CHAPTER 6

Habitats and Land Use as Determinants of Plant Invasions in the Temperate Zone of Europe

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6.1 Introduction

In the current literature on plant invasions, solid information on macroecological patterns has accumulated, which contributes to our understanding of the invasion process. For example, it has been firmly established that temperate mainland regions are more invaded than tropical mainland, islands are more invaded than corresponding areas of mainland, and that the proportion of naturalized alien species to native species in temperate zone decreases with latitude and altitude (see Pyšek and Richardson 2006 for a review). It is symptomatic that these generalizations are based on the numbers of alien species, mostly naturalized, in individual regions or states, and ignore that the emergent patterns on the coarse scale can be an outcome of patterns and processes occurring on finer scales, namely of differences in the level of invasion among different habitats.

Because large-scale quantitative information on the distribution of species, not only alien but also native, in habitats is scarce, the extent to which individual habitats are invaded was sometimes estimated from expert assignments of alien plant species represented in a regional flora to their respective habitats (Crawley 1987; Rejmánek *et al*. 2005; Walter *et al*. 2005). This approach essentially defines alien species pools of individual habitats (Zobel 1992; Sádlo *et al*. 2007), but has a disadvantage that sizes of the regional species pools of aliens cannot be simply scaled down to individual sites so that their level of invasion can be quantified.

In the present chapter, we review studies dealing with invasions in habitats and, by using an extensive dataset from the Czech Republic, we demonstrate differences between the level of invasion (defined as the actual representation of alien species, Chytrý *et al*. 2005; Richardson and Pyšek 2006) and invasibility (defined as the inherent vulnerability of habitats to invasion, Lonsdale 1999). We classify individual habitats according to these two measures and explore the relative importance of factors which determine both the level of invasion and invasibility. In analyses, two traditional groups of European aliens are considered, distinguished on the basis of residence time (Pyšek *et al*. 2004): archaeophytes (arrived before 1500 AD, mainly from the Middle East and Mediterranean), and neophytes (arrived after 1500 AD, mainly from North America and Asia). Finally, the potential for application of the knowledge of invasion in individual habitats is discussed and possibilities of using it in risk assessment outlined.

6.2 Overview of studies on the level of invasion in habitats

Until recently our knowledge of which habitats are invaded, and how much, was based on anecdotal evidence rather than rigorous testing. A pioneering study documenting quantitatively invasions in

various habitats was published by Kowarik (1995) for the city of Berlin, and papers comparing several habitats over large areas, using large numbers of vegetation plot records, started to appear only recently. Quantitative data on the representation of alien species in various habitats are still surprisingly scarce; only a few such assessments are available from Europe (Chytrý *et al*. 2005, 2008a, b; Maskell *et al*. 2006; Vilà *et al*. 2007) and the United States (Stohlgren *et al*. 1999, 2006; Spyreas *et al*. 2004). Most surveys conducted at a landscape scale, are performed within habitat types (Gilbert and Lechowicz 2005) or biased towards particular habitats, which makes the range of habitats considered limited (DeFerrari and Naiman 1994; Planty-Tabacchi *et al*. 1996; Sobrino *et al*. 2002; Brown and Peet 2003; Campos *et al*. 2004; Pyšek *et al*. 2005). Such studies therefore cannot provide broader insights into the differences in the level of invasion among habitats.

6.2.1 Representation of alien species in habitats

Despite some differences in plot size and habitat classification systems, European studies that evaluated invasions in individual habitats, based on thousands of vegetation plots, yielded consistent results in terms of the representation of alien species in the most invaded habitats. Chytrý *et al*. (2005), working on the scale of units to hundreds m^2 and using 32 habitat types in the Czech Republic, found that the 6 most invaded habitats harbored on average 4.4–9.6 per cent of neophytes (2.3 per cent on average across all vegetation types). For Catalonia, Vilà *et al*. (2007), using 34 habitat types and plot size of ca 20–90 m^2, also found a low mean number of neophytes per plot (less than 2.0 per cent pooled across habitats, and less than 9.0 per cent in the most invaded habitats). The highest proportions of neophytes of the total species numbers per plot were reported from the UK, with maxima of 10.0–24.8 per cent in the 3 most invaded of 19 habitat types (Chytrý *et al*. 2008b). There are also regional surveys, where percentages of alien species higher than 10 per cent are reported, but this is because these studies deliberately focused on highly invaded habitats such as riverine (Sobrino *et al*. 2002; Planty-Tabacchi *et al*. 1996) and coastal (Campos *et al*. 2004).

Outside Europe, the most extensive studies on the occurrence of alien and native species were done on 37 natural vegetation types in 7 states in the central United States (Stohlgren *et al*. 1999; Stohlgren 2007) in plots ranging in size from 1 to 1000 m^2. In several of these vegetation types, the proportion of alien species considerably exceeded 10 per cent (Stohlgren *et al*. 2006). The figures given by these authors can be compared with data from the Czech Republic, Catalonia, and Britain, because "exotic" and "alien" species in the US studies (Stohlgren *et al*. 1999, 2006) correspond to neophytes in the European studies (Chytrý *et al*. 2005, 2008b; Vilà *et al*. 2007). It is striking that the proportion of aliens in US natural vegetation types is often much higher than in vegetation of human-made habitats in Europe.

