



The biogeography of naturalization in alien plants

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ABSTRACT

Aim This paper reviews the main geographical determinants of naturalization in plants.

Location Global.

Methods Comparative studies of large data sets of alien floras are the main source of information on global patterns of naturalization.

Results Temperate mainland regions are more invaded than tropical mainland regions but there seems to be no difference in invasibility of temperate and tropical islands. Islands are more invaded than the mainland. The number of naturalized species in temperate regions decreases with latitude and their geographical ranges increase with latitude. The number of naturalized species on islands increases with temperature. Naturalized species contribute to floristic homogenization, but the phenomenon is scale-dependent.

Main conclusions Some robust patterns are evident from currently available data, but further research is needed on several aspects to advance our understanding of the biogeography of naturalization of alien plants. For example, measures of propagule pressure are needed to determine the invasibility of communities/ecosystems/regions. The patterns discussed in this paper are derived largely from numbers and proportions of naturalized species, and little is known about the proportion of introduced species that become naturalized. Further insights on naturalization rates, i.e. the proportion of aliens that successfully naturalize within regions, and on geographical and other determinants of its variation would provide us with better understanding of the invasion process. Comparative studies, and resulting generalizations, are almost exclusively based on numbers of species, but alien species differ in their impact on native biodiversity and ecosystem processes.

Keywords

Alien plants, biological invasions, climatic factors, global patterns, invasibility, latitude, plant invasions, propagule pressure, temperate regions, tropics.

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SPECIES INVASIVENESS AND COMMUNITY INVASIBILITY: TWO SIDES OF THE SAME COIN

Invasion ecology, the study of the human-mediated transfer of organisms to areas outside their natural dispersal range and the consequences of such transfers, is a rapidly developing field of ecology. The starting point for the systematic study of invasions was Elton's (1958) book *The ecology of animal and plant invasions*. The modern foundation for invasion ecology

was established by the SCOPE programme in the 1980s (Drake *et al.*, 1989) and the last two decades have seen an explosion of research that has radically improved our understanding of invasions. Considerable effort is being devoted to practical aspects such as predictions of which species will invade (Křivánek & Pyšek, 2006 and references therein), and to designing appropriate management and control strategies for particular species (e.g. Wittenberg & Cock, 2001). Nevertheless, the two basic questions that have fascinated ecologists

since biological invasions emerged as a pressing global issue are still at the forefront of the research agenda. First, the question 'Which species will invade and under which conditions?' has stimulated the search for traits that separate successful from less successful invaders (the 'species invasiveness issue'; Rejmánek & Richardson, 1996; Williamson & Fitter, 1996; Keane & Crawley, 2002). Second, the question 'What features of ecosystems makes them prone to, or resistant to, invasions?' has spurred attempts to define the set of community characteristics and environmental situations under which invasion is realized (the 'community invasibility issue'; Lonsdale, 1999; Davis *et al.*, 2000). At the start of the modern era of invasion studies, the two issues were generally explored separately, but it is now widely recognized that these are two sides of the same coin (Richardson & Pyšek, 2006). Traits contributing to the success of taxa as invasive aliens are not universal and need to be related to the features of the invaded community, geographical conditions and a set of external factors, including propagule pressure (Higgins & Richardson, 1998; Davis *et al.*, 2000). Social and economic factors are crucial at the introduction stage, biogeographical and ecological factors are of eminent importance at the stage of naturalization (see also Mack, 2000), and ecological and evolutionary principles are crucial mediators of invasiveness (see also Perrings *et al.*, 2005).

There are limited opportunities for experimental studies of biological invasions when searching for large-scale biogeographical principles and macroecological patterns. This is not only for technical reasons, where the same constraints apply as for biogeography in general, but also because of ethical issues associated with introducing new, potentially invasive and damaging organisms. Invasion ecology therefore must rely on historical data and comparative studies of alien floras from different parts of the world; much of the field's theoretical foundation is based on such data. This approach has been crucially important for describing patterns and generating hypotheses for testing using other approaches (Lonsdale, 1999) and for historical analyses (Forcella, 1985; Kowarik, 1995; Pyšek *et al.*, 2003). Natural experiments are another very valuable source of information in invasion ecology (Brown & Sax, 2004). There are, however, numerous constraints, and only recently have attempts been made to evaluate the opportunities and limitations (e.g. Richardson *et al.*, 2004).

