Habitat invasion research: where vegetation science and invasion ecology meet

Petr Pyšek & Milan Chytrý

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Pyšek, P. (corresponding author, pysek@ibot.cas.cz): Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43, Průhonice, Czech Republic, and Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44, Praha 2, Czech Republic
Chytrý, M. (chytry@sci.muni.cz): Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37, Brno, Czech Republic

Abstract
In the last decade, habitat-oriented studies of plant invasions, performed at broad scales and using large data sets of vegetation plots, have focused on quantifying the representation of alien species in vegetation or habitat types, identifying factors underlying invasions, and exploring the pools of species available for invasion into particular habitats. In this essay we summarize what we have learned, discuss constraints associated with this kind of data and outline promising research topics to which a macroecological perspective of habitat invasions can contribute. Such topics include, among others: integrating species-specific information on invasion status, residence time in the region, biological and ecological traits and phylogenetic relationships into habitat invasion research to better capture the context-dependence of invasions; focusing on the functional role that alien species, relative to natives, play in plant communities; and obtaining insights into the role of pre-adaptation for invasion by comparing the functional composition of habitat species pools in the native range. There is still a strong geographic bias, with detailed assessments across broader ranges of habitat types in large regions available only from Europe, the United States and New Zealand, which call for extension of this research to other continents.

Introduction
The knowledge of distribution of species introduced by humans to new regions is important for understanding biological invasions. It is nevertheless typical that generalizations about geographic patterns are usually based on the number of naturalized alien species in individual regions or states, which ignore that the emergent patterns on a coarse scale are an outcome of processes occurring at finer scales, namely differences in the levels of invasion among different habitat or vegetation types (Pyšek et al. 2010a,b). However, comprehensive large-scale information on the distribution of species, not only alien but also native, across habitat types is generally scarce. Thus, the extent to which individual habitats are invaded is sometimes estimated from expert assignments of alien plant species represented in a regional flora to their respective habitats (Crawley 1987; Walter et al. 2005; Arianoutsou et al. 2010b; Aikio et al. 2012), which rather reflects alien species pools of individual habitats (Zobel 1992; Sádlo et al. 2007) than the degree to which particular sites are invaded. It is surprising that although the question of what makes some habitats more invasible than others has been addressed since invasion biology started to rapidly develop in the late 1980s (Crawley 1987; Rejmánek 1989), and issues related to habitat invasibility continue to be a key part of invasion theory (Catford et al. 2012; Rejmánek et al. 2013), quantitative assessment of the levels of invasion in particular habitats only started to appear in the last decade. This period has seen intensive research to quantify the occurrence of alien species in plant communities associated with particular habitats, as well as to generalize the observed patterns and identify mechanisms underlying differences in invasibility among habitats. There is still a strong geographic bias, with detailed assessments across broader ranges of habitat types in large regions available only from Europe (Kowarik 1995; Chytrý et al. 2005, 2008a,b; Masek et al. 2006; Vilà et al. 2007, 2010; Pyšek et al. 2012a;
Sirbu et al. 2012; Campos et al. 2014; Medvecká et al. 2014), the United States (Stohlgren et al. 1999, 2006; Spyreas et al. 2004) and New Zealand (Wiser et al. 2011).

While in the US quantitative knowledge of alien species distribution in habitats is largely based on results of one research group (Stohlgren et al. 1999, 2006), the recent progress in Europe was made possible due to the use of large databases of vegetation plots (Schaminée et al. 2009; Dengler et al. 2011). For decades, records from phytosociological plots were used nearly exclusively for the purpose of classifying and mapping vegetation, but such records have enormous potential as a data source for macroecological research (Beck et al. 2012). Stimulated by the EU-funded ALARM project (Settele et al. 2005), and/or encouraged by the rapid development of computer-based technologies and emergence of extensive databases, phytosociological data started to be used in research on alien plants to gain insights into the patterns of habitat invasions at regional to continental spatial scales (Chytrý et al. 2005, 2008a,b; Pyšek et al. 2005).