6.2.2 Which habitats are most invaded?

A study summarizing levels of invasion based on vegetation plot data from three European regions, and using standardized classification of habitats (Chytrý *et al*. 2008b), showed that habitats generally associated with human- and water-induced disturbances, high fertility, and high propagule pressure, exhibit the highest levels of invasions. Pooled across regions, arable land, coastal sediments, and ruderal habitats—including trampled areas—harbor the highest proportions of neophyte species. This is in accordance with regional and habitat-specific studies (DeFerrari and Naiman 1994; Planty-Tabacchi *et al*. 1996; Sobrino *et al*. 2002; Campos *et al*. 2004; Chytrý *et al*. 2005; Vilà *et al*. 2007; Simonová and Lososová 2008). The highest level of invasion in Europe was found in coniferous woodlands (with 24.8 per cent of neophytes), arable land (14.3 per cent) and coastal sediments (10.0 per cent) in Britain (Chytrý *et al*. 2008b). Two subtypes of annual anthropogenic vegetation in the Czech Republic also contained on average 17–22 per cent of neophytes (Simonová and Lososová 2008). However, coniferous woodlands were highly invaded only in Britain, where most of them are plantations of exotic conifers, while native and even

planted coniferous woodlands in the other countries had very low proportions of alien species. In a study of the British countryside, Maskell *et al*. (2006) also investigated temporal trends in the representation of alien and native species and concluded that changes such as eutrophication, nitrogen deposition, and increased fertility in infertile habitats currently benefit native species more often than aliens.

The figures reported for archaeophytes are much higher, reaching 55.5 per cent, 35.5 per cent, and 21.8 per cent on arable land, ruderal vegetation, and trampled habitats in the Czech Republic, and 16.2 per cent on arable land in Britain. British habitats generally contain less archaeophytes than Czech habitats, which reflects the differences in the total pools of archaeophytes in the two countries (Sádlo *et al*. 2007; Chytrý *et al*. 2008b).

6.2.3 Importance of scale

When assessing the role of alien species in vegetation, the effect of scale must be taken into account (Chytrý *et al*. 2005; Stohlgren *et al*. 2006; Stohlgren 2007). The proportional representation of alien species has been traditionally assessed in larger areas, such as countries (Essl and Rabitsch 2002; Pyšek *et al*. 2002b), counties (Stohlgren *et al*. 2005), bioregions (Dark 2004), cities (Pyšek 1998), or grid squares of floristic mapping (Deutschewitz *et al*. 2003; Kühn *et al*. 2003; Pino *et al*. 2005), but much less so in vegetation plots ranging in size from units to hundreds of square meters. In general, the shift to a finer scale strongly affects the representation of alien species. For example, neophytes make up 26.8 per cent of the flora of the Czech Republic (Pyšek *et al*. 2002b) and 25.2 per cent of the flora of an average Central European city (Pyšek 1998), but only 2.3 per cent of the species found in an average vegetation plot (Chytrý *et al*. 2005). In the same vein, the 2 per cent of neophytes per vegetation plot recorded by Vilà *et al*. (2007) in Catalonia are much less than the mean of 6.9 per cent reported from 10 km grid cells sampled in the same region (Pino *et al*. 2005). The multi-scale plot design adopted by Stohlgren *et al*. (1999, 2006), who used four nested plot sizes of 1, 10, 100, and 1000 m^2, allows for a rigorous assessment of the effect of scale on the richness of alien species. For example, in the most invaded habitat, irrigated shortgrass prairie, the mean number of aliens per plot increased from 2.9, 5.2, 6.9, to 10.0 from the smallest to largest plots, and the pattern was consistent across habitats. In addition, not only numbers of alien species but also their proportions depend on the scale of observation (Stohlgren *et al*. 2006).

The above examples point to the importance of choosing an appropriate scale for studying the level of invasion in habitats. A test of commonly used rangeland quadrat sampling methods revealed that small quadrats failed to capture about half of the native and alien plant species occurring in several prairie and grassland habitats (Stohlgren *et al*. 1998). The plot size ranging from 10s to 400 m^2, common in phytosociological studies and used in the comparative assessment of European habitats (Chytrý *et al*. 2008b) and in the analysis of factors determining their level of invasion (Chytrý *et al*. 2008a), seems optimal for this purpose. Plots of this size capture a reasonably high proportion of species present in the habitat, and the scale allows for a fine assessment of the effects of environmental variables, because detailed information on environmental settings can be obtained in each sampling site—something that cannot be achieved at larger scales where average values for, for example, regions or states, embody a great variation among sites. To get an insight into factors determining habitat invasibility, it is necessary to obtain good information on habitat variables, because invasions of alien species are determined by a multitude of factors that are likely to co-vary with spatial and temporal scales such as climate, vegetation structure, micro- and macro-disturbances, resource availability, species pools and propagule pressure, and associated ecosystem processes (Stohlgren *et al*. 2006).

