invasions (Schwartz *et al.* 2006, but see Kühn & Klotz 2006).

At the community level, the suppression of native plants is a phenomenon resulting from the dominance invasive species achieve in invaded habitats (Richardson *et al.* 1989, Pyšek & Pyšek 1995, Daehler 2003). Surprisingly, studies measuring

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*Correspondence author. E-mail: pysek@ibot.cas.cz the community level effects of invasive plants are rather scarce (Tickner *et al.* 2001). Recently, papers measuring the effect of the invasions of *Impatiens glandulifera* (Hejda & Pyšek 2006, Hulme & Bremner 2006) and *Mimulus guttatus* (Hejda & Pyšek 2008) have been published, which indicate that the impact on species diversity and composition of invaded communities differs among individual invaders. Studying the community level impacts in the field, by comparing invaded and uninvaded plots, can identify potential effects of an invading alien species and provide valuable information for landscape management and nature conservation (Gordon 1998, Manchester & Bullock 2000).

The present paper examines the invasion of 13 invasive neophytes (alien species introduced after 1500 AD, see Richardson *et al.* 2000, Pyšek *et al.* 2004 for definitions) in a variety of plant communities in the Czech Republic, Central Europe, and describes the associated changes in species composition and diversity in these invaded communities. We ask: Do invasive species vary in their effect on species diversity? If so, what is the range of this effect and what are the major determinants of this impact?

Methods

RATIONALE OF PLOT SELECTION

Field work was done between 2004 and 2007. For each of the 13 invasive neophytes (Table 1), the impact of invasion was studied in various regions of the Czech Republic (See Appendix S1 in Supporting Information). For each species, 10 pairs of adjacent 4 × 4-m vegetation plots were sampled. The plots were chosen so as to cover a range of site conditions and vegetation types in which the invader achieves dominance in the invaded communities (Appendix S1). In each vegetation type, one plot of the pair was placed in heavily invaded vegetation ('invaded plots') where the invader was dominant and had a high cover (Table 1) and the second plot in a neighbouring vegetation, where the invader had no cover ('uninvaded plots'). The uninvaded plot was chosen so as to have as similar site conditions as possible to the invaded plot, which could have been assumed with reasonable certainty due to the uninvaded plot being located in close proximity to the invaded plot. In a few cases, very low amounts of the invader occurred in the uninvaded plot, which could not have induced any changes to vegetation structure and species composition. In total, 260 vegetation plots were sampled in regions ranging from lowland alluvial meadows to sub-alpine meadows at the highest altitudes of the Czech Republic (Appendix S1).

SAMPLING AND MEASURING IMPACT

In each plot, all species of vascular plants were recorded and their covers (%) estimated. Species covers were used as importance values for calculating the Shannon diversity index H' and evenness J. Evenness was calculated as $H'/\ln S$, where S is the species richness expressed as the number of species (Magurran 1983). Differences in species richness S, Shannon index H' and evenness J between invaded and uninvaded plots were used to measure the effect of invasion on these community characteristics. To assess the impact of invasion on species composition and relative covers of resident species, we calculated the Sørensen index of similarity between each plot pair, based on species covers (Chao *et al.* 2005). The invading neophyte was excluded from the calculation of community characteristics (Hejda & Pyšek 2006) and so were species in the shrub and tree layers, which were only rarely present.

The species richness S was taken as a measure of diversity at the plot scale. In addition, for each invasive species studied, the total numbers of species recorded in all plots with invaded and uninvaded vegetation (S_{tot}) were used as a measure of the impact of invasion on diversity at the landscape scale.

To assess the effects of population characteristics of the invading species on species richness at the plot scale, the invader's height (cm) and cover (%) were measured in each invaded plot. To compare the absolute performance of the invader with its relative performance in comparison with a dominant native species, height and cover of the dominant native species were also measured and differences in both characteristics between the invading and native dominant species calculated.

STATISTICAL ANALYSIS

Differences in species richness S were tested by paired t-tests of invaded and uninvaded plots on square rooted data (e.g. Sokal & Rohlf 1995, pp. 352–356), using the correction for multiple comparisons based on the Bonferroni method, where the achieved significance levels are multiplied by the number of inferences to obtain conservative tests that eliminate type I error inflation (Daalgard 2002, p. 116). The correlation between reduction in species richness S and Sørensen index of similarity was tested by Pearson's correlation.

Differences in impacts among the invasive species were assessed by one-way ANOVAS. Differences in species richness S, Shannon's diversity H' and evenness J between each pair of invaded and uninvaded plot were the response variables, and the individual invasive species a factor. Differences among the influence of the species were then compared by *a posteriori* multiple comparisons among means using SNK tests (Underwood 1997, pp. 234–242).

Population characteristics determining the impact were first evaluated by ANCOVAS. Response variables were the differences within pairs in species richness S, Shannon's diversity H' and evenness J between uninvaded and invaded plots. The explanatory variables were (i) individual invasive species as a factor, and (ii) height and cover of the invasive species and (iii) differences in height and cover between the invasive and native dominant species as covariates. The modelling of ANCOVAS started with fitting maximal models that included the interaction of each covariate with each species and all one-level interactions among the covariates. The aim of the analyses was to determine the minimal adequate model (MAM), in which all explanatory variables are significantly different from zero and from one another, and all non-significant explanatory variables are removed (e.g. Crawley 1993). This was achieved by a step-wise process of model simplification, beginning with the maximal model and then proceeding by eliminating non-significant terms (using deletion tests), and retaining significant terms (e.g. Pyšek *et al.* 2005).