The value of large-scale analyses depends on the quality of available data, which are often collated with insufficient attention to details that are crucial when exploring alien floras (Pyšek *et al.*, 2004b). Good checklists of alien species and regional floras, atlases and data bases with detailed information on introduced plants are becoming more widely available (Essl & Rabitsch, 2002; Klotz *et al.*, 2002; Preston *et al.*, 2002; Pyšek *et al.*, 2002b) and it is encouraging to note that research approaches, including those dealing with the classification of alien species according to the stage of the invasion process they have reached, are starting to follow similar principles, designed with an effort to use biological criteria (Richardson *et al.*, 2000; Daehler, 2001; Pyšek *et al.*, 2004a).

The outcome of introductions to a given region is determined by several sets of features: (1) biological and ecological traits of the species, (2) dispersal possibilities and the availability of suitable vectors (Rejmánek *et al.*, 2005), (3) resistance or vulnerability of recipient habitats (Lonsdale, 1999; Davis *et al.*, 2000), (4) historical circumstances, including the effect of residence time (Rejmánek, 2000a; Castro *et al.*, 2005; Pyšek & Jarošík, 2005), and (5) geographical determinants such as the position of the target region, climate or latitudinal patterns (Rejmánek, 1996a; Chown *et al.*, 1998; Sax, 2001). Few studies have sought to determine the relative roles of each of these factors and the interactions between them in explaining invasion patterns (but see Thuiller *et al.*, 2006). In this paper our main interest is the last of the issues mentioned above, large-scale geographical patterns in plant invasions. One aspect that we do not address in this paper is the concentration of plant invasions in hotspots of native diversity. There is good evidence that the number of alien, naturalized and invasive plant species is positively correlated with native plant-species richness at the scale of landscapes or regions; see Sax & Gaines (2006) for a global review of the phenomenon and a range of possible explanations, and Richardson *et al.* (2005) for an assessment of patterns for South Africa.

THE NATURALIZATION–INVASION CONTINUUM CONCEPT

Various definitions of native and alien species have been suggested (e.g. Colautti & MacIsaac, 2004; Pyšek *et al.*, 2004a), but the crucial distinguishing factor between native and alien is whether the taxon in question is present in a region because of human activities. This criterion clearly excludes from the concept 'alien' those taxa that 'invade' a region via natural means, e.g. migration following disturbances such as glaciation (such movements are better termed migrations, range expansions or range extensions; Pyšek *et al.*, 2004a), and taxa that increase in abundance or distribution by colonizing newly available habitats within their natural regions (Rejmánek, 2000a; Pyšek *et al.*, 2004a). The dynamic processes that drive any change in the distribution/abundance of organisms are similar, but those involved in the spread of organisms transferred to new biogeographical realms should be distinguished from those driving changes in distribution/abundance of native species. To avoid confusion the latter should not be termed invasive.

Following this approach, native species are those that have originated in a given area without human involvement or that arrived there without intentional or unintentional intervention of humans from an area in which they are native. Alien (exotic, non-native, non-indigenous) plants, on the other hand, are taxa in a given area whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien (Pyšek *et al.*, 2004a; Richardson & Pyšek, 2004).

Human involvement is a crucial aspect in the conceptualization of the invasion process, which can be viewed as a

sequence of barriers that an alien species must overcome, e.g. the geographical barrier between the region of origin and that of introduction is generally overcome with the help of humans (see Richardson *et al.*, 2000 for a detailed classification of barriers). Another crucial facet in the conceptualization of invasions is the ability of an organism to reproduce in the new region without the assistance of humans (or despite human activities that work against establishment). Successful reproduction is a prerequisite for any invasion, and it is the overcoming of the reproductive barrier that separates casual alien species from those that naturalize and can become invasive (Richardson *et al.*, 2000). The capacity for reproduction is closely associated with habitat compatibility and, for a successful invasion, dispersal possibilities are a necessary prerequisite; those are the remaining key principles of the suggested scheme (Richardson *et al.*, 2000). Concerning habitat compatibility, recent studies have shown that for an alien species, demographic changes in the new region may be coupled with evolutionary changes. Natural selection can lead to evolution in a species niche, as opposed to niche conservatism. Species may often be ‘rescued’ by evolutionary processes if their preferred niche is not too different from the one they are introduced into (Holt *et al.*, 2005). Moreover, it has been demonstrated that evolutionary change in some alien invaders can be very rapid (Huey *et al.*, 2005).