6.2.4 Native–alien relationship

Strongly associated with the issue of scale is the relationship between the numbers of native and alien plant species. Within a vegetation type, native species richness and cover may vary considerably (Stohlgren *et al*. 2006). With increasing spatial scale invasions of alien species and their coexistence with native plants are likely to increase (Stohlgren

et al. 1999, 2006; Knight and Reich 2005). At subcontinental scales there is convincing evidence of strong positive relationships between native and alien plant species richness (Stohlgren *et al*. 2003; Richardson and Pyšek 2006). These results complement regional landscape-scale observational studies (e.g. Stohlgren *et al*. 1999; Brown and Peet 2003; Keeley *et al*. 2003), but do not provide an understanding of the factors that determine the patterns of alien species diversity and the mechanism for the observed patterns across scales (Levine *et al*. 2003, 2004).

Generally, positive relationships between native and alien species richness strengthen at scales of more than 1 m^2, becoming more significant at scales of more than 100 m^2. This is consistent with null models of community invasibility, which show that the relationship between native and alien species richness tends to be negative at small spatial scales, but more positive at larger scales (Fridley *et al*. 2004; Herben *et al*. 2004). It has been proposed that similar factors to those associated with the increase in native species with area, such as habitat heterogeneity, extensions of environmental gradients, and increased probabilities of encountering disturbed habitats are also responsible for increasing establishment of alien species (Stohlgren *et al*. 1999, 2001, 2002, 2003). The positive relationship can be explained by the similarity of native and alien species in the abundance of propagules entering a community (Levine 2000) or by both groups of species occurring more frequently in resource-rich and moderately disturbed sites (Davis *et al*. 2000, Vilà *et al*. 2007). Stohlgren *et al*. (2006) suggested that in the invasion of any area greater than 1 m^2 native species outnumber newly arriving invaders, but their biotic resistance (Elton 1958; see Richardson and Pyšek 2006 for a review) becomes overwhelmed by biotic acceptance, where co-existence is a stronger force than competitive exclusion, resulting in the broad-scale establishment of many alien species. The Theory of Biotic Acceptance (Stohlgren *et al*. 2006) suggests that where environmental heterogeneity, environmental gradients, disturbance, and species turnover increase with spatial scale, natural ecosystems tend to accommodate alien species despite the presence and abundance of native species.

Recent European studies arrived at similar conclusions on the prevailing positive relationship between native and alien species richness at the scale of units to hundreds of square meters (Chytrý *et al*. 2005; Maskell *et al*. 2006). In addition, a similar positive relationship exists between archaeophytes and native species, and even more strongly between neophytes and archaeophytes. Neophytes are found commonly in habitats also occupied by archaeophytes, and archaeophytes can thus serve as predictors of the neophyte invasion risk (Chytrý *et al*. 2005, 2008b). However, the relationships between the numbers of neophytes and native species were mostly positive only if individual plots were compared separately within habitats; the correlations calculated with habitat mean values were non-significant (Chytrý *et al*. 2005). Vilà *et al*. (2007) found both high and low numbers of alien species at intermediate values of native species richness and low values at both extremes of native species richness.

6.3 Theoretical background of community invasibility

If we want to obtain a deeper insight into community (or habitat) invasibility, we face a major limitation. The majority of data reported in the literature are species numbers—how many alien species are present in a given habitat (ecosystem, region), or what is the proportion of aliens to all species. For this measure the term *level of invasion* was suggested (Hierro *et al*. 2005; Chytrý *et al*. 2005; Richardson and Pyšek 2006). However, the level of invasion cannot be used to infer whether or not, and to what extent certain habitat is prone to invasion. Therefore it is necessary to distinguish this measure from *invasibility*, that is, habitat susceptibility to invasion.

As pointed out by Williamson (1996), looking for real differences in invasibility requires looking at the residuals from the regression between invasion success and propagule pressure. From this it follows that successful invasion of a habitat requires dispersal, establishment, and survival, with the number of species determined by the balance between extinction and immigration

(Lonsdale 1999). The number of alien species existing in the habitat, A, is given by the product of the number of alien species introduced to the habitat, I, and their survival rate S, which differs in individual habitats based on their properties:

$$A = I \times S$$

The survival rate S, which is the measure of habitat invasibility, is determined by several components:

$$S = S_v \times S_h \times S_c \times S_m$$

These components represent losses, or constraints to invasion, due to competition with species already present in the habitat (in natural and semi-natural habitats majority of them are native), S_v, the effects of herbivores and pathogens, S_h, chance events, including extreme climatic events, S_c, and maladaptation, S_m. To invade, the species must survive the effect of all these factors; hence the overall survival rate is a product of all the factors listed above (Lonsdale 1999). To compare the invasibility of two habitats, we need to compare their S values rather than their A values. A habitat is more prone to invasions (i.e. more invasible) if the survival rate of alien species, introduced by means of propagule pressure, is higher than in another habitat with lower S.