Invaders' heights were ln-transformed, their proportional covers angular-transformed (e.g. Sokal & Rohlf 1995) and all covariates standardized to zero mean and unit variance to achieve their comparable influence. Using these standardized values, collinearity was checked by a matrix of correlation coefficients, and then by calculating tolerance values (Quinn & Keough 2002, p. 128). All fitted models were checked by plotting standardized residuals against fitted values, and by normal probability plots (e.g. Crawley 1993). Their explained variance was expressed both as R^2 based on sum of squares, and as R^2_{adj}, based on mean squares, following Quinn & Keough

Table 1. The invasive alien species studied, their life form (rp – rhizomatous perennial, mp – monocarpic perennial, a – annual; all species are dicots), region of origin (NA – North America, A – Asia, E – Europe) and impact on community characteristics. The range of covers of the invading species in invaded plots and the number of species (mean ± SD, $n = 10$) in invaded (S inv) and uninvaded plots is shown (S uninv). At the plot scale, the impact on species richness S is expressed as the mean percentage reduction of species number in invaded plots compared to uninvaded (100%). Positive value indicates a higher species number in uninvaded, negative in invaded vegetation. At the larger scale, the impact is expressed as the percentage reduction of the total number of species recorded in invaded (S_{tot} inv) plots and related to that recorded in uninvaded plots (S_{tot} uninv = 100%). Mean Sørensen similarity index, calculated as an average value for 10 pairs of plots, indicates the impact of invasion on species composition; the lower the similarity the less similar is the invaded and uninvaded vegetation. Species are ranked according to the decreasing reduction in S. Significant differences in species richness S between invaded and uninvaded plots, corrected for multiple comparisons using the Bonferroni method, are shown: $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$

Species	Life form	Origin	Cover range (%)	S uninv†	S inv	Impact on S (%)	S_{tot} uninv	S_{tot} inv	Impact on S_{tot} (%)	Sørensen similarity
Fallopia sachalinensis (F. Schmidt) Ronse Decraene	rp	A	70–100	13.3 ± 4.9	1.8 ± 1.6	86.4***	70	10	85.7	0.17
F. japonica (Houtt.) Ronse Decraene	rp	A	100	12.1 ± 3.5	3.3 ± 2.8	73.0**	76	21	72.4	0.23
F. × *bohemica* (Chrtek & Chrtková) J. P. Bailey	rp	A	40–100	14.8 ± 7.3	5.4 ± 5.0	65.9*	75	37	50.7	0.36
Heracleum mantegazzianum Sommier & Levier	mp	A	90–100	16.7 ± 4.5	7.4 ± 3.1	52.6**	91	40	56.0	0.33
Rumex alpinus L.	rp	E	75–100	12.6 ± 2.5	7.7 ± 2.4	39.1***	51	34	33.3	0.42
Aster novi-belgii L. agg.	rp	NA	60–90	14.1 ± 4.8	8.9 ± 6.3	38.7	80	54	32.5	0.34
Helianthus tuberosus L.	rp	NA	50–100	12.7 ± 6.5	8.0 ± 4.9	33.7	57	39	31.6	0.59
Rudbeckia laciniata L.	rp	NA	80–100	10.6 ± 2.6	6.9 ± 3.0	29.8	45	34	24.4	0.60
Solidago gigantea Aiton	rp	NA	70–100	16.4 ± 6.7	12.0 ± 6.3	25.5	92	62	32.6	0.51
Imperatoria ostruthium L.	rp	E	50–80	14.3 ± 5.6	9.9 ± 2.6	21.4	61	39	36.1	0.63
Lupinus polyphyllus Lindl.	rp	NA	60–95	21.1 ± 2.3	16.4 ± 3.8	21.2	93	71	23.7	0.62
Impatiens glandulifera Royle	a	AS	60–90	10.9 ± 1.8	9.5 ± 2.6	12.3	49	46	6.1	0.75
Mimulus guttatus DC	rp	NA	30–40	17.2 ± 7.4	17.1 ± 7.6	–6.3	93	90	3.2	0.61

†Neophytes were excluded from calculations of species numbers in plots.

(2002, p. 139). In the latter case, larger values of R^2_{adj} indicated better fits taking into account sample sizes and number of predictors.

To provide understandable and generally interpretable results of the interactions between explanatory variables, regression trees (Breiman *et al.* 1984, De'ath & Fabricius 2000, Chytrý *et al.* 2008) were constructed by repeatedly splitting the response variables using binary recursive partitioning in CART® v. 6.0 (Steinberg & Colla 1995). To find the best tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was grown, and their re-substitution relative errors, corresponding to residual sums of squares, were estimated. Tenfold cross-validation was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the minimum cost tree was selected as the best tree (Steinberg & Colla 1995). Following De'ath & Fabricius (2000), a series of 50 cross-validations was run, and the modal (most likely) single tree chosen for description. Total variance explained by the best single tree was calculated as $R^2 = 1$ – re-substitution relative error. The best trees were represented graphically, with the root Node 1 standing for undivided data at the top, and the terminal nodes, describing the homogeneous groups of data, at the bottom of the hierarchy. The quality of each split was assessed by improvement, corresponding to the proportion of the total sum of squares explained by the tree at each node. To reduce the splitting power of the high categorical variable species (13 factor levels, corresponding to the individual species), the species were adjusted to have no inherent advantage over continuous variables, following penalization rules of Steinberg & Colla (1995).