Other schemes have been proposed for conceptualizing the various barriers that an introduced species must overcome, and the phases that it must go through to reach different levels of success in a new region (Heger & Trepl, 2003; Colautti &

MacIsaac, 2004). Such conceptualization, based on unequivocal criteria, is vitally important for focusing research effort in invasion ecology. Following the scheme proposed by Richardson *et al.* (2000) and elaborated by Pyšek *et al.* (2004a), it is sensible to classify alien plants according to their ‘invasion status’. Here we distinguish three categories:

1. *casual alien plants* are those that may flourish and even reproduce occasionally away from cultivation in an area, but that eventually die out because they do not form self-replacing populations. Persistence depends on repeated introductions;
2. *naturalized plants* sustain self-replacing populations without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets capable of independent growth;
3. *invasive plants* are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and thus have the potential to spread fast over a large area.

The advantage of the above framework of definitions is that it facilitates the labelling of taxa using reasonably objective criteria, according to their position along the ‘naturalization–invasion’ continuum (Richardson *et al.*, 2000 and their Fig. 1). The definitions rely solely on biological and ecological criteria, and no assessment of ‘impact’ is required. Clearly, many invasive species have substantial impacts in their new range. However, recent efforts to define ‘invasive’ by invoking some measure of impact (e.g. Davis & Thompson, 2000, 2001) appear unfortunate to us, especially if the ‘impact’ alluded to is economic (Rejmánek *et al.*, 2002). Introducing impact criteria

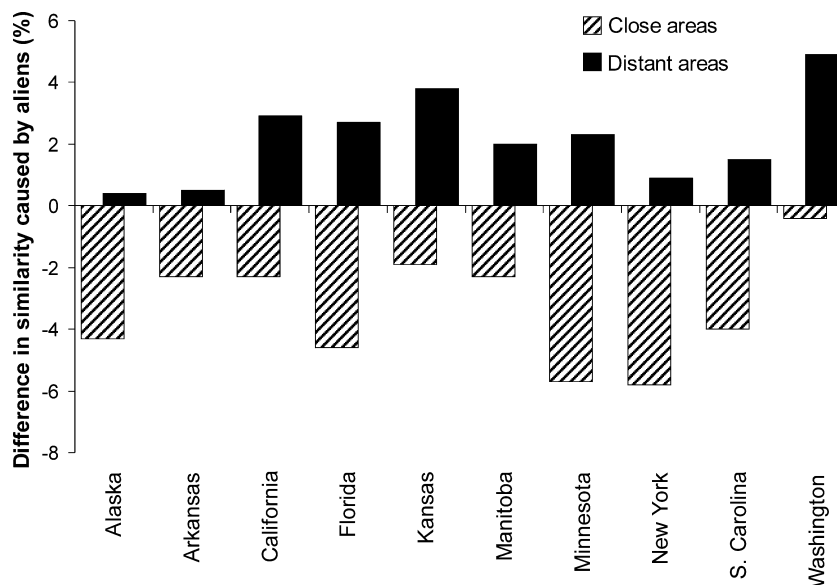


Figure 1 The effect of exotic taxa on floristic similarity of selected states in Canada and the USA, expressed by Jaccard’s index. The height of the bar reflects the difference between the indices computed with and without naturalized alien species. The zero line indicates that the similarity of the floras compared would be the same, regardless of whether the flora is based only on native species or on all species, including naturalized aliens. Positive values indicate that aliens have caused similarity to increase, whereas negative values indicate that aliens have caused similarity to decrease. These measures are shown for states that are adjacent to each other (hatched bars) and for those that are more than 1000 km distant from each other (black bars). Each bar represents the comparison of the given state (e.g. Alaska) with a randomly selected neighbouring (British Columbia) and distant (California) state. Pairs of states selected are based on data in Rejmánek (2000b).

which are based on human value systems or even political considerations (such as the US President's Executive Order No. 13112, <http://invasivespecies.gov/laws/exeorder.shtml>) clouds the key issues. We argue that the invasive status of a species in a given region should be based exclusively on measures of population growth and spread; definitions based on such features capture biogeographical/ecological processes that can be confirmed with simple measurements, leading to greater agreement among ecologists and better progress in understanding invasions as ecological phenomena (Daehler, 2001; Rejmánek *et al.*, 2002; Richardson & Pyšek, 2004). Furthermore, general acceptance of such a framework for definitions would also align the concepts of invasiveness and invasibility.