In this essay, we summarize achievements from a decade of studies focusing on habitat invasions by alien plants, discuss constraints associated with this kind of data, and outline research topics we consider promising and to which a macroecological perspective of habitat invasions can contribute. We focus here on broad scales and large data sets, as noted above, leaving aside experimental studies of habitat invasions. This is because the latter rarely provide a complete picture, due to limitations in terms of the area sampled, habitat completeness and number of replicates (although we acknowledge their utility for assessing invasion mechanisms at smaller scales). For more details on patterns of habitat invasions discussed below we refer the reader to a previous review of the topic (Pyšek et al. 2010b) and to original studies.

Exploring vegetation-plot data: what has it told us?

Habitat-oriented studies of plant invasions were recently developed along two main lines of research. The first focused on quantifying the representation of alien species in vegetation plots, with associated analyses aimed at identifying factors underlying invasions in particular habitats. Studies based on species and environmental data from vegetation plots, characteristics of their surrounding landscape that served as proxies for propagule pressure, and climatic characteristics, have allowed separation of the level of habitat invasion (the actual number or proportion of alien species in the community, or proportional abundance of alien species in the community) from invisibility, defined as an inherent property of the plant community occurring in a given habitat (Williamson 1996; Lonsdale 1999; see Richardson & Pyšek 2006; Chytrý et al. 2008a for definitions and discussion of differences between the two metrics). The results revealed that habitats differ considerably in levels of their invasion. These patterns reported for Europe were consistent across different regions (Chytrý et al. 2008b); the same habitats had either high or low levels of invasion in all geographic locations examined, which was confirmed by later studies from other regions that used similar schemes of habitat classification (Sirbu et al. 2012; Medvecká et al. 2014). The differences in level of invasion were mainly caused by inherent habitat properties, and to a lesser extent by propagule pressure and climatic differences among regions (Chytrý et al. 2008a). The most invasible habitats were those with fluctuating availability of resources, especially nutrients, and most of these habitats were frequently and/or strongly disturbed (Chytrý et al. 2008a; Pyšek et al. 2012a), which is consistent with the theory of fluctuating resource availability (Davis et al. 2000). This general pattern was confirmed through another analysis of vegetation plots across a broad range of habitats, which related the level of invasion to species indicator values rather than to habitat classification (Jansen et al. 2011). There was an overall correspondence between the level of invasion and habitat invasibility, with the most invaded habitats also being highly invisible. However, invisibility of some moderately invaded habitats appeared to be low, with their resistance to invasion overcome by high propagule pressure (Chytrý et al. 2008a; Pyšek et al. 2010a,b). The occurrence of archaeophytes (species introduced to the target European regions before AD 1500, mainly from the Middle East and Mediterranean; Pyšek et al. 2012b) is to a large extent deterministic, depending mainly on habitat types, while propagule pressure is less important. The occurrence of neophytes (arriving after AD 1500, also from North America and more distant regions of Asia) was more stochastic; propagule pressure was more important than in archaeophytes, yet habitat type was also the most important predictor for this group (Chytrý et al. 2008a). Overall, the percentage of neophytes in European habitats rarely exceeds 10%. This is strikingly different from the US, where the proportion of aliens in natural vegetation types is often much higher than in human-made habitats in Europe (see Pyšek et al. 2010a,b for a review of available data on levels of invasion).

Such consistent results associated with habitat invasibility from different biogeographic regions (Chytrý et al. 2008b) provided an opportunity for mapping plant invasions to produce regional maps as well as a map for the whole of Europe (Chytrý et al. 2009a,b). In Europe, high levels of invasion are observed in the industrialized west and in lowland agricultural regions in the east, while montane zones, oceanic areas in the northwest and the boreal zone are relatively little affected. By linking this research with integrated scenarios of future socioeconomic
development in Europe based on land-use patterns projected for 2020, 2050 and 2080 (Spangenberg et al. 2012), projected future levels of plant invasions were mapped for Europe (Chytrý et al. 2012). The results indicate that implementation of sustainability policies would not automatically restrict the spread of alien plants; rather, such policies might increase invasions in less productive areas by supporting agriculture and associated invasion-conducive land use.

