

**Community level impacts of alien invasive plants and the role of
native range habitats in plant invasions**

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Introduction

Biological invasions and associated homogenization of biota is a very rapid and apparent aspect of the global environmental change (Meyer 2004, Schwartz et al. 2006). Although the environmental consequences may be the main motiff for studying biological invasions, systematic data documenting these consequences are still lacking (Tickner et al. 2001, Richardson & van Wilgen 2004). Therefore, it is difficult to make more general assumptions about various invasive species impacts and to compare the environmental hazards associated with various invasive species invasions.

The community level consequences of an invasion are a convenient synthetic characteristics of its overall environmental impact, since the dominant plant species, such as most target invaders, tend to dominate the invaded sites and therefore set the conditions for most other organisms. Vice versa, the changes in the plant species composition and its diversity reflect the changes in site conditions associated with the invasion. The data on community level impact of invasions may be even a good base for land management decisions (Gordon 1998, Manchester & Bullock 2000) and represent an example of the link between the primary research and applications.

Methodological and logistic constrains may be the main cause of the lack of systematic data on the community level impacts of plant invasions. There are two basic ways how to approach this problem: comparative and experimental. The experimental approach is formally and methodologically more correct, since the causal relationship between the invasion and its consequences can be unambiguously proved only by experimental manipulation. However, field experiments are demanding on working capacity and therefore usually cover only a small part of conditions, under which the invasion of a particular species takes place. Moreover, removal experiments often suffer from artefacts induced when invasive species are removed from the plots. This concerns mostly clonal invaders with a massive rootsystem, such as *Rumex alpinus* or *Reynoutria* species. Annual invaders (*Impatiens* species) can be more easily removed from the invaded site without a severe soil disturbance.

However, to restrict the research focus to such species only would severely bias the general idea about the consequences of invasions. Additive field experiments with invasive species are constrained for ethical reasons. Another problem is that it is very difficult to distinguish the long-term equilibrium state of the community from the direct response to the removal of the invader, which is usually dominating the invaded community (Richardson et al. 1989, Pyšek & Pyšek 1995, Bímová et al. 2004). The sites from which the invader was removed can be quickly colonized by pioneering species (Morrison 2002, Hulme & Bremner 2006) and the original resident community need not necessarily recover after the removal (Harms & Hiebert 2006). The *ex situ* experiments

can be questioned about whether the experimental field simulates the site conditions properly, since even small deviations can seriously bias competitive relationships among the plant species. The *ex situ* experiments often address the competition of an alien with one or a few selected native species (e.g., Meekins & McCarthy 1999, Alcock 2002, Lenz et al. 2003, Sher & Marshall 2003). Therefore, such experiments give an idea about the competitive influence of an invader on certain native species, but not on the whole plant community.

On the other hand, comparative approaches are often criticised for poor proof of the causality between observed effects and the invasion, because it is not clear to what degree the differences between the invaded and adjacent uninvaded vegetation are attributable to the invasion itself and to what degree to different site conditions prior to the invasion. Moreover, it may be difficult to separate the causes and effects of the invasion, since the characteristics of the community prior to the invasion are thought to influence the degree and probability of invasion (Lonsdale 1999). Some studies relate the diversity and/or species composition of various invaded localities to the abundance of invasive species (e.g., Kwiatkowska et al. 1997), but this approach neither excludes the possible influence of confounding factors nor separates the cause and effects of the invasion. Only exceptionally, it is possible to relate the site prior and after the invasion, for example due to historic vegetation records or aerial photographs (see for example Lambrinos 2000, Denoth & Myers 2007).