The issues mentioned above show that despite the recent increased interest in biological invasions among researchers, practitioners and the public (Simberloff, 2003), a seemingly simple question, 'What is an invasive species?' is clouded by much confusion (Richardson & Pyšek, 2004). Even when applying objective criteria, there is much uncertainty when deciding about status of individual species (Pyšek *et al.*, 2004b). Nevertheless, comparative studies would be greatly simplified if the same concepts were used worldwide; this would facilitate the adoption of a clear theoretical framework to which real data could be accurately related.

INHERENT COMMUNITY CHARACTERISTICS AND PROPAGULE PRESSURE DETERMINE COMMUNITY INVASIBILITY

Studies aimed at identifying patterns in plant invasions at the scale of regions by comparing different regions of the world traditionally rely on the *numbers* of alien/naturalized/invasive species recorded in regional floras. But these results need to be considered with more caution than is generally applied because variations in the level of invasion (reflected by the number of recorded species) could be simply due to differences in the number of aliens arriving in a given region (Williamson, 1996; Lonsdale, 1999). Whether a region is more invulnerable than another cannot be evaluated simply by looking at whether it has more alien/naturalized/invasive species, as this does not indicate its intrinsic susceptibility to invasions (Lonsdale, 1999; Chytrý *et al.*, 2005). The intrinsic invasibility can only be determined if processes of immigration and extinction are considered. Most introduced species fail to establish away from sites where they are nurtured by humans (Williamson & Fitter, 1996; Williamson, 1996; Mack, 2000; Richardson *et al.*, 2000), so the number of casual, naturalized and invasive species in a region is determined by the number of alien species introduced, their survival rate in the new environment (Lonsdale, 1999) and the time elapsed since introduction (Rejmánek, 2000a; Pyšek & Jarošík, 2005). Survival rate is affected by losses attributable to competition, herbivory, chance, pathogens and maladaptations associated with release of a species into an unsuitable environment (Lonsdale, 1999). *More invaded* (harbouring more naturalized/invasive species)

does not necessarily mean *more invulnerable* (offering alien species a higher chance of surviving, becoming established and spreading). Real differences in invasibility between regions can only be assessed by analysing residuals from the relationship between invasion success and propagule pressure (Williamson, 1996; Lonsdale, 1999).

At smaller spatial scales, and for individual species, it is clear that immigration rates are important for shaping alien biotas (Williamson, 1989; Lonsdale, 1999). Propagule pressure is a crucial ingredient for successful invasion (Crooks & Soulé, 1999; Richardson, 1999; Rejmánek, 2000a; Foxcroft *et al.*, 2004). Unfortunately, propagule pressure is extremely difficult to measure, especially at large spatial scales and for entire alien floras (Lonsdale, 1999). At the global scale, regions differ in propagule pressure depending on the intensity of human activities. At a very coarse scale there is clear evidence of the driving role of propagule pressure in invasions. Those societies currently experiencing the biggest problems with invasive alien species are those wealthy Western human societies that typify Dasmann's (1988) concept of 'biosphere people' – societies whose wealth, access to technology and cultural background have led them to rely on resources derived from every corner of the globe. Societies at the other end of the continuum, Dasmann's 'ecosystem people', have historically relied less on commodities and organisms drawn from distance biomes. There has thus been less propagule pressure, and these societies currently experience less severe problems with invasive alien taxa.