The second approach to studying habitat invasions stemmed from the assumption that the level of invasion depends on the global pool of species that are available for invasion in a given habitat. An analysis of a large vegetation-plot database and plant indicator values has shown that Central European species that invade other continents often originate from productive habitats (Dostál et al. 2013). This implies that corresponding productive habitats on other continents have a higher probability of being invaded because of the large species pool of introduced species compatible with these habitats. This has been tested by comparing the habitats in which species occur in their native and invaded ranges. Among species invading Central Europe, those confined in their native range to productive habitats with frequent disturbance were identified as the most successful invaders (Hejda et al. 2009). The same result was obtained when European natural habitats were compared as donors of alien species to other continents (Kalousová et al. 2013). Of these habitats, alluvial forests and coastal dunes provide a disproportionately higher number of successful invaders to other parts of the world than other natural habitats, with the lowest number of invaders provided by arctic, alpine and other low-productive and relatively undisturbed habitats. Obviously species adaptations to particular habitats correlate with traits that facilitate successful invasion: species originating in habitats that are frequently disturbed and/or (at least temporarily) rich in resources and highly productive tend to be the most successful invaders. In the recipient regions, these species invade similar habitats as found in their native range but also many others, extending their habitat niche (Hejda et al. 2009; Kalusová et al. 2013). In particular, species originating from habitats with fluctuating resources can often successfully invade not only similar habitats, but also habitats with consistently low resource levels or very rare resource pulses, as exemplified by Eurasian Bromus species in deserts of the southwestern USA (Schlesinger et al. 1996). The correspondence between habitats in native and invaded ranges is also reflected by the fact that European habitats donating the highest proportions of invasive species to other continents also tend to be most invaded in Europe by alien plants originating from other continents (Kalousová et al. 2013).

Avenues of future research: What else can we learn?

Based on the recent progress in habitat invasion research, we suggest that improved understanding of the mechanisms and processes determining habitat invasibility, and of some general issues in invasion biology, can be achieved by focusing on the following topics:

1. Integrating species-specific information on invasion status, residence time in the region and biological and ecological traits would make it possible to better capture the context-dependence of invasions. So far, habitat-focused studies mostly have not distinguished between species at different stages of invasion (Blackburn et al. 2011), lumping all alien species together and using species richness as currency. Yet, different traits are likely to play varying roles in particular habitats (Dainese & Bragazza 2012; Jauni & Hyvönen 2012) and in different stages of the invasion process, from casual through naturalized to invasive (Williamson 2006; Richardson & Pyšek 2012). The role of habitat characteristics in shaping the naturalization process, a key stage preceding invasion, remains largely unexplored, yet the habitat in which naturalization takes place is a key component of invasion success (Richardson & Pyšek 2012).

2. Incorporating species’ habitat affinity in both the native and invaded ranges into models explaining species invasiveness and habitat invasibility would deepen current understanding of the role species traits play in invasion success, and of the context-dependence of trait-related processes (Pyšek et al. 2009).

3. Focusing on the functional role that alien species, relative to native, play in plant communities (Hejda & de Bello 2013), and taking into account differences in abundance of species belonging to particular functional groups would improve our understanding of the functional role of new species in plant communities. It is especially relevant with respect to the concept of ‘novel ecosystems’, based on the notion that native and alien species occur in combinations and relative abundances that have not occurred previously within a given biome (Hobbs et al. 2006, 2009).

4. The source area approach, based on examining the success of invaders originating from the pool of species native to a certain region (Pyšek et al. 2004, 2009), can provide insights into the role of pre-adaptation for invasion by comparing the functional composition of habitat species pools in the native range. These pools are of different composition and size, hence species from different habitats vary in the range of functional traits that they sample by interacting with species of plant communities in the native range (Sax & Brown 2000). Linked to this line of research are phylogenetic relationships between invading species and native floras, so far explored mainly at the scale of regions (Fridley 2008), while studies addressing these
relationships at fine scales and at habitat level are still rare (Gerhold et al. 2011).

