

11 From Ecosystem Invasibility to Local, Regional and Global Patterns of Invasive Species

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11.1 Introduction

Distribution patterns of species are a consequence of long evolutionary histories. Biogeographical barriers have resulted in separate developments of biota with specific adaptations to their native ecosystems and associated environmental conditions. Especially during the past centuries, human activity has helped species to surmount these natural barriers, so that present-day patterns of alien species result from natural drivers as well as man's history of land exploitation and construction of traffic routes. Humans created new pathways of species introductions (Chaps. 2 and 3), and also new habitats. Introduced species were thus able to invade both (semi-)natural and human-made habitats, which differ considerably in their proportion of alien species (e.g. Chytrý et al. 2005).

With the arrival of aliens in a novel environment, interactions between resident species are disrupted, and interactions among resident and invading species have to be newly established. Though unplanned and mostly unwanted, biological invasions are considered to be an important ecological experiment, well suited for ecological studies. Because many aspects are better known in alien species than in native ones (e.g. time of isolation from the original gene pool, and we have replications by introductions into multiple localities), species invasions provide a unique opportunity to test general ecological theories as an alternative approach to focused experimental manipulations which might be more constrained by time, space, research budgets, etc. (Rice and Sax 2005).

Here, we employ this approach by using habitat availability, and the fact that habitats differ in their proportion of alien species across a multitude of ecosystems and spatial scales to investigate the question of spatial patterns of alien species distribution, and the consequences of invasions for communities and ecosystems. Many of these ideas were outlined initially by Elton (1958),

who provided a set of key observations and hypotheses in this field of research. In this chapter, we will discuss the invasibility of ecosystems as well as local, regional and global patterns of alien species occurrence as a tool to understand two different niche theories and general biogeographical patterns. In this context, alien species are here defined as exotic (non-native) species which have been intentionally or unintentionally introduced into an area after the discovery of the Americas by Columbus.

11.2 Background

In his famous book ‘The ecology of invasions by animals and plants’, Elton (1958) laid the foundation for modern invasion biology. He describes why relatively simple communities are “more easily upset than richer ones; that is, more subject to destructive oscillations in populations, especially of animals, and more vulnerable to invasions” (Elton 1958: 145). The idea that species-rich communities are more resistant to invasions than are species-poor communities has challenged generations of ecologists.

Particularly important for invasion biology is the question whether ecological communities are saturated or unsaturated, and whether the more invaded ones are less saturated. This aspect is directly coupled with that of the ecological niche. The concept of the ‘ecological niche’ is considered to be among the most important in ecology (Cherrett 1989). However, there are essentially at least two different niche concepts, based on the ideas of Grinnell (1928), on the one hand, and Hutchinson (1957) on the other. Grinnell (1928) used the term ‘niche’ to characterise species-specific requirements. Besides habitat, these can be nutrients, mating places or other resources and requisites associated with a species’ occurrence (Brandl et al. 2001). Grinnell (1928) defines a niche as an ...”ultimate distributional unit, within which each species is held by its structural and instinctive limitations, these being subject only to exceedingly slow modification down through time”. According to this concept, the niche has an autecological character – any community to which a species belongs is of less importance. However, even Grinnell had pondered on whether all niches are necessarily occupied within a community (Grinnell and Swarth 1913). Grinnell’s theory was mainly used to describe and to understand changes in species distributions in relation to environmental variability. Jäger (1988) directly applied Grinnell’s idea to invasion problems. He characterised the introduced range of a species by the properties of its native range. This idea also forms a basis for species distribution modelling using climate envelopes.

Hutchinson (1957) introduced a new concept to niche theory. He stated that basic autecological (environmental) factors are not the only ones determining niche dimensions. The role of a species in its community is an impor-

tant additional factor influencing the presence or absence of a species at a given site. The difference between the Grinnell and the Hutchinson approach can be viewed as that between an address (Grinnell) and a profession (Hutchinson). Hutchinson (1957) described the niche as an n -dimensional hyper-volume characterised by several niche dimensions such as nutrients and other resources. The fitness of a species may vary along these niche axes, which may lead to a reduction in available niche space. He thus distinguished between the fundamental niche and the realised niche. The former covers all potential resources and requisites, the latter only the resources and requisites available to a species within a given community.