Studies that have used quantitative surrogates for propagule pressure, such as human population size or density (Pyšek *et al.*, 2002a; McKinney, 2004a; Taylor & Irwin, 2004), amount of trade and tourism (Thuiller *et al.*, 2005) or economic activity (Dalmazzone, 2000; Vila & Pujadas, 2001; Taylor & Irwin, 2004) show that these variables are reasonable proxies that reflect differences between regions, indicating an important effect of the propagule pressure on invasion patterns, allowing us to draw conclusions about the invasibility of regions and habitats (Lonsdale, 1999; Pyšek *et al.*, 2002a; McKinney, 2004b). However, as sophisticated and more exact measures of propagule pressure are seldom available, the results related to alien floras must be interpreted with this limitation in mind.

Species invasiveness (including their invasion history), inherent invasibility of a region (resulting from the invasibility of different plant communities) and propagule pressure (reflecting a wide array of human activities) are three major determinants of plant invasions, acting in concert to shape patterns of distribution and abundance of invasive plants in the world.

GLOBAL PATTERNS OF PLANT INVASIONS AND LARGE-SCALE GEOGRAPHICAL DETERMINANTS OF NATURALIZATION

Although global overviews of alien species distribution are constrained by a limited availability of good data from some areas (especially Asia and parts of South America), the

distribution of invasive alien plants across the globe is far from random. Despite the considerable idiosyncrasies inherent in biological invasions, fairly robust geographical patterns do exist. The recent research interest in invasions, together with the increasing availability of data, has facilitated several far-reaching analyses that have uncovered interesting patterns. These are summarized in Table 1 and illustrated below.

Temperate regions are more invaded than the tropics

Rejmánek (1996a) plotted the numbers of naturalized alien species in floras worldwide against the gradient of latitude and found that on mainlands of both hemispheres, tropical areas have accumulated fewer naturalized aliens than temperate areas (see also Lonsdale, 1999; Sax, 2001). The pattern was different on islands; those in the tropics are as invaded (having a similar number of alien species) as those in extratropical areas. Of possible explanations for the higher number of naturalized species in extratropical areas, such as differences in intensity and extent of disturbance, number of propagules and higher resistance in the tropics due to natural biotic and abiotic factors (Rejmánek, 1996a; Lonsdale, 1999), the latter seems to be most plausible. Some tropical areas are highly disturbed and large numbers of naturalized alien species on tropical islands show that diaspores do reach these regions. The high production of biomass of native species and rapid recovery of wet tropical vegetation after disturbances seems the most probable explanation of the lower level of invasions into tropical ecosystems than merely their high species diversity (Rejmánek, 1996a).

Islands are more invaded than mainland areas

The assumed high invasibility of islands is traditionally explained by their geographical and historical isolation and the various consequences of this isolation, namely the low diversity of resident biota resulting in interaction with and adaptation to only limited numbers of species through evolutionary time, and high levels of natural disturbances and human exploitation (Elton, 1958; Fox & Fox, 1986;

Rejmánek, 1996a; Sax & Brown, 2000). That islands tend to harbour more alien species than equivalent mainland sites suggests that they may be more invulnerable (due to the properties of resident species and/or due to high levels of disturbance), or that they simply have experienced higher propagule pressure (Lonsdale, 1999). The relatively low numbers of native plant species on islands, often suggested as one of the reasons for islands being easily invaded, was questioned by the results of Lonsdale (1999). In his data set of 104 globally distributed sites, the higher level of invasion on islands was not explained by low native species density.

The higher inherent invasibility of islands has not been proved using real data (Simberloff, 1997), simply because good information on propagule pressure for islands relative to mainland sites is lacking; its effect cannot therefore be statistically filtered out from analyses (Lonsdale, 1999). Available surveys do, however, suggest that islands not only have more invaded species than mainlands but that they are also more invulnerable (Loope & Mueller-Dombois, 1989; Bergstrom & Chown, 1999; Vila & Muñoz, 1999; Hulme, 2004). If island invaders indeed have greater invasion potential and native species on islands less resistance to disturbance (Lonsdale, 1999), differences in evolutionary history between these groups may be an important reason for the observed patterns. An inherent superiority of dominant mainland species from species-rich regions has been suggested as a clue for the high invasibility of islands and explanation for a seeming paradox that alien invaders displace native species that are well adapted to their environment (Sax & Brown, 2000). Such superiority may have been acquired through the evolutionary history of dominant mainland species, by them sampling more variation than biota on islands. This might have equipped such species to tolerate a wide range of abiotic conditions, use a broad spectrum of resources and resist a large number of potential enemies. This hypothesis has two important implications for invasions. First, the same attributes that allowed these species to dominate most habitats in their native range also allow them to dominate in invaded environments. Second, because they are abundant and widespread, dominant mainland species are