To reveal net effects of invaders, independent of species identity, the effect of individual invasive species was removed from the analyses. This was done by refitting the individual invasive species in the ANOVAS, and calculating Pearson's standardized residuals of these models (Hastie & Pregibon 1993, p. 205). Residuals from these models were then examined as the response variables (Lonsdale 1999, Chytrý *et al.* 2008) by the step-wise backward procedures aimed to determine the MAMs, beginning with the maximal model which contained all possible interactions among the explanatory variables. Significant interactions of the differences between the cover of invading and dominant native species with the cover of invading species were then examined by regressing simple slopes on increasing differences between the cover of invading and dominant native species at varying values of the cover of the invading species: its mean, and mean plus and minus its sample standard deviation (Quinn & Keough 2002, pp. 131–133). Analysis of these interactions was made using centred variables (Quinn & Keough 2002, p. 131).

Results

IMPACT ON SPECIES COMPOSITION AND STRUCTURE OF INVADED COMMUNITIES

The impact of invasion on the invaded communities markedly differed among the 13 invading species; significant differences in species richness between invaded and uninvaded plots were found for five species. Species exhibiting the greatest impact reduced species numbers per plot (S) and the total number of species recorded in the communities sampled (S_{tot}) by almost 90%. In contrast, some invaders exhibited very low or no impact on both measures of diversity (Table 1). The measures of impact of invading species on community characteristics were correlated. As expected from the nested arrangement of S within S_{tot}, invasions associated with a strong reduction in species richness at the plot scale were also associated with a marked reduction in the total number of species S_{tot} at the landscape scale (Table 1). Reduction in species richness S also decreased similarity between invaded and uninvaded vegetation (Fig. 1).

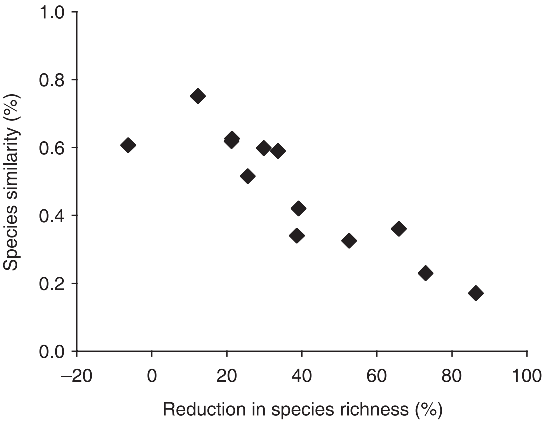

Fig. 1. Correlation between the impact of the neophyte species studied on species composition (expressed as mean Sørensen similarity between invaded and uninvaded plots in a pair) and species richness S: $r = -0.89$, $t = 6.41$, d.f. = 11, $P < 0.001$.

The greatest impact on species composition of invaded communities was recorded for *Fallopia sachalinensis* and *F. japonica*, resulting in only 17% and 23% similarity between invaded and uninvaded plots, respectively. The invasion by *Heracleum mantegazzianum*, *Aster novi-belgii* and *F.* × *bohemica* also resulted in profound changes in species composition and low (33–36%) similarity between invaded and uninvaded plots. For the remaining species, the similarity between invaded and uninvaded plots ranged from 42% to 75%, with *Impatiens glandulifera* exhibiting the smallest effect (Table 1).

The impact of individual invading neophytes on species richness S, Shannon diversity H' and evenness J exhibited a similar pattern, with taxa of the genus *Fallopia* and *Heracleum mantegazzianum* usually exerting the strongest impact (Fig. 2). The invasion of *Impatiens glandulifera* and *Mimulus guttatus* always had a minimum effect and for diversity and evenness the SNK tests consistently confirmed that the impact of these two species was significantly ($P < 0.05$) smaller than that of all the other species (Fig. 2b,c). The species impacts were generally weakest when measured as a decrease in species richness (total variance explained by one-way ANOVA: $R^2 = 0.37$) and stronger when measured as diversity ($R^2 = 0.50$) and evenness ($R^2 = 0.53$).

FACTORS DETERMINING THE IMPACT ON SPECIES RICHNESS

The decrease in species richness in invaded plots depended on the identity of the invading neophyte, but also significantly interacted with species-specific differences in cover between