The main differences between these two concepts are

1. Grinnell highlights the distributional range (geography) of a species to characterise the niche (regional concept). Hutchinson stresses the use of resources within a given community (local concept).
2. Following Hutchinson, the niche of a species depends on other species in a community. Grinnell's concept emphasises the fundamental niche, Hutchinson's the realised niche.
3. Hutchinson defined the niche in terms of species characteristics and community structure. By definition, there exists no vacant niche within a community.

One conceptual problem with Hutchinson's niche concept is the idea that 'vacant niches' do not occur. Indeed, it is obvious that, in some systems, there may be possibilities for species to exist which, due to evolutionary constraints, are simply not made use of. A prominent example are large herbivores represented in African savannahs by ungulates, in Australian grasslands by marsupials but which were absent on the pre-Columbian South American pampas.

In addition, both these classical concepts consider species as static entities, and assume that communities are saturated and therefore in equilibrium (i.e. species gains are compensated by losses). However, these assumptions are both usually not met. Species evolve continuously, and microevolution can occur over short time periods. Furthermore, an ecosystem is rarely in equilibrium, and this for several reasons: for example, systems in temperate regions may not have reached their full set of species after the last glaciation (i.e. they are unsaturated), the climate changes continuously, systems are disturbed more or less frequently by natural or human processes, and propagule pressure ensures a steady influx of new species.

Nevertheless, these two niche concepts facilitate a wider understanding of scale-dependent processes in biological invasions, as their underlying processes work at different scales. Grinnell's concept is more regional and describes a species' potential impact whereas Hutchinson's concept is more local and describes a species' existing requirements within a community.

11.3 Case Studies on Ecosystem Invasibility

There are several case studies shedding light on the patterns and processes of biological invasions. Ecosystems can be invaded if there is a 'vacant niche', i.e. resources which are not utilised. A good example for this is the Central European aquatic mammal community (Brandl et al. 2001): the water vole (*Arvicola terrestris*) and European beaver (*Castor fiber*) are native herbivores of these inland waters, where humans successfully introduced the North American muskrat (*Ondatra zibethica*) and South American coypu (*Myocastor coypus*). Why was this possible – was there a 'vacant niche'? It has been suggested that, in vertebrates, resource use correlates with body mass (Brown 1975). The difference in resource use between the beaver (over 20 kg body mass) and water vole (ca. 0.1 kg) is substantial: a beaver feeds on trees, a water vole on grass. Between these two extremes are some resources which are evidently unutilised and thus available for the muskrat (ca. 1 kg body mass) and coypu (ca. 7–8 kg). This shows that increasing species numbers can lead to more complete resource use. Therefore, more species would mean less 'vacancies'.

This example shows why we may expect a negative relationship between species richness and invasion resistance, but leaves room for other explanations as well. Indeed, it is useful to review some more patterns which (1) derive from a larger sample size, (2) are robust to statistical testing and (3) encompass different groups of organisms and different spatial scales. Gido (in Brown and Lomolino 1998) found a significant negative correlation between native and introduced fish species in North American rivers. A similar observation was made by Case and Bolger (1991) for reptiles on islands. They reported that, on islands with only few native reptile species, there were more invasive reptile species than on islands with many native reptile species. However, in both these fish and reptile datasets, native–invasive relationships were not linear, species-poor communities showing a higher variability in the number of invading species. This means that alien species which can potentially invade do not necessarily do so. An analysis of macrozoobenthos of German waterways again showed a significant negative correlation between native and alien species numbers (reported by Brandl et al. 2001) but the proportion of alien species decreased with increasing number of native species (see also Chap. 15). By contrast, Welter-Schultes and Williams (1999) found no significant relationship between species richness of native and alien species for molluscs of the Aegean islands. For plant species, most of the published studies report that species-rich habitats were also more strongly invaded, i.e. the rich became richer (Stohlgren et al. 2003). As an example, Stadler et al. (2000) analysed native and alien tree species richness in Kenya, reporting a positive correlation between native and alien tree species numbers. In a more complex approach, Chytrý et al. (2005) investigated over 20,000 vegetation plots, ranging in size from 1–100 m² in 32 habitats of the Czech Republic. They

found no significant relationship between native and alien plant species numbers when analysing across all habitats but, within habitat types, mostly positive relationships were recorded.