6.4 Separating the level of invasion from invasibility

Lonsdale's model (1999) implies that a certain fraction of the variation in alien species richness among sites can be attributed to propagule pressure, defined as the rate of influx of alien propagules into the target site. To answer the question why some habitats are more invaded than others, one must separate the effects of habitat properties from those of propagule pressure and from other potentially confounding factors, such as climate (Chytrý *et al*. 2008a). Up to now, surprisingly little was known about the importance of habitat properties, relative to that of propagule pressure and other factors, mostly due to methodological reasons. Seed addition experiments, which suggest that increased propagule pressure strongly contributes to the level of invasion (e.g. Tilman 1997; Kennedy *et al*. 2002) are usually confined to a single habitat and single site, and do not explain differences between broader ranges of habitats. Observational studies have not provided significant insights either, as they are mostly restricted to a few habitats, a single or a few species, use limited numbers of replicates, or do not attempt to separate the effects of habitat properties from those of propagule pressure.

However, recent compilations of large databases of vegetation survey plots (e.g. Font and Ninot 1995; Hennekens and Schaminée 2001; Chytrý and Rafajová 2003; Firbank *et al*. 2003), which include thousands of records of species composition from all the major habitats of a country or a large region, provide an excellent opportunity to rigorously compare the levels of invasion between habitats. Continental Europe is a region with a strong phytosociological tradition—classification of vegetation into units is based on field data collated in a standard way. Over several decades phytosociologists collected huge amount of data which can now, profiting from the development in computing facilities, be used to study macroecological questions, if some limitations such as preferential sampling or varying plot size are taken into account (Chytrý 2001; Knollová *et al*. 2005; Roleček *et al*. 2007; Haveman and Janssen 2008).

6.4.1 Comparison of the levels of habitat invasions with their invasibility

Vegetation plots accumulated over the past 30 years of phytosociological vegetation surveys were used in a study of invasions in habitats of the Czech Republic (Chytrý *et al*. 2005, 2008a, b; see Fig. 6.1 for the outline of methods). Due to its geographical position and variety of habitats (Sádlo *et al*. 2007), the results can be considered as representative of a wider temperate region of Central Europe. Regression tree analysis (see Chytrý *et al*. 2008a for details) identified habitats with the highest and lowest levels of invasion in the Czech Republic. The lowest proportion of neophytes (on average 0.3 per cent) is found in natural and semi-natural habitats at altitudes above 465 m above sea level (a.s.l), while the highest proportion of neophytes (20.3 per cent) occurs in human-made

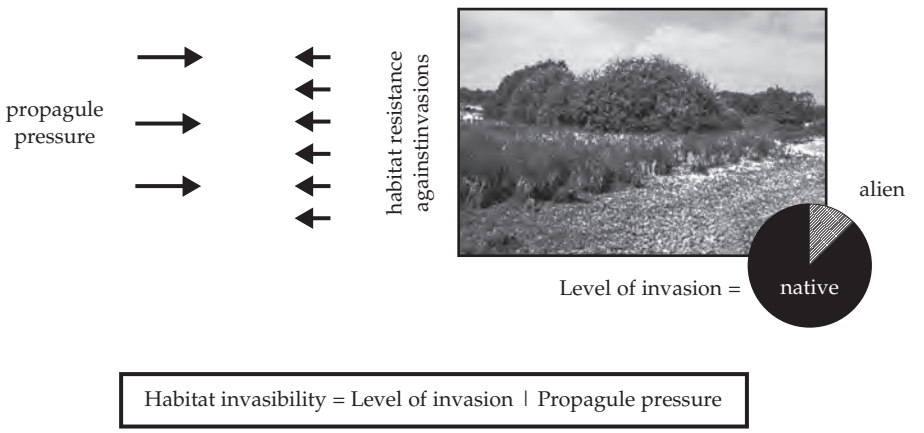

Figure 6.1 A conceptual model for studying the relationship between the level of invasion (an actual number or proportion of alien species present in a habitat) and the invasibility (inherent vulnerability of a habitat to invasion, when the effect of propagule pressure is held constant). To translate Londsdale's equation (see text) into the terminology used in this paper, the Level of Invasion (number or proportion of alien species we observe in a habitat) is a product of Propagule Pressure (number of species introduced there) and Habitat Invasibility (survival rate of invading species). The level of invasion was expressed as proportional numbers of aliens in 20,468 vegetation plots collected by phytosociologists on a regional scale of 78,000 km^2 (Czech Republic) in the last three decades, and stored in the national phytosociological database (Chytrý and Rafajová 2003). To study habitat invasibility, the effect of habitat (classified into 32 types using the standard classification of European habitats, EUNIS; Davies & Moss 2003, available at http://eunis.eea.europa.eu/habitats.jsp) on the level of invasion was tested, holding the effect of propagule pressure and climate, expressed by mean annual temperature and precipitation in the given site, constant. To account for the effect of propagule pressure, the following proxies were measured within 500 m circles around each plot: human population density; proportion of the area that is residential, industrial or agricultural; the distance of a site from the nearest river; and the altitudinal floristic region from the national classification, which reflects the history of human colonization. See Chytrý *et al*. (2008a) for details.