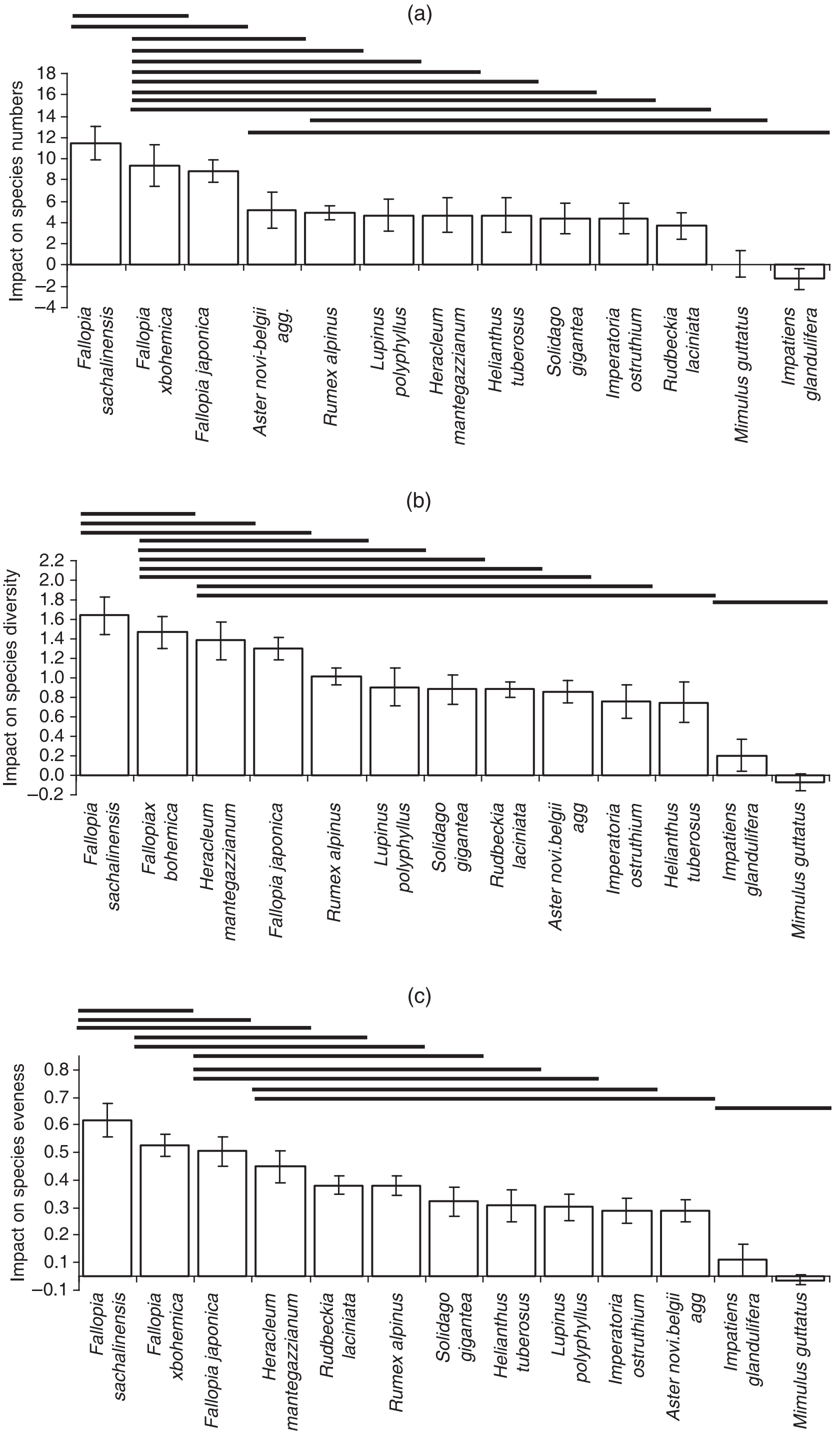

Fig. 2. The impact of individual invading neophytes on species numbers S (a), Shannon diversity H' (b) and evenness J (c), measured as a difference within 10 pairs of invaded and uninvaded plots for each species. Differences in one-way ANOVAS: $F = 5.83$; d.f. = 12, 117; $P < 0.001$ (a); $F = 9.68$; d.f. = 12, 117; $P < 0.001$ (b); $F = 10.98$; d.f. = 12, 117; $P < 0.001$ (c). Bars are means ± standard errors. Lines above the bars show groups of species not significantly different; lines that do not overlap with others show means significantly ($P < 0.05$) different in *a posteriori* SNK tests.

the invading and native dominant species (Appendix S2). The regression tree for the decrease in species richness (Fig. 3) explained 44% of variance ($R^2 = 0.44$), with most of this impact (81.3% of the explained variance based on the improvement values at the individual nodes) attributed to the identity of invading species. The taxa of the genus *Fallopia* had the largest average impact and *Impatiens glandulifera* and *Mimulus guttatus* had no impact. The taxa of the genus *Fallopia* further split based on differences in cover between the invading and native dominant species (Fig. 3).

FACTORS DETERMINING THE IMPACT ON SPECIES DIVERSITY

The decrease in species diversity, H', of invaded plots significantly depended on interactions among invading species and their height, differences in height between invading species and dominant native species, and the cover of invading species. There were also significant interactions between height, cover and differences in height and cover (Appendix S2). The regression tree on the decrease of Shannon diversity H'