Using both an observational and an experimental approach, Levine (2000) found two different patterns in native–alien relationships in his analysis of riverine Californian plant communities. He investigated tussocks of the sedge *Carex nudata*, which can host more than 60 native and three alien plant species (*Agrostis stolonifera*, *Plantago major*, *Cirsium arvense*). As a first approach, he counted the proportion of native tussocks in which the alien species occurred (i.e. invader incidence), finding a significant positive relationship with plant species richness (excluding the invaders). In a second approach, he manipulated the tussocks; specifically, he removed all species from randomly selected tussocks and assigned these to one of five species richness treatments. Then, he added 200 seeds of each alien plant species to the surface of the experimental tussocks. Here, with increasing native species richness, the number of alien seeds which germinated and survived two growing seasons decreased. Thus, in a controlled experiment but in a natural setting, Levine (2000) was able to separate effects of species richness from covarying effects of natural heterogeneity.

The examples above do not show a clear pattern. It therefore is necessary to have a closer look at the different factors driving the invasibility of habitats and ecosystems. This can help to understand which processes are relevant for invasibility, and to decide which niche concepts are best able to explain small-to large-scale invasion patterns.

11.4 Scale Dependence of Invasibility and the Importance of Environmental Factors

On a local scale, the main factors identified to date in explaining habitat invasibility are evolutionary history, disturbance, propagule pressure, abiotic stress, and community structure (Alpert et al. 2000).

Local patterns of invasibility differ strongly around the globe. For example, Europe is less affected by biological invasions whereas regions of North America, Australia and especially oceanic islands can be heavily affected. This can be explained by different evolutionary histories. It is argued that species and habitats which have shared a long co-evolutionary history with human land uses (such as agriculture) are better (pre-)adapted to biological invasion. Thus, these species had already been selected for their tolerance to disturbance. Therefore, regions such as the Mediterranean, with a long history in agriculture, may be less prone to biological invasions than others (di Castri 1990). By contrast, natural grasslands such as the North American prairies evolved under a regime of only little disturbance by native grazers and, there-

fore, under today's strong grazing pressure, are particularly susceptible to invasions (Mack and D'Antonio 1998). Likewise, islands which have been most strongly affected by invasions were often least disturbed before human colonisation. Island biota are evolutionary distinct from mainland biota, and have evolved very specific community structures and species traits. For one, oceanic islands are considered to host habitats showing relaxed selection for competitive ability (Loope and Mueller-Dombois 1989). In the presence of invading species, specific interactions are therefore more heavily affected in island biota than in mainland biota, which makes islands much more susceptible to invasions than mainland areas.

In numerous studies, disturbance is considered to be a key factor in biological invasions, but one which can act in several ways: disturbance can remove native competitors, facilitate a flush of surplus resources (Davis et al. 2000), such as light or nutrients, or can create completely new habitats. In many cases, therefore, increasing disturbance promotes invasibility. However, invasions can occur also without disturbance, and there are cases when suppressing disturbance can even increase invasions. Thus, it can be hypothesised that it is not necessarily disturbance per se which increases invasibility but rather the deviation from a typical disturbance regime (Alpert et al. 2000).

Lonsdale (1999) argues that invasion patterns are a function not only of habitat invasibility – as an idiosyncratic characteristic – but also of different propagule pressures (see also Williamson 1996). Therefore, the number of exotic species would be a function of the frequency and magnitude of intentional and unintentional introduction events, and of the ability of these species to successfully reproduce. The importance of propagule pressure for invasion patterns has been invoked in several analyses (e.g. Pyšek et al. 2003; Thuiller et al. 2005). Locally, propagule pressure can explain exotic species cover better than can environmental factors (Rouget and Richardson 2003). For birds, it is known that invasion success is higher when more species have been introduced into a target region (Duncan et al. 2003).