habitats, disturbed woodlands, or cliffs and walls at altitudes below 365 m a.s.l. that are surrounded by urban and industrial land and have open vegetation cover, less than 23 per cent (Chytrý *et al*. 2008a). Central European habitats can be divided into three groups based on the level of invasion, increasing from low levels in alpine and subalpine habitats, bogs and coniferous woodland, through intermediate in most grasslands and broad-leaved woodlands, to high in human-made habitats, including arable land, and deciduous plantations. In general, the pattern found for archaeophytes and neophytes is similar, although some habitats are more invaded by one group of aliens or the other (Table 6.1).

Then, between-habitat comparisons of invasibility were made using statistical models in which habitat was the predictor variable and the residuals from the regression of the level of invasion on the confounding variables (i.e. measures of propagule pressure and climate) were the response variables (see Chytrý *et al*. 2008a for details). Habitats were ranked by (i) the actual proportions of aliens in habitats, that is the level of invasion, and (ii) the residuals after subtracting the effect of confounding variables, that is invasibility. This comparison indicates that there is an overall correspondence between the two measures of invasion—the most invaded habitats are also highly invasible, but some habitats differ markedly if their levels of invasion and invasibility are compared (Fig. 6.2). This especially concerns some moderately invaded habitats whose invasibility is actually low (Table 6.1), but the resistance to invasion is overcome by a high propagule pressure. Consistent with the theoretical models (Alpert *et al*. 2000; Davis *et al*. 2000; Shea and Chesson 2002), the pattern we found can be interpreted in terms of disturbance regime and resource availability (Table 6.1):

(i) Most invasible habitats are strongly and/or frequently disturbed. In arable land, disturbance completely removes the above-ground biomass at least once a year. Vegetation of ruderal and trampled sites is also strongly and frequently

Table 6.1 Central European habitats grouped according to their level of invasion and invasibility and characteristics of disturbance regime and nutrient availability. Where the group (archaeophytes, neophytes) is not specified following the habitat name, the pattern holds for all alien plants. See Fig. 2 for quantitative comparison of the level of invasion and invasibility in individual habitats

Habitat	Disturbances	Nutrient availability
High level of invasion, very high invasibility		
Arable land	Frequent, strong	High, frequent and strong pulses due to external input
High level of invasion, high invasibility		
Annual ruderal vegetation	Frequent, strong	High, pulses due to external input
Trampled areas	Frequent, strong	High, pulses due to external input
Perennial ruderal vegetation	Frequent	High, pulses due to external input
Deciduous plantations (neophytes)	Strong at the initial establishment	High, pulses at the initial establishment
Intermediate level of invasion, intermediate invasibility		
Coniferous plantations (archaeophytes)	Strong at the initial establishment	Pulses at the initial establishment
Deciduous plantations (archaeophytes)	Strong at the initial establishment	High, pulses at the initial establishment
Disturbed woodlands	Strong	High, pulses after disturbance
Screes	Frequent	Low, occasional pulses
Riverine scrub	Common	High, frequent pulses
Running waters (neophytes)	Common	Medium, rare pulses
Sedge-reed beds	Occasional	High, occasional pulses
Standing waters (neophytes)	Occasional	High, occasional pulses
Moist tall-herb grasslands	Occasional	High, rare pulses
Temperate scrub	Occasional	Medium to high, rare pulses
Base-rich fens (neophytes)	Occasional	Low, occasional pulses
Cliffs and walls	Occasional	Low, occasional pulses
Wet grasslands (neophytes)	Infrequent, predictable	High, low pulses
Fen scrub	Rare	Low, rare pulses
Mixed woodlands (neophytes)	Rare	High, rare pulses
Intermediate level of invasion, low invasibility		
Saline marshes	Occasional	Medium, rare pulses
Dry grasslands	Occasional	Low, rare pulses
Woodland fringes	Occasional	Low, rare pulses
Mesic grasslands	Infrequent, predictable	High, occasional pulses
Wet grasslands (archaeophytes)	Infrequent, predictable	High, low pulses
Saline grasslands	Infrequent, predictable	Medium, rare pulses
Base-rich fens (archaeophytes)	Infrequent, predictable	Low, occasional pulses
Deciduous woodlands	Rare	High, rare pulses
Low to zero level of invasion, probably low invasibility		
Coniferous plantations (neophytes)	Strong at the initial establishment	Pulses at the initial establishment
Running waters (archaeophytes)	Common	Medium, rare pulses
Standing waters (archaeophytes)	Occasional	High, occasional pulses
Subalpine scrub	Occasional	High, occasional pulses
Subalpine tall forbs	Occasional	High, occasional pulses
Temperate heaths	Occasional	High, occasional pulses
Mixed woodlands (archaeophytes)	Rare	High, rare pulses
Alpine grasslands	Rare	Low, rare pulses
Bogs	Rare	Low, rare pulses
Coniferous woodlands	Rare	Low, rare pulses
Poor fens	Rare	Low, rare pulses