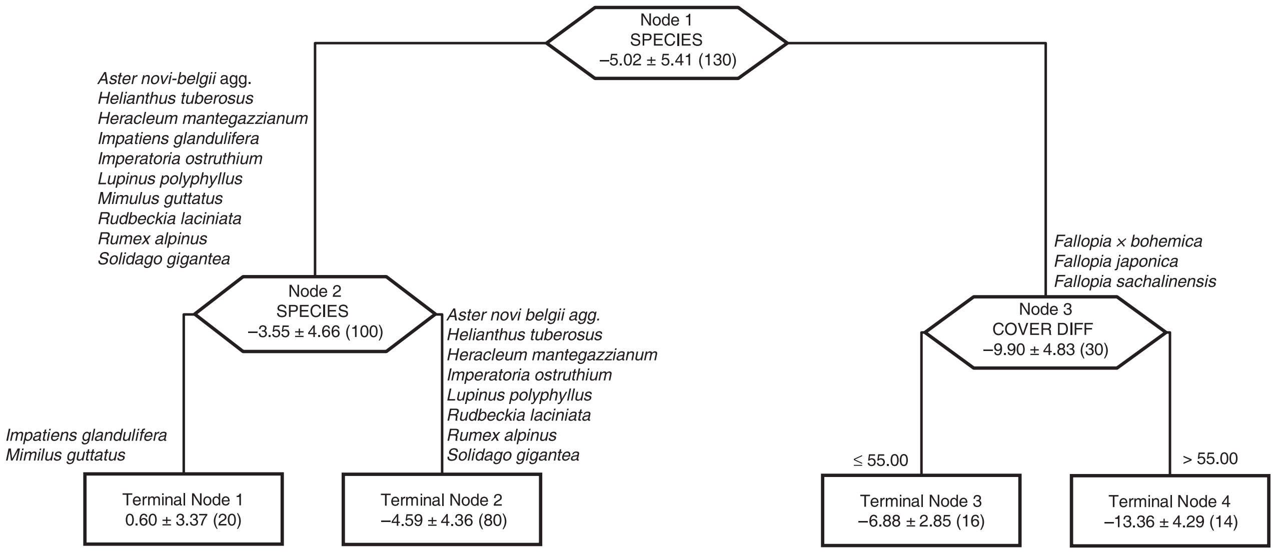

Fig. 3. Regression tree describing the impact of invading species on species richness S in invaded plots. Each node shows node number, mean ± standard deviation of the difference in species richness between invaded and uninvaded pairs of plots (negative value indicates a decrease due to invasion), and number of plots in brackets. Splitting node (polygon) shows the name of the splitting variable, with splitting criteria indicated. Terminal nodes are shown as rectangles. COVER DIFF = difference in cover of the invading species and that of the dominant native species in uninvaded plots (in %).

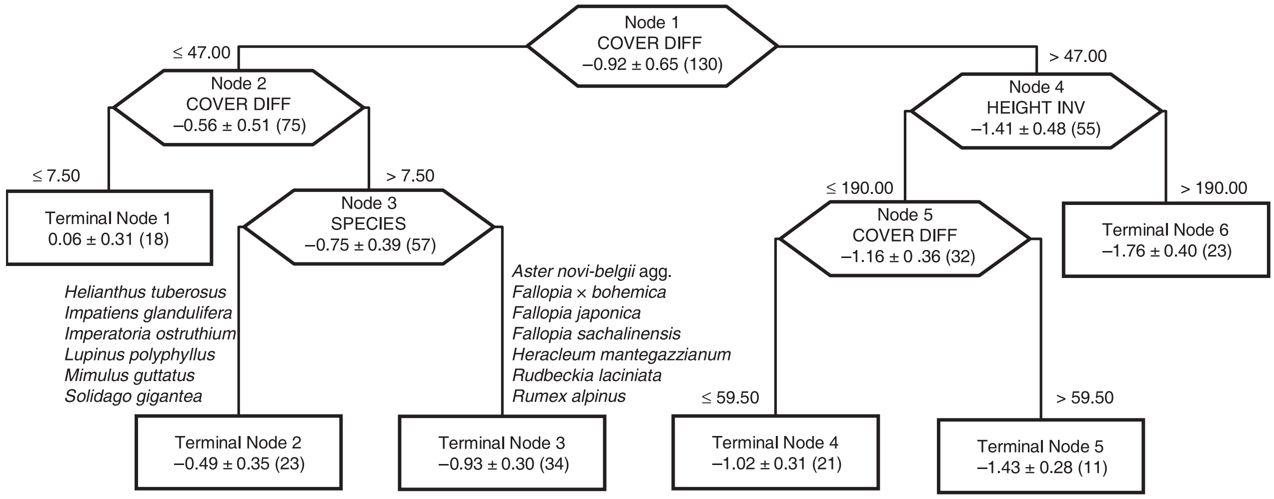

Fig. 4. Regression tree describing the impact of invading species on species diversity H' in invaded plots. Each node shows node number, mean ± standard deviation of the difference in species diversity between invaded and uninvaded pairs of plots (negative value indicates a decrease due to invasion), and number of plots in brackets. Splitting node (polygon) shows name of the splitting variable, with splitting criteria indicated. Terminal nodes are shown as rectangles. COVER DIFF = difference in cover of the invading species and that of the dominant native species in uninvaded plots (in %); HEIGHT INV = height of the invading species (cm).

(Fig. 4) explained 74% of variance, with 81.7% of this impact attributed to the differences in cover between invading and dominant native species, 11.7% to the height of the invading species and only 6.5% to the identity of the invading species. The impact was first divided based on a cover difference of approximately 50% (≤ 47.0%). The group with the small differences in cover exhibited no impact on H' if the cover of the invading and native dominant differed by ≤ 7.5%; for cover differences between 8% and 47%, the impacts were species-specific (Fig. 4). The group with differences in cover above 47% indicated the absolutely highest impact on H' value if the invading species was taller than 190 cm. If the invading species was shorter than 190 cm, the impact on H' value was further divided based on differences in cover (Fig. 4).