Be that as it may, the idea that causality is derived from an empiric comparison is widely used (see for example de Winton & Clayton 1996, Kwiatkowska et al. 1997, Lenz & Taylor 2001, Kourtev et al. 2002, Brockerhoff et al. 2003, Badano & Pugnaire 2004, Henderson & Naeth 2005) and to condemn it would deprive ecology substantially. For these reasons, I used both experimental and comparative approach if it was possible to remove the invader from the invaded stands easily and with minimum soil disturbance, which was the case of *Mimulus guttatus* and *Impatiens glandulifera*. Moreover, these two species deserved special attention since their impact was expected to be low (Hulme & Bremner 2006). Since it is not really possible to prove the non-existence of a phenomenon, it was highly desirable to inspect the impact of these two species in more detail and achieve a higher statistical power of the tests. For remaining 11 invasive species studied, I used only the comparisons of the invaded and adjacent uninvaded vegetation. This approach is often used in ecological studies dealing with succession, where it is called the “space for time substitution” approach (Prach et al. 1997, Alvarez & Cushman 2000, Badano & Pugnaire 2004). This indicates that two different sites of a different age are considered as representing different stages of the same process over time, prior and after the invasion in this case.

Following this logic, the heavily invaded stands were compared to adjacent uninvaded or slightly invaded vegetation with the site conditions as similar to the invaded site as possible.

Therefore, a pair of vegetation relevés with a heavily invaded and adjacent uninvaded vegetation were considered as replicates in the analysis. Sometimes, the invasion was confounded with a decrease of management intensity and consequent nitrification. In order to ensure the best possible match of the site conditions between the invaded and uninvaded vegetation, the invaded vegetation was compared with the degraded nitrophilous vegetation dominated by native species. This approach made the impacts of certain target invaders lower than expected, since it separated the effects of the invader from the effects of changes due to management intensity. This concerned mostly grassland vegetation where especially *Heracleum mantegazzianum*, *Imperatoria ostruthium*, *Lupinus polyphyllus* and *Rumex alpinus* invade.

Despite the methodological constraints discussed above, the fact that the impact of a number of invasive species was sampled in the same way and on the same scale makes it possible to compare these species' community level impacts, because potential biases in data are likely to be consistent for all the species sampled. Species alien to Central Europe which spread rapidly, form continuous stands with a high cover and are not restricted to human-made sites were selected for the comparative study.

It is clear that a community level impact of a plant invasion is a multi-stage process and there are several aspects of it, which need to be separated from each other. The impact on α and β diversity can be expressed as the differences in species richness, Shannon diversity H' and evenness J' indices (Magurran 1983) between the invaded and adjacent uninvaded vegetation. On the other hand, differences in the total numbers of species found in the vegetation invaded by a certain species with that found in the adjacent uninvaded vegetation provides an insight into the floristic homogenization of sites due to invasion. This is reflected by the invader's impact on β diversity and points to the environmental hazards at the landscape scale. This is an important point, since it shows how the results scale up to coarser spatial scales (Hulme & Bremner 2006).

The impact on both α and β diversity can differ from the invader's impact on species composition. Abundance-based Sørensen similarity index (Chao et al. 2005) calculated for the invaded and adjacent uninvaded vegetation or multi-dimensional methods were used to detect the impact on species composition. The multi-dimensional methods used to detect the impact of *M. guttatus* and *I. glandulifera* were performed twice: with species covers as importance values to detect the invader's impact on species abundances and with binary presence/absence data to detect its impact on species composition in qualitative terms.

The impact of an invader on invaded communities is associated with its ability to form dense stands over considerable areas, in short, with its dominance in the invaded community (Richardson et al. 1989, Pyšek & Pyšek 1995, Bímová et al. 2004). Such ability is very likely to be determined by its dispersal and competitive ability, the way it utilizes, accommodates and allocates resources or

tolerates stressful factors. It is clear that all these traits are a result of a long-term adaptation of the invading species to site conditions in the region of its native distribution. In this way, the site conditions of habitats in the native range could determine the dynamics, extent and hence the impact of invasion due to these preadaptations. To understand the invasive success in a broader evolutionary context, information about habitats in the native range can provide some insights, for example about how and why the preadaptations advantageous for invasion evolved. Therefore, the information about native range habitats was obtained for a sample of almost 300 species alien to Central Europe. This dataset was restricted to species, for which where the information about habitats in the native range was detailed enough. The narrative information about the character of native range habitats was transformed into a slightly modified EUNIS classification system (Davies & Moss 2003).