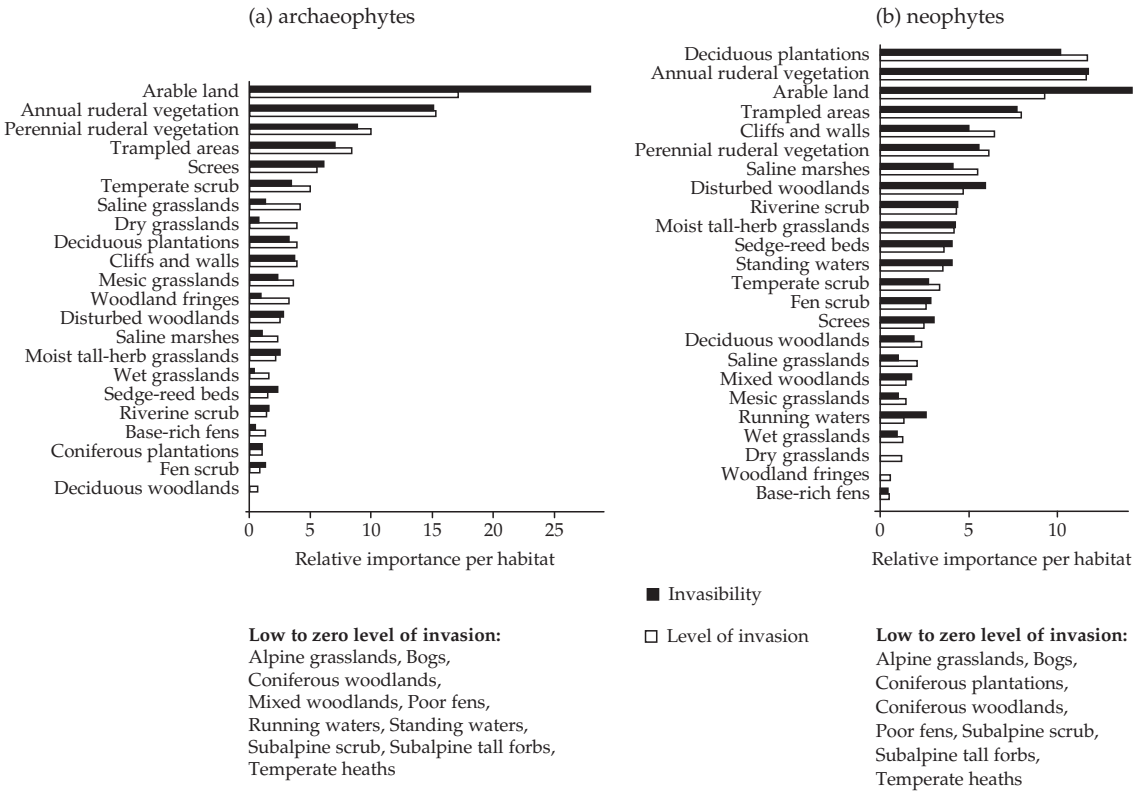

Figure 6.2 Comparison of the level of invasion and invasibility of Czech habitats by two groups of alien plants, archaeophytes and neophytes. The level of invasion is defined as the mean proportion of archaeophytes or neophytes to all species encountered in the vegetation survey plots belonging to particular habitats. Invasibility is defined as the same measure keeping propagule pressure and climate constant across the plots; it was quantified by using residuals of the linear model that subtracted the effects of propagule pressure and climate from the relation between the level of invasion and invasibility. To make both measures comparable, they were normalized to an equal sum across all the habitats (level of invasion after arcsin transformation, invasibility after converting residuals to positive numbers). Habitats are ranked according to the decreasing level of invasion, those with the lowest levels are not shown. Based on data reported in Chytrý *et al*. (2008a).

disturbed by human activities, and forest clearings are created by tree felling. Disturbance in these habitats is coupled with temporary increases in resource availability, e.g. fertilization of arable land, nutrient input into ruderal vegetation or increased light availability after opening the woodland canopy. Pulses of a high nutrient availability from external sources are typical of highly invasible habitats.

(ii) In contrast, least invasible are those habitats that are little disturbed. Most of the resistant habitats are perennial grasslands, which are also disturbed by grazing or mowing. However, such disturbances do not result in a significant temporary increase in nutrient availability, because vegetation is never disturbed completely and the resident plants respond to damage by rapid uptake of free nutrients to support their fast regrowth (Chytrý *et al*. 2008a). Many habitats of the low invasibility group do not experience any significant pulses of resource input from external sources, for example, alpine grasslands, mires, and oligotrophic grasslands and heathlands. However, nutrient input in these habitats (e.g. fertilizer application in an oligotrophic grassland) may cause a rapid shift towards other habitats (e.g. mesotrophic to eutrophic grassland) and such transitional habitats may indeed become highly invasible.