FACTORS DETERMINING THE IMPACT ON SPECIES EVENNESS

The decrease in species evenness, J, in invaded plots depended on almost all possible one-way interactions among invading species, their height and cover, and differences between height and cover of invading and dominant native species (Appendix

S2). The regression tree on the decrease in evenness (Fig. 5) explained 81% of variance, with 74.4% of it attributed to the differences in cover between invading and dominant native species, 16.7% to the differences in height between invading and dominant native species, 6.5% to the cover and 2.4% to the height of the invading species. No variance was attributed to the identity of the invading species. There was no impact on evenness if the difference in cover was ≤ 7.5% (Terminal Node 1: –0.03 ± 0.08; $N = 18$).Within the range of 8–37% differences in cover, however, evenness was most reduced in plots with extremely high covers of the invading species (Terminal Node 4). Otherwise (Terminal Nodes 2 and 3) the impact depended on the differences between heights of invading and dominant native species. If differences in cover were above 37%, the decrease in evenness was determined by differences in the height of invading and dominant native species. The invasion resulted in the highest recorded impact on evenness if the invader was taller than 225 cm and its height exceeded that of the native dominant species by > 110 cm (Terminal Node 8). For a height difference of ≤ 110 cm the impact of evenness again increased with increasing difference in cover between invading and dominant native species (Fig. 5, Terminal Nodes 5 and 6).

IMPACT INDEPENDENT OF SPECIES IDENTITY

Net effects of invasion were examined on residuals after removing species-specific effects of invading species. There were significant negative effects, independent of the identity of invading species, on species diversity H' and evenness J (Table 2), but not on species richness S. The effect of invasion resulting in a significant decrease in species diversity and evenness in invaded plots was mostly manifested by the difference between the cover of invading and dominant native species. These differences significantly interacted with the cover of invading species (Table 2) and their effect became stronger as the cover of invading species increased (Table 3).

Discussion

MEASURING THE IMPACT OF INVASIONS BY COMPARING INVADED AND UNINVADED SITES

Measuring the impact of invasive species on resident communities by comparing invaded and uninvaded sites (Levine *et al.* 2003) makes it possible to collate large data sets, which cover the variation in response of the invaded community over a wider range of environments. However, this approach brings about some uncertainty over the character of invaded plots prior to invasion, i.e. to what extent are they comparable with uninvaded control plots as the plots may differ in factors other than the invasion. In the present study, the uninvaded plots were selected to be in close vicinity of the invaded stands with habitat conditions matching as closely as possible. Evidence that the plots were very similar is provided by the large portion of variance explained by the impact of invasion, especially so for diversity (regression tree: $R^2 = 0.74$; MAM:

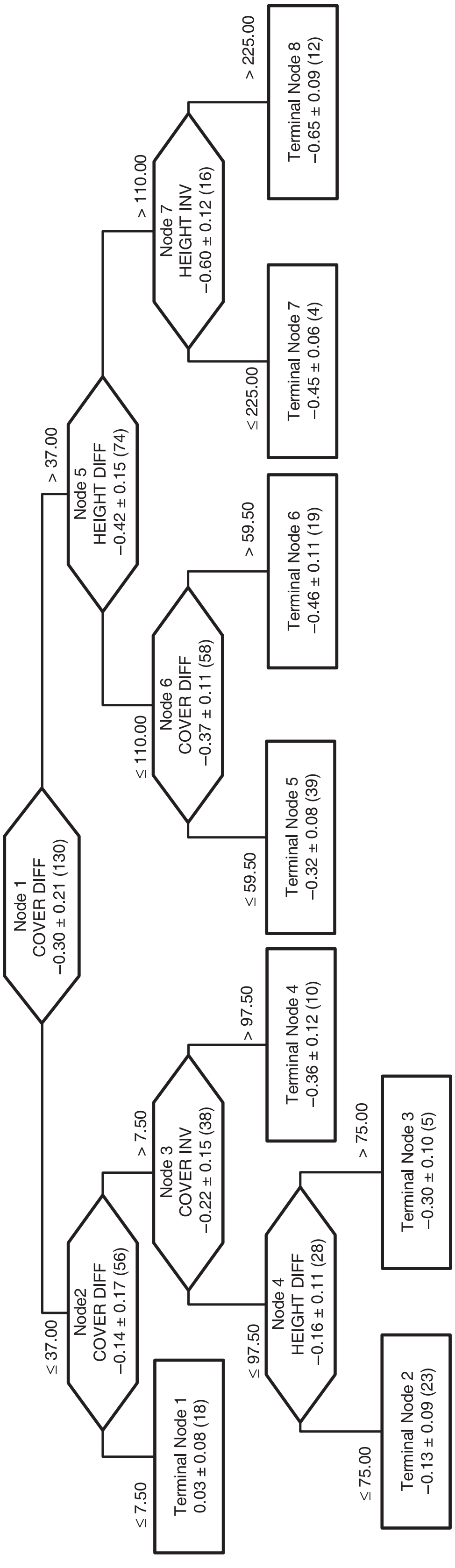

Fig. 5. Regression tree describing the impact of invading species on species evenness J in invaded plots. Each node shows node number, mean ± standard deviation of the difference in species evenness between invaded and uninvaded pairs of plots (negative value indicates a decrease due to invasion), and number of plots in brackets. Splitting node (polygon) shows name of the splitting variable and splitting criteria. Terminal nodes are shown as rectangles. COVER DIFF = difference in cover of the invading species and that of the dominant native species in uninvaded plots (in %); HEIGHT INV = height of the invading species (cm); HEIGHT DIFF = difference in height of the invading species and that of the dominant native species in uninvaded plots (in cm).