All the data were collected within the framework two international projects: DAISIE, aimed at inventoring European alien species; and ALARM, aimed at assessing large scale environmental hazards. Both these interdisciplinary projects brought together experts from various European countries and resulted in creating large datasets using standardized approaches. These datasets are being used not only for research purposes, but are open to land managers, local authorities and general public as well and represent another connection of primary research and applications.

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Conclusions

Categorization of the species studied according to their impact on invaded communities

This study focused on neophytes, species introduced after 1500 A.D., because their impact on native vegetation is higher and more obvious than that of archaeophytes, introduced before that date, due to considerable invasion dynamics and relatively short residence time (Pyšek et al. 2002). The target neophytes, included in the study, differ strongly in their community level impacts. *Impatiens glandulifera* had a miniscule impact on species diversity and composition, both in the removal experiment and comparative study (Chapter I). This small impact is likely to be associated with this annual species' lower competitive strength, which has a modest root system and forms stands that are not homogeneous in terms of cover. The density of *I. glandulifera* populations is known to decrease during the vegetation season, as plants fall due the weight of climbers, which are common in invaded riparian communities (*Calystegia sepium*, *Cuscuta europaea* – see Beerling & Perrins 1993). Moreover, the character of communities in which *I. glandulifera* invades, mostly riparian nitrophilous vegetation, does not provide opportunities for competitively weak species even if they are not invaded. This vegetation is dominated by tall, competitive native nitrophilous species (*Urtica dioica*, *Carduus crispus*, *Chaerophyllum bulbosum*) and competitively weak species, which would be otherwise prone to competitive exclusion by *I. glandulifera*, cannot thrive in these communities due to the suppression by these native nitrophilous dominants.

Similarly, *Mimulus guttatus* has no impact on species diversity and composition both in the removal experiment (Chapter II) and comparative study (Chapter III). The invasion of this species in the Czech Republic is restricted to heavily disturbed riparian terraces, which is the only place where *M. guttatus* forms dense stands. Even though the cover of *M. guttatus* exceeded 70% in some of the experimental plots, the overall cover of all plant species rarely reached 100%, which suggests that the development of the closed vegetation cover is limited by the riparian disturbance regime rather than the invasion by *M. guttatus*. At the same time, the intensive disturbance could reduce the competitive effect of native vegetation and enable the alien species to form stands, which are otherwise rarely observed in Central Europe.

The situation is different in the Atlantic part of Europe, where *M. guttatus* is often seen invading wet meadows and dense riparian vegetation (Truscott et al. 2008). It is very likely that the species thrives in the Atlantic climate of the British Isles and is more competitive there which allows it to successfully penetrate into dense native vegetation. The parts of the Czech Republic where *M. guttatus* is found invading riparian vegetation (SW and N Bohemia, NE Moravia – Slavík 2000) are climatically somewhat similar to the Atlantic Europe because of high summer

precipitation. However, the neophytes are supposed to go through a rapid adaptation process during the invasion (Lee 2002; Daehler 2003; Bossdorf et al. 2005), so it is possible that populations of *M. guttatus* better adapted to Central European climatic conditions will appear in the future.

The comparative study measuring the community level impact of 13 neophytes alien to Central Europe (Chapter III) revealed that these neophytes differ strongly in their impacts. The stands of *Fallopia sachalinensis* harboured on average almost 90% less species than adjacent uninvaded vegetation, and the effect of this species on β diversity was similarly suppressive. Low similarity between invaded and uninvaded vegetation indicates also severe impact on species composition. The other species from the genus *Fallopia* (*F. japonica* and *F. x bohemica*) and *Heracleum mantegazzianum* all exhibited more than 50% reduction of both α and β diversity and are alien invaders with the most severe impact on the invaded community.

Rudbeckia laciniata, *Solidago gigantea*, *Imperatoria ostruthium*, *Lupinus polyphyllus* represent species with moderate impact on invaded vegetation; their invasion resulted in less than 40% reduction of both α and β diversity. Their effect on floristic similarity was also moderate. The invasion by *Aster novi-belgii* resulted in a similar reduction of α and β diversity, but was associated with a strong impact on species composition. The opposite was true for *Helianthus tuberosus*: invasion of this species was associated with moderate impact on α and β diversity, but relatively modest impact on species composition.