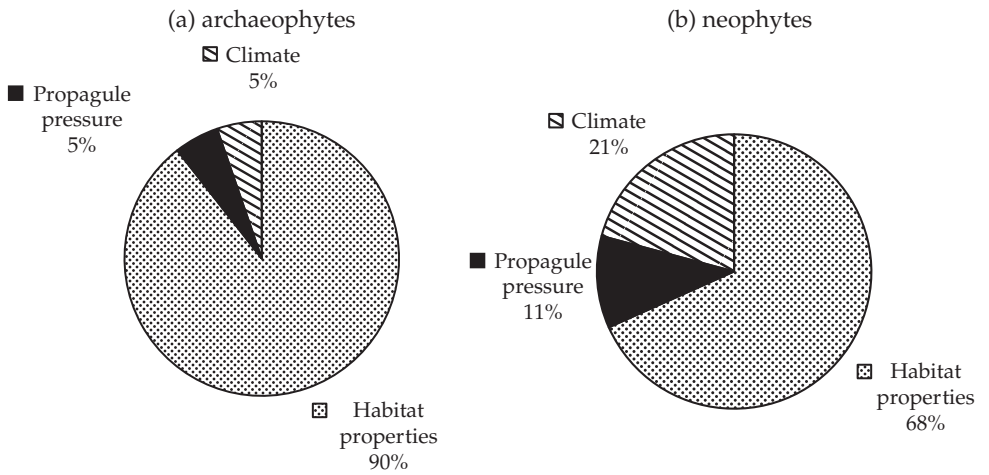

Figure 6.3 Proportional effect of the major determinants of the level of invasion by alien plants in habitats in the Czech Republic; the total proportion of variation explained by the models was 86.4% for archaeophytes (a) and 28.3% for neophytes (b); here it is recalculated to 100%. Predictor variables are in three groups, related to habitat properties, propagule pressure, and climate (see Fig. 6.1). Habitat properties also included the foliar cover of vegetation in the given habitat; this characteristic was included as an important component of community structure, with an assumed effect on community invasibility. Based on analyses presented in Chytrý *et al*. (2008a, their Table 2).

The results summarized in Table 6.1 support the notion that not all disturbances are necessarily conducive to invasions. In many habitats, invasions result from the alterations of the typical disturbance regime rather than from disturbances which are inherent to given habitat, for example, tree falls in forests or mowing in meadows (Hobbs and Huenneke 1992; Alpert *et al*. 2000). Patterns of invasibility observed across habitats are consistent with The Theory of Fluctuating Resource Availability (Davis *et al*. 2000). According to this theory, new species can invade a community if there are temporary pulses of unused resources. These pulses can be due to an increased supply of resources from external sources, a decreased uptake by resident vegetation, or both. Examples of the increased resource supply from external sources which increase community invasibility include fertilizer application in agricultural habitats, nutrient accumulation from atmospheric deposition, or nutrient input with flood sediments. Examples of the increased resource availability due to decreased uptake by resident vegetation are most frequently caused by disturbances, for example, herbiciding, floods, or tree felling.

6.4.2 Relative importance of factors determining the level of invasion

The analysis of the level of invasion in Central European habitats (Fig. 6.1; Chytrý *et al*. 2008a) quantified the effect of factors determining to what extent particular habitats are invaded. These factors act differently when archaeophytes and neophytes are examined separately. For archaeophytes, the joint effect of climate and propagule pressure is very low relative to that of habitats, and the total explained variation in their occurrence in the habitats is high. The occurrence of neophytes is less deterministic, with less variation explained, but habitat type is still the most important predictor. In spite of that, decrease in the level of invasion with increasing altitude and with decreasing proportion of urban and industrial land in the surroundings is notable. The proportional contribution of the joint effects of the three groups of predictor variables gives a different picture from that in archaeophytes. In neophytes, climate and propagule pressure are important in determining the level of invasion, accounting for about one third of the total variation explained (Fig. 6.3; Chytrý *et al*. 2008a).

As climate has been repeatedly shown to be one of the most important determinants of species composition or proportion of alien plants in Central European plant communities (Pyšek *et al*. 2002a, 2005; Lososová *et al*. 2004), this comparison of the relative effects of propagule pressure and climate suggests that the selected proxy variables provide a reasonable approximation to the actual propagule pressure, even though they certainly explain less variation in the proportion of aliens than would be the case if propagule immigration rate was directly measured. Interestingly, little variation is shared between habitats and climate (3.9% for archaeophytes and 3.4% for neophytes) even though different habitats occur in different climatic regions.