Table 2. ANOVA tables and deletion tests for minimal adequate models (MAMs) of ANCOVAs describing population characteristics determining the impacts on diversity and evenness, independent on identity of invading species

	ANOVA on MAM				Deletion tests on MAM		
Source of variation	d.f.	SS	MS	$R^2 (R^2_{adj})$	*F*	d.f.	*P*
Net effects on diversity *H′*							
Cover	1	0.5211	0.5211		4.6700	1, 127	0.03
Differences in cover	1	9.4988	9.4988		73.6500	1, 127	< 0.001
Cover × Differences in cover	1	0.7302	0.7302		5.4500	1, 127	0.02
Residuals	126	16.8711	0.1339				
Total	129	27.6212		0.39 (0.38)			
Net effects on evenness *J*							
Cover	1	0.0989	0.0989		1.6800	1, 127	0.20 (NS)
Differences in cover	1	0.9062	0.9062		73.3600	1, 127	< 0.001
Cover × Differences in cover	1	0.1200	0.1200		9.6100	1, 127	0.002
Residuals	126	1.5735	0.0125				
Total	129	2.6986		0.42 (0.41)			

Table 3. The decrease in species diversity *H′* and evenness *J* with increasing differences between the cover of invading and dominant native species (slope) for small (mean + standard deviation), medium (mean) and high (mean – standard deviation) cover of the invading plant. Net effects on residuals, after removing effects of individual invading species, were calculated on centred values

	Impact on diversity *H′*				Impact on evenness *J*			
Cover of invading plant	Slope	Standard error	*t*-test	*P*	Slope	Standard error	*t*-test	*P*
Small	–0.001	0.002	5.45	< 0.001	–0.095	0.012	7.81	< 0.001
Medium	–0.014	0.002	8.58	< 0.001	–0.105	0.012	8.74	< 0.001
High	–0.018	0.002	7.86	< 0.001	–0.115	0.013	9.06	< 0.001

$R^2 = 0.83$, $R^2_{adj} = 0.76$) and evenness ($R^2 = 0.81$ and 0.91, respectively; $R^2_{adj} = 0.79$). Therefore, we believe that our data provide a solid background for comparing the differences among a reasonably large set of invasive species, for which a standardized quantitative estimation of their impact on resident communities has not been made before. To minimize the bias, data were collated using the same methods and on the same scale. However, bearing the above limitations in mind, we consider it more appropriate to interpret our results of the comparison of invaded and uninvaded plots as changes associated with invasion, without temporal inferences of the invasion process.

VARIATION IN INVADER EFFECTS

Fallopia spp. and *Heracleum mantegazzianum* had the strongest impacts on invaded communities in terms of both species diversity and composition. It is likely that the vigorous growth of these species, which reach a high cover and are much taller than members of invaded resident communities, is responsible for their strong impact (Brabec & Pyšek 2000, Pyšek *et al.* 2007). The extensive and dense rhizome system of *Fallopia* taxa also plays a role in the competitive exclusion of native species from invaded communities (Sukopp & Schick 1993). The ability to form homogenous stands, which is typical of *Heracleum mantegazzianum*, seems to be another effective means of suppressing native vegetation.

Our results confirm that *Mimulus guttatus* and *Impatiens glandulifera* exhibit minor impact on the characteristics of the invaded communities studied (Hulme & Bremner 2006, Hejda & Pyšek 2006, 2008, Truscott *et al.* 2008). For the rhizomatous perennial *M. guttatus*, the negligible effect can be linked to the rather low cover this species achieves in invaded communities. The low impact of *Impatiens glandulifera* can be attributed to a combination of factors; although also tall and fast growing, this species does not develop homogenous stands. As the only annual among the species studied, *I. glandulifera* is not able to compete effectively for underground space by means of rhizomes. Individual plants form clusters and this spatial pattern of invading populations, explained by individual mortality (Beerling & Perrins 1993) leaves space for native species to survive in the community after the invasion (Hejda & Pyšek 2006).

The type of the invaded community is another factor that can explain differences in the impact exerted by individual species of invasive neophytes. *Impatiens glandulifera* invades riparian habitats, where native communities are dominated by tall nitrophilous species and the impact of the invader is not much different from the competitive influence of these native tall nitrophilous dominants (Hejda & Pyšek 2006). The same seems to be true for *Helianthus tuberosus*, another invasive species of riparian habitats with relatively low impact, despite its tall stature, high cover and dense rhizome system. *Heracleum mantegazzianum*, on the other hand, massively invades species-rich sub-montane meadows with many vulnerable, competitively weak species, which are not present in invaded sites (Pyšek & Pyšek 1995, Thiele & Otte 2007).