Table 1 Summary of some key generalizations in plant invasions related to geographical variables

Generalization	Scale	Source
Temperate mainland regions are more invaded than tropical mainland regions	Global	Rejmánek (1996a), Lonsdale (1999)
There is no difference in invasibility of temperate and tropical islands	Global	Rejmánek (1996a), Lonsdale (1999)
Islands are more invaded than the mainland	Global	Rejmánek (1996a), Lonsdale (1999)
Number of naturalized species in temperate regions decreases with latitude	Continental: Europe	Sax (2001)
Geographical ranges of naturalized species in temperate zone increase with latitude	Continental: Europe	Sax (2001)
Number of naturalized species on islands increases with temperature	Southern Ocean islands	Chown <i>et al.</i> (1998)
Naturalized species contribute to floristic homogenization	Continental: North America	Rejmánek (2000b), McKinney (2004c)
Clonal species increase their representation in alien floras with latitude	Global	Pyšek (1997)

Only results documented by statistical analyses of data are presented. Size of data sets: Lonsdale (1999) 184 regions; Rejmánek (1996a) 63 island and 52 mainland sites; Sax (2001) 3000 species; Rejmánek (2000b) 10 US states; Chown *et al.* (1998) 25 Southern Ocean islands; Pyšek (1997) 19 regional floras.

more likely to be dispersed than species that are rare and less widely distributed (Sax & Brown, 2000). As most invasions of islands have been by species from mainlands, the hypothesis seems plausible for explaining, at least partly, the apparent susceptibility of islands to invasions.

Latitudinal patterns in distribution of naturalized species

Besides the latitudinal patterns that can be explained by the distribution of climatic zones over the globe, namely that of tropical and extratropical areas (Rejmánek, 1996a), the number of naturalized species decreases with latitude, even within temperate zones (Sax, 2001; see also Sax & Gaines, 2006). This is not surprising as the latitudinal gradient of species diversity in many taxonomic groups is one of the most robust patterns in biogeography (see Sax, 2001 for references). Latitude affects not only the number of naturalized alien species but also their geographical ranges. In Europe, the geographical range sizes of naturalized species have been shown to correlate positively with latitude (Sax, 2001). This biogeographical pattern is known as Rapoport's rule. This pattern was originally suggested for mammalian subspecies by Rapoport (1982) and later shown to hold within temperate zones for various taxa of animals and plants, including trees (Stevens, 1989; Stevens & Enquist, 1998; Gaston, 2003).

Latitude affects not only the degree to which regions are invaded and the character of geographical ranges of naturalized aliens but also their species traits. Depending on the environmental conditions in the target area, that change with latitude, the importance of some traits favourable for invasion follows a clear trend along the gradient of latitude. For example, the proportion of species with ability to propagate clonally among all aliens within a flora increases with latitude in both hemispheres (Pyšek, 1997). The same pattern, i.e. a higher proportion of clonal species in northern latitudes, is known for native species (van Groenendael & de Kroon, 1990), but the obvious trend in the proportional representation indicates that constraints imposed by latitudinal gradients act more severely upon aliens.

Do naturalized species contribute to floristic homogenization?

Plant invasions affect the species diversity of invaded regions in two ways. Initially, introductions (by definition) increase diversity at small spatial and temporal scales. Interactions with resident organisms over longer time-scales often dampen the increased diversity by causing local extinctions. The net effect on species diversity therefore depends on the spatial and temporal scale under consideration, and on the balance between naturalization and extinction (Sax *et al.*, 2002; Sax & Gaines, 2003). At local scales, the evidence is mixed and the species diversity, despite the extinction of some native species, tends to increase with invasions of alien species (Davis, 2003). At the regional scale, no general decreases in diversity are

known to have occurred (Sax & Gaines, 2003) and empirical evidence suggests that net plant species diversity has increased due to introductions, both on oceanic islands and within regions on continents, in the past few centuries (Sax *et al.*, 2002). Nevertheless, at the global scale, biological invasions are reducing species diversity because rates of species extinction exceed those of speciation (Sax & Gaines, 2003).