6.4.3 Habitat vs. propagule limitation and methodological pitfalls

Since invasions are human-mediated processes, the effect of propagule pressure on a broad geographical scale, for a variety of habitats and a large species pool of potential invaders, can be quantified through proxy variables that reflect the degree of human activity. Proxy variables representing the intensity of human activities are difficult to interpret as measures of propagule pressure in studies which focus on larger, internally heterogeneous sampling units, such as nature reserves (Macdonald *et al*. 1988; Lonsdale 1999; Pyšek *et al*. 2002a; McKinney 2004) or grid mapping cells (Deutschewitz *et al*. 2003; Kühn *et al*. 2003; Pino *et al*. 2005). Such studies usually report a positive correlation of those proxies with the number and/or proportion of alien species, but at that scale proxy variables may represent both increased propagule pressure and increased disturbance in more densely populated or urbanized areas. In our study, we controlled for disturbance effects by focusing on small, internally homogeneous plots, and on individual habitats, which themselves differ in disturbance regimes. In our models, most of the variation attributable to disturbance is therefore included in the effect of habitat. In addition, by including total vegetation cover as a predictor variable we were able to control for the variation in disturbance within individual habitats. We can therefore safely assume that the proxy variables used in this study measure the propagule pressure rather than the rate of disturbance.

The relatively low effect of propagule pressure detected here is in contrast with the results of Rouget and Richardson (2003), who reported higher importance of propagule pressure than of environmental variables for the distribution of three invasive tree species in South Africa. This difference points to the importance of the context in which invasibility is studied: while Rouget and Richardson (2003) studied recently established patterns of spread of individual populations, in which offspring usually tend to establish near to their parents, our study focused on multi-species alien assemblages which are outcomes of at least tens or hundreds years of invasion history.

6.5 Habitat-based mapping of plant invasions in Europe and prediction of future trends: the next step?

Data on the level of invasion in vegetation survey plots from Great Britain, Catalonia (NE Spain), and the Czech Republic, amassed during the European Union ALARM project (Settele *et al*. 2005), made it possible to sample a range of basic European climates, from Mediterranean to sub-continental and oceanic (Chytrý *et al*. 2008b). All three datasets consisted of several thousand vegetation plots from a range of different habitats, providing a robust assessment of the level of invasions in European habitats. The comparison of the three regions showed that (i) although there were large differences in the species composition of alien floras among the regions, patterns of habitat invasion were remarkably consistent. (ii) Extreme habitats with low nutrients were little invaded; frequently disturbed habitats with fluctuating resource availability were highly invaded. (iii) The most invaded habitats were arable land, coastal sediments, trampled areas, ruderal vegetation, sedge and reed beds, and cliffs and walls.

Inter-regional consistency of the habitat invasion patterns makes habitat a good predictor for invasion risk assessment. This assumption is supported by the result reported above (Chytrý *et al*. 2008a); for entire alien floras and the whole range of habitats across large regions, habitat properties are a much more important predictor of the level of invasion than climate or proxy measures of propagule pressure. Therefore the data from a comparative study of British, Catalonian and Czech habitats (Chytrý *et al*. 2008b) were used to produce a European map of invasions by alien plants, based on habitats (Chytrý *et al*., 2009). This was done by translating habitat types to CORINE land-cover classes (Moss and Wyatt 1994), which had been previously mapped across Europe from the interpretation of satellite images. The data from the three regions were extrapolated to other parts of Europe, using the framework of European biogeographical regions. The overall pattern indicates high levels of invasion in industrialized western Europe and in lowland agricultural regions in the east of the continent, and with montane zones, oceanic areas in the north-west, and the boreal zone relatively little affected (Chytrý *et al*., 2009).

Using habitats as mapping units is suitable because this approach takes into account landscape structure; habitat data allow the extrapolation of quantitative estimates of the level of invasion to other regions, based on climatic similarities—something that cannot be done with country-wise data. Finally, sampling by phytosociological method is intensive, which makes the regions studied well sampled; the results based on such data are robust. This allows reasonable precision to be achieved and provides a solid background for the assessment of risk from plant invasions, for monitoring and for modeling future changes under various scenarios of climate and land-use change.

6.6 Conclusions

1. Habitats differ considerably in their invasibility. The differences in the level of invasion between Central European habitats are mainly caused by inherent habitat properties, and to a lesser extent by propagule pressure and climatic differences between regions.
2. Patterns of habitat invasion are consistent across different regions of Europe. The same habitats usually have either high or low level of invasion despite their geographical location.
3. The most invasible habitats are those with fluctuating availability of resources, especially nutrients; most of these habitats are frequently and/or strongly disturbed.
4. The occurrence of archaeophytes is to a large extent deterministic; it mainly depends on habitat types, while propagule pressure is less important. The occurrence of neophytes is more stochastic; propagule pressure is more important than in archaeophytes, yet habitat type is still the most important predictor.
5. An approach using ecoinformatics and linking large sets of spatially explicit data from vegetation survey plots can produce robust information on macroecological patterns of plant invasions. Spatially explicit information on habitat invasions can be used to identify the areas of highest risk of invasion so as to support effective monitoring and management of alien plants; combined with scenarios of future land-use change, it may also be used for prediction of invasion risks in the future.

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