5. Incorporating information on species’ habitat affinities in their native ranges, with corresponding knowledge of shifts in their habitat niches, into risk assessment schemes (e.g. Leung et al. 2012) could improve accuracy of prediction and identification of potentially invasive species.

6. Extending research on habitat invasions using vegetation-plot data from large areas, as described herein, to continents other than Europe may provide important new insights. The studies done so far have been strongly geographically biased to Europe, but invasion patterns can differ considerably in other parts of the world, and mechanisms not considered for Europe can play a role.

**Constraints and limitations**

The issue of habitat invisibility is a complex one, with outcomes determined by a number of factors and their interactions (Rejmánek et al. 2013). It is clear that vegetation-plot data can provide answers only to a subset of questions related to the role of habitats in plant invasion. There are some constraints and limitations to the outlined approach, some of which are difficult to overcome.

1. Differences in habitat classifications used in different regions, and lack of appropriate classification in some regions. For Europe, the EUNIS system of habitat classification (Davies et al. 2004) proved to be a convenient platform (Chytrý et al. 2005, 2008b; Vilà et al. 2007; Arianoutsou et al. 2010a,b; Gassó et al. 2012; Sirbu et al. 2012; Medvecká et al. 2014). Its underpinning by the phytosociological system of vegetation classification, started by Rodwell et al. (2002) and further developed by the IAVS Working Group European Vegetation Survey in cooperation with European Environment Agency, provides a direct link between this broadly accepted system of habitat classification and data from hundreds of thousands of vegetation plots stored in European databases (Schaminée et al. 2009; Dengler et al. 2011). However, current lack of similar systems of habitat or vegetation classification and vegetation-plot data in many regions outside Europe imposes limitations, both on the assessment in the biomes not present in Europe, especially tropical and subtropical, and on intercontinental comparisons of habitat invasions. Systems of vegetation and habitat classification generally consistent with those established in Europe, and supported by analyses of large amounts of vegetation plots, are now emerging on other continents (Jennings et al. 2009; Wiser et al. 2011; Li et al. 2013). Such systems and underlying data can greatly facilitate habitat invasion research in the near future; however, vegetation studies outside Europe are still mainly focused on natural vegetation, although most invaded sites tend to be in human-made habitats.

2. The nature of the data from vegetation plots stored in large databases. Varying size of the plots, non-random and non-systematic sampling schemes used, and the error in ocular cover estimations may introduce bias to the analyses (Dengler et al. 2011), although the patterns found are often sufficiently robust. In any case, appropriate data stratifications should be used before the analyses, and interpretations of the results based on such data should be done with utmost caution (Michalcová et al. 2011).

3. Failure to capture changes in the level of invasion over time, despite the vegetation-plot data going back to the early 20th century. This is partly due to the fact that vegetation plots from different time periods were sampled at different sites, which were selected subjectively (Chytrý et al. 2014), and partly due to inaccurate location of the historical plots, which precludes the opportunity of repeated sampling. Also, alien species in older times were probably less likely to be sampled, and stands with dominant aliens may often have been avoided on purpose and ignored (Michalcová et al. 2011).

**Conclusions**

We argue that a decade of research at the interface between vegetation science and invasion ecology, using ecoinformatics approaches and linking large sets of spatially explicit records from vegetation survey plots, has proved useful in producing robust information on macroecological patterns of plant invasions. The approach can be further developed by including species-specific information on traits of both alien and native representatives in plant communities, taking functional and phylogenetic relationships into account, considering species invasion history in a region, and comparing habitat affinities in both native and invaded ranges. Further possibilities lie in harmonizing data available in other regions of the world and extending the biogeographical scope of analyses. Moreover, spatially explicit information on habitat invasions can be used to identify the areas at highest risk of invasion so as to support effective monitoring and management of alien plants. Combined with scenarios of future land-use change, such information may also be used for predicting invasion risks in the future.

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