Measures and determinants of the community-level impact

The impacts of invading neophytes on α diversity correlates with that on β diversity and on species composition. The fact that the impact on α diversity is negatively correlated with abundance-based Sørensen similarity between invaded and uninvaded vegetation proves the time for space substitution approach to be right: when the impact of invasion is low, the species composition of invaded vegetation resembles that of the vegetation which is uninvaded and was considered to mimic the situation before the invasion.

The impact of the invader is determined by its height and cover; these characteristics can be used as surrogates for biomass production. The spatial homogeneity of the invaded stands is another important factor, since non-homogeneous populations of the invading species, such as *I. glandulifera*, provide opportunities for native species to survive in the invaded vegetation. This is likely to be the mechanism behind the assumption that the impacts of the invasive species are scale dependent.

The impact on diversity differs according to its measure. When the differences in species numbers are considered, the impact depends mostly on the identity of the invading species. On the

other hand, when the differences in Shannon evenness and diversity are used as the measures, the impact positively correlates with the differences in height and cover of the invading neophyte and that of the native species dominating the adjacent uninvaded community, hence assumed to dominate the community before the invasion. In other words, if the invader imposes substantially stronger dominance over the community than the native dominant species present prior to invasion, the community level impact of invasion is especially strong. In this way, the character of the community prior to invasion determines the overall community level impact of the invasion as well – the communities with strong dominants prior to the invasion tend to be impacted less, because such communities do not contain many competitively weak species, that would be easily eliminated following the invasion. The species actually present in such communities are less likely to be excluded from the community, because the competitive influence of the invader is not much different from that of the native species dominating the community prior to invasion. In contrary, communities without strong native dominants tend to be impacted more, because they contain more species that cannot cope with the competitive effect of the invader. Similar pattern was observed for the influence of invasion on soil (Dassonville et al. 2008). In this study, soils that were oligotrophic prior to invasion were affected more and the impact of invasion was context-dependent.

Considering that the community level impacts are likely to be context-dependent, hence to a large extent determined by the characteristics of the community prior to invasion, the impact of *I. glandulifera* might change in the future. When the data for this study were collected (season 2004–2005), *I. glandulifera* was observed to form dense stands almost exclusively in riparian vegetation. Nowadays, it is observed to colonize wet meadows, submontane tall forb vegetation and wet hemerobic vegetation (Drescher & Prots 2003). If this species continues to invade such vegetation in the future, its community level impact might be different from that observed in the riparian vegetation.

The character of uninvaded vegetation also needs to be considered when evaluating conservation hazards associated with invasion. Most target neophytes were found to invade disturbed and/or nitrophilous habitats and their dominance was mostly at the expense of ruderal species and other neophytes (see also Hulme & Bremner 2006). On the other hand, some neophytes with relatively mild impact, assessed in quantitative terms, can seriously deprive communities of a high conservation value, harbouring rare native species. This is the case of *Lupinus polyphyllus*, *Heracleum mantegazzianum* and *Rumex alpinus* that were most often found to invade semi-natural and natural communities.