Associated with changes in species diversity is the issue of biotic homogenization, i.e. the gradual replacement of distinct native biotas by locally expanding non-natives (Olden *et al.*, 2004); those declining as a result of human activities are being replaced by a much smaller number of expanding species promoted by global transport and thriving in human-altered environments (McKinney & Lockwood, 1999; Lockwood & McKinney, 2001; Olden & Le Roy Poff, 2003). At the regional scale (up to 2500 km distance), it has been documented that alien species in local areas in the USA tend to homogenize plant communities because they are more commonly shared among them (McKinney, 2004c). Moreover, introductions from nearby sources are more frequent and species introduced from less distant sources have a greater homogenization effect than species introduced from a larger distance, as McKinney (2005) documented for three different scales by comparing the homogenization effect of introductions within the USA with those from outside the USA.

On the other hand, the comparison of complete floras of selected states in Canada and the USA (Rejmánek, 2000b) showed that the presence of naturalized aliens decreased the floristic similarity of neighbouring states, thus acting against homogenization of their floras, but distant states have consistently more similar floras (Fig. 1). Although the results for the comparison of neighbouring states do not accord with those of McKinney (2004c), and indicate that a different approach can lead to contradicting conclusions, at the geographical scale of the continent naturalized alien species contribute to the homogenization of regional floras (Rejmánek, 2000b). This corresponds to the fact that in the past centuries plant species richness in US states has increased by an average of c. 20% (Sax & Gaines, 2003). Since successful naturalized species have rather wide geographical ranges (Rejmánek, 1996b), it follows that homogenization results from these species being more commonly shared between distant states than is the case for native species.

The fact that alien species do not always homogenize communities, and in some cases they rather tend to increase floristic dissimilarity, seems to be related to sampling and the extent to which the compared regions are invaded. As shown by McKinney (2004d), when compared floras have relatively few aliens, there is a tendency for aliens to produce differentiation whereas homogenization is predicted when the naturalized/native species ratio is high.

PRIORITIES FOR FUTURE RESEARCH

The present overview indicates that rigorously analysed plant geographical data sets are still rather scarce but some robust

generalizations do emerge (Table 1). We believe that the following issues deserve attention in future research on biogeography of biological invasions.

1. Our review focused on plants, but several recently published studies suggest that the basic biogeographical principles outlined here apply across a wide range of taxa, including plants and various groups of animals (Chown *et al.*, 1998; Sax, 2001; Sax *et al.*, 2002; Sax & Gaines, 2003). The absence of common definitions of naturalization and invasion for all taxa is hampering further generalization and the identification of important contrasts between taxa.

2. Estimates and measures of propagule pressure are needed to define the invasibility of communities/ecosystems/regions. Numbers of recorded aliens do not allow for robust comparisons of invasibility. However, given the complexity of modes of introduction pathways into different regions and the variety of factors that determine whether a propagule reaches a certain community/habitat, it seems that at biogeographical and global scales surrogates related to various aspects of human activities, as mentioned above, are the only possibility for studying this issue.

3. The patterns discussed in this paper were derived from numbers and proportions of *naturalized* species and little is known about the rates at which introduced species become naturalized. To study this, information on the total number of aliens, including *casuals*, is needed. These two groups of species can provide different results, as illustrated by Fig. 2. If the number of naturalized species in floras is plotted against latitude, there is a trend for high numbers of naturalized aliens to occur in middle latitudes (Fig. 2a; see also Rejmánek, 1996a). However, the naturalization rate, expressed as the percentage of naturalized species among all aliens including casuals, decreases with latitude, which explains 38% of variation in the same data set (Fig. 2b). Further research on naturalization rates, i.e. the proportion of all aliens that successfully naturalize, for different taxa and on variation in rates between taxa and regions, would provide us with better understanding of the invasion process, species invasiveness and community/region invasibility.