DETERMINANTS OF THE IMPACT ON INVADED COMMUNITIES

Of the two components of species diversity, richness and evenness (Magurran 1983, Stirling & Wilsey 2001), the focus of invasive species impacts has been primarily on richness (Levine *et al.* 2003, Hulme & Bremner 2006). However, changes in species evenness may influence invasion resistance, productivity and local plant extinction rates (Wilsey & Potvin 2000, Smith *et al.* 2004). Our results show that the impacts of invasion on these structural characteristics of plant communities are determined by both species identity of the invader and its population characteristics, such as stand height and cover, acting in concert with those of the native dominant species, and that the relative importance of these determinants on species richness, evenness and diversity differs.

With the exceptions of *Impatiens glandulifera* and *Mimulus guttatus*, species richness was reduced by invasion. This effect of invasion is largely species-specific, and the severity of impact depends almost exclusively on the identity of particular invading species; net effects on species richness independent of species identity were not significant. This is consistent with impacts of individual invading species on species richness being weaker, and explaining less variance in analyses of population determinants of the impact, than those on species diversity and evenness.

The decrease in species evenness, and consequently diversity, is mostly driven by the cover and height of invading species, independently of species identity. However, it is rather the difference between the cover and height of the invader and native dominant species that determines the degree to which species diversity and evenness are reduced in invaded communities. In our plots invading species have on average higher cover (median 90%, lower and upper quartile 70 and 100%, respectively, $n = 130$) and height (158.2 ± 73.8, mean ± SD) than native dominants (cover: median 40%, lower and upper quartile 30% and 60%; height: 109.0 ± 34.7). The impact of an invasive species is usually associated with the degree of its dominance (Richardson *et al.* 1989, Pyšek & Pyšek 1995) and our results suggest that the advantage of monopolizing relatively more space in the community than occupied by the native dominant is directly associated with the impact of invasion. This is manifested by the difference in cover, as a population characteristic closely related to biomass. The difference in cover is the most important determinant of the impact on species evenness and diversity; invasions by neophytes, which increase the dominance in the community by approximately 40–50%, have the most profound effect, especially if the invading species is tall.

IMPLICATIONS FOR MANAGEMENT OF INVASIVE SPECIES

The results reported here are based on a limited set of 13 species, yet they represent the so far most comprehensive quantitative analysis of the impact of plant invaders on the composition and structure of resident vegetation. The species included in the study are invasive in most Central-European countries (Lambdon *et al.* 2008) and may therefore be considered broadly as representative of plant invasions in the temperate zone.

Native species differ in their resistance to invasion; some are excluded from invaded communities more easily than others (Standish *et al.* 2001, Stinson *et al.* 2007). The strong impact on species richness is correlated with that on species composition, measured as the similarity between invaded and uninvaded vegetation. It has previously been reported that even for invasions with a limited effect on species richness, species composition changes and that it is resistant ruderal species that increase their representation in invaded communities (Hejda & Pyšek 2006). Thus, conservation or management decisions based on impact need to (i) realize that the effect of individual invasive species largely differs, (ii) the effect on community characteristics is determined by the character of the invaded community, especially the dominance of the native dominant relative to that of the invader, and (iii) it is more appropriate to measure the impact of invasion by examining the traits of species forming the post-invasion community than simply the number of species lost due to invasion. Consequently, conservation hazard associated with invasion of a particular species can differ from its community-level impacts. Some neophytes can have a decisive community-level impact, however, the loss of biodiversity associated with that particular invasion concerns mostly weeds or other alien species (Hulme & Bremner 2006). This is the case of *Fallopia* species and *Solidago gigantea*, which often invade semi-ruderal communities with prevalence of widespread weeds. In the contrary, a species with a low community impact can seriously impair species diversity of species-rich communities with a number of rare species. *Lupinus polyphyllus* is an example of such type of impact; this species often invades wet oligotrophic montane and sub-montane meadows of a high conservation value. Unlike most other neophytes, it is able to massively invade low nutrient sites, probably because of its nitrogen-fixing ability. *Rudbeckia laciniata*, *Heracleum mantegazzianum* and *Rumex alpinus* also invade communities with a high conservation interest. In general, when evaluating the conservation risk associated with the invasion of a particular neophyte, the conservation value of invaded communities needs to be taken into account.

Moreover, the correlation between impact at the two scales and the comparably strong effect of the species with the highest impact on species richness at both the plot scale and landscape scale indicate that the impact of such invaders is not restricted to the community level, but represents a serious hazard also at the landscape scale (Hulme & Bremner 2006).

Acknowledgements

We thank Jan Pergl and Zuzana Sixtová for technical assistance, reviewers for helpful suggestions, and Scott Wilson and Andrea Baier for improving our English. This work was supported by the FP6 EU Integrated Project ALARM (GOCE-CT-2003–506675, Settele *et al.* 2005), FP7 EU project PRATIQUE (KBBE-212459), grant no. IAA600050811 and institutional long-term research plans no. AV0Z60050516 from the Academy of Sciences of the Czech Republic and nos. MSM0021620828 and LC06073 from the Ministry of Education of the Czech Republic.

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Received 12 September 2008; accepted 18 December 2008
Handling Editor: Scott Wilson

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Overview of plots used in the study

Appendix S2. ANOVA tables and deletion tests for minimal adequate models