The role of habitats in the native range

The link between the character of the native range habitats and invasion success in Central Europe is distinctive, even though it is masked by the effect of other factors, such as residence time, life form, and geographical origin. Species recruited from (i) riverine terraces, eroded slopes and banks and avalanche tracks and (ii) deciduous forests and, at the same time, from riparian scrubs are, in relative terms, most likely to become successful invaders. Another native range habitats with a high proportion of successful invaders are (iii) subalpine tall forbs, (iv) cultivated gardens and parks, (v) trampled and other intensively disturbed areas and (vi) wet grasslands. In contrary, most of the neophytes recruited from (i) coastal sand and dune habitats, (ii) sedge and reedbeds, (iii) dry grasslands and (iv) ruderal and other anthropogenic habitats only occur as casuals in the invaded range. From their native habitats, these neophytes seem to be adapted to effective dispersal and possess competitive strength resulting from vigorous growth. In their native range, they usually grow on nutrient-rich sites with a high intensity of disturbance, rapid succession and therefore intensive competition, such as riparian habitats or subalpine tall forbs. The riverine terraces and riparian scrub can be seen as one habitat in different part of a successional sere – the riparian scrub develops on riverine terraces. In this context, an ideal invader seems to be an opportunistic colonizer of newly exposed substrata, which is, at the same time, competitive enough so as to persist in the rapidly developing nitrophilous vegetation. The importance of the rapid dispersal is likely to be connected with the fact that random disturbance events, such as floods, promote the invasion (Truscott et al. 2006). Similar habitats in Central Europe suffer from the invasions most intensively (Chytrý et al. 2005). The character of native range habitats with the highest proportions of casual neophytes (i.e., the least successful invaders) suggests that neophytes recruited from such habitats are more adapted to tolerating stressful factors rather than towards effective dispersal and competitiveness.

The correspondence between the habitats in the native and invaded ranges changes with the invasive success. Casual neophytes invade a limited spectrum of habitats compared to that they occupy in the native range. This is rather trivial fact, associated with the limited spread of casual neophytes – limited distribution is correlated with a limited spectrum of habitats occupied in the invaded range. Naturalized neophytes invade a spectrum of habitats comparable to that they inhabit in the native range; the naturalisation process is most likely to be successful in the same conditions as the species occupies in the native range, since those are the site conditions it is best adapted to. The most successful invaders seem to expand their original niche and invade a broader scale of habitats than they occupy in their native ranges. Although these successful invaders typically recruit from a few habitats described above, the spectrum of habitats they occupy in the invaded range is

broader. Part of this phenomenon can be attributed to them being widespread – the larger the area a species occupies, the more types of habitats it is likely to sample and colonize, although this relationship is not straightforward and linear. However, besides this, it is likely that invasive neophytes expand their original niche during invasion. This “primary niche expansion“ of the most successful invaders can be explained by ecological plasticity of these species as well as their ability to adapt rapidly to the conditions encountered in the invaded range. The rapid evolution, assumed to take place during the invasion process (Lee 2002, Daehler 2003, Bossdorf et al. 2005) may be an important factor responsible for the rapid spread of the invasive species.

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Participation in Projects

- 2005–2008 DAISIE – Delivering Alien Invasive Species Inventories for Europe;
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Authorship statement

Hejda M. & Pyšek P. (2006): What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological conservation* 132: 143 – 152

The first author presented the basic idea of the paper, collected and analyzed the data, and took share in writing the paper.

Hejda M. & Pyšek P. (2008) Estimating the community level impact of the riparian alien species *Mimulus guttatus* by using a replicated BACI field experiment. In: Rabitsch W., Essl F. & Klingenstein F. (Eds.): *Biological Invasions – from Ecology to Conservation*. *NEOBIOTA* 7 (2007): 251 – 258

The first author designed the removal experiment, collected and analyzed the data, and took share in writing the paper.

Hejda M., Pyšek P., Pergl J., Sádlo J., Chytrý M. & Jarošík V. – Habitats in the native distribution range as predictors of the invasion success of alien plants.

The first author brought the basic idea of the paper, prepared the data and took share in the analysis and interpretation of results, and writing of the paper.

Hejda M., Pyšek P. & Jarošík V. – Impact of invasive plants on the species richness, diversity and composition of invaded communities.

The first author brought the basic idea of the paper, collected the data, contributed to data processing and took a major share in writing the paper.

Publications

Hejda M. (2005): Charakteristika populací a výskytu *I. glandulifera* na Křivoklátsku. Zpr. Čes. Bot. Společ. 39: 431 – 452

Hejda M. & Pyšek P. (2006): What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation 132: 143–152

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In revision

Hejda M., Pyšek P., Pergl J., Sádlo J., Chytrý M. & Jarošík V. Habitats in the native distribution range as predictors of the invasion success of alien plants. Global Ecology and Biogeography.

Hejda M., Pyšek P. & Jarošík V. Impact of invasive plant species on the characteristics of invaded communities.