4. Besides the lack of data from some regions, there is another limitation to obtaining a more precise picture of invasions on a global scale. Comparative studies, and resulting generalizations, are almost exclusively based on numbers of species. However, alien species differ considerably in their impacts on native biodiversity (Manchester & Bullock, 2000), ecosystem processes (Vitousek & Walker, 1989; Brooks *et al.*, 2004) and also human well-being. Invasions result in substantial costs to regional (Zavaleta, 2000) and global economics (Pimentel, 2002). A region invaded by a single species with heavy impact can incur huge costs even if the overall diversity of the invasive flora in the region is low, and vice versa, areas harbouring numerous invaders need not be markedly transformed by alien plants if the invaders have only a limited impact. On the other hand, because of a sampling effect, the more aliens invade a region the higher is the probability that some will become serious invaders or transformers (*sensu* Richardson *et al.*, 2000). Consequently, patterns revealed by analysing species

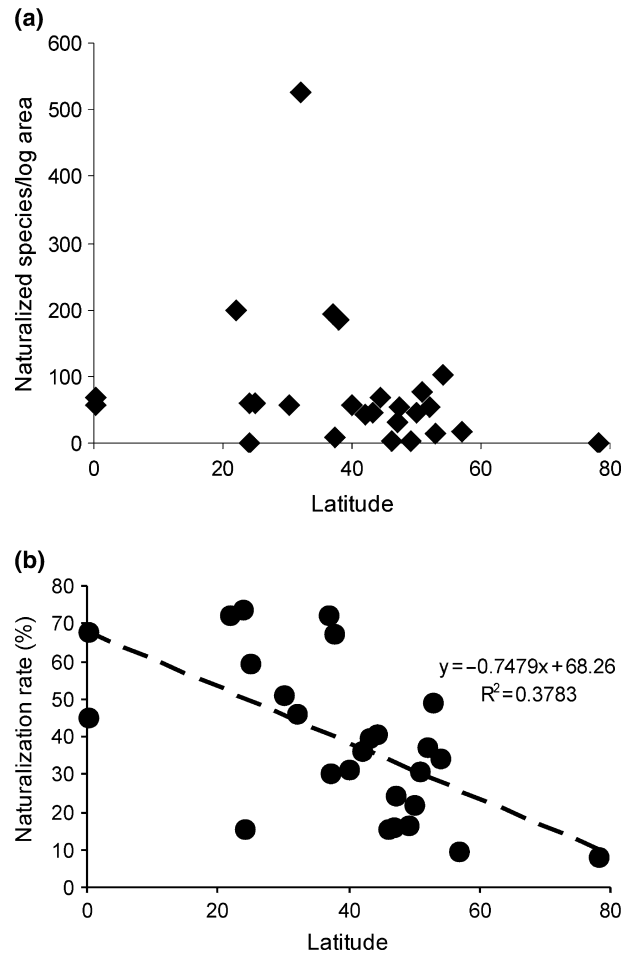


Figure 2 Latitudinal patterns in the number of naturalized species (top panel) and in naturalization rate (bottom panel) are shown for 27 floras (Amsterdam Island, Austria, Azores, California, Carnac Island, Corsica, Czech Republic, Flanders – Belgium, Galapagos, Great Britain, Hawaiian Islands, Henderson Island, Hungary, Kerguelen Island, Kermadec Island, La Possession Island, Nauru Island, Pitcairn Island, Poland, Queen Charlotte Islands, Sardinia, Scotland, Svalbard, Taiwan, Var Island and Wisconsin; P. Pyšek *et al.*, unpublished data). These floras were selected because data were available for each that distinguished (or allowed the authors of this work to distinguish) between alien species that are naturalized and those that are only casuals; where the original conception of categories of alien species status differed from those in Richardson *et al.* (2000), species lists were re-evaluated according to the criteria outlined in this paper. Naturalization rate is expressed as the percentage of naturalized species among all aliens (including casuals). Note the strong contrast between the numbers versus rate of naturalized species. Although the trend is not particularly strong, the greatest numbers of naturalized species are found at middle latitudes, which is consistent with patterns found by Rejmánek (1996a). In contrast, the naturalization rate of alien species clearly decreases with latitude.

numbers are probably relevant for gaining a broad-scale view of the overall impact of invasions in different regions, but little work has been done in this area.

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BIOSKETCHES

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