As another factor, environmental stress is hypothesised to be important for ecosystem invasibility. Stress can be caused by specific factors which are limiting for plant growth, such as the availability of nutrients, water and light, by the presence of toxins (incl. saline soils) or by other extreme conditions. The majority of studies found that ecosystem invasibility decreases with increasing stress or that invasion increases when limiting resources, such as nutrients, are provided (Alpert et al. 2000). Therefore, adding nutrients such as nitrogen or phosphorus can raise invasibility and promote a smaller number of faster-growing species. Depending on interactions with other factors, a complete shift of community structure was observed in several directions (Alpert et al. 2000 and references therein). For one, there is evidence of some interaction between stress and disturbance. When stress is low (i.e. resource availability is high), only little change in a typical distur-

bance regime is needed to facilitate invasions whereas when stress is high, a high deviation from the typical disturbance regime is needed (Alpert et al. 2000).

In terms of specific community structure, ecosystem invasibility involves several processes. Still, the basic concept behind this idea is that of the niche. The realised niche of a species may be altered by specific members of a community within the potential given by the fundamental niche. One classical example is Ellenberg's (1953) experiment, where he showed that several grass species (amongst others, *Bromus erectus*, *Arrhenatherum elatius* and *Alopecurus pratensis*) had the same optimal growth along a water gradient in single-species plots but displayed a considerable shift in multi-species plots (e.g. *Bromus erectus* towards dryer sites and *Alopecurus pratensis* towards moister sites). Also, different members of a community can have very strong interactions which may either inhibit invasions (e.g. due to the depletion of resources) or facilitate these (e.g. nitrogen-fixing acacias, Holmes and Cowlings 1997; see also Chap. 10).

Besides effects on resources, community structure can also determine the availability of natural enemies, thus creating a 'natural enemy escape opportunity' (Shea and Chesson 2002). This is explicitly explained by two important hypotheses – the enemy release hypothesis (ERH; Keane and Crawley 2002), and the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995). The former states that plant species in their introduced range should experience a decrease in regulation by herbivores and other natural enemies when their specific enemies are absent. This would result in higher abundances and, thus, wider distributions of alien species in their introduced range. The latter hypothesis states that introduced species do not need to invest resources in the defence against enemies. They can therefore invest these resources in the evolution of increased competitive ability (Blossey and Nötzold 1995). There are examples both corroborating and rejecting these hypotheses (Chap. 6).

Important – though long overlooked – interactions exist between soil micro-organisms and macro-organisms. These seem to play an important role in the invasibility of ecosystems. Callaway and Aschehoug (2000) found that *Centaurea diffusa*, a noxious alien weed in North America, had much stronger negative effects on grass species from North America than on closely related grass species from communities to which *Centaurea* is native. On sterile soils, these differences disappeared. They argue that *Centaurea*'s advantage against North American species appears to be due to differences in the effects of its root exudates, indicating that micro-organisms are responsible for the invasion success of the species in its introduced range. More recently, Klironomos (2002) was able to show several interactions between soil micro-organisms and plant species. Rare native plant species cultivated in their own soils were smaller than those cultivated in soils of other species. Invasive species, on the other hand, grew better (cf. relative increase in growth) in their

home soils than in soils of other species. Klironomos also found that rare native plant species accumulated species-specific pathogens quickly in their own soils and, therefore, maintained low densities. By contrast, invasive species benefited from interactions with mycorrhizal fungi.

The examples above show that biodiversity plays a major role in community structure and community susceptibility to biological invasions. Indeed, following the ideas of Elton (1958), biological diversity is considered to be a key element of invasion resistance. In a recent review, Levine et al. (2002) showed that in most experimentally assembled systems, species diversity enhances invasion resistance whereas those studies examining natural invasion patterns more often reported positive correlations between natural species diversity and invasion, rather than negative ones. This apparent contradiction has been widely discussed in the literature, and has spawned some idiosyncratic views of invasion processes and invaded systems. Nevertheless, this contradiction can be resolved within a general conceptual framework by distinguishing between local factors affecting biodiversity and those factors associated with diversity patterns across communities, i.e. on a larger scale (Shea and Chesson 2002; Levine et al. 2002). In the model of Shea and Chesson (2002), negative relationships between alien and native species numbers can be observed in each case for groups of locations where a given group shows little variation in environmental factors. When these data are combined across several groups together spanning highly variable environmental factors, the result is a large-scale positive relationship (Fig. 11.1). Levine et al. (2002) consider that small-scale diversity as such causes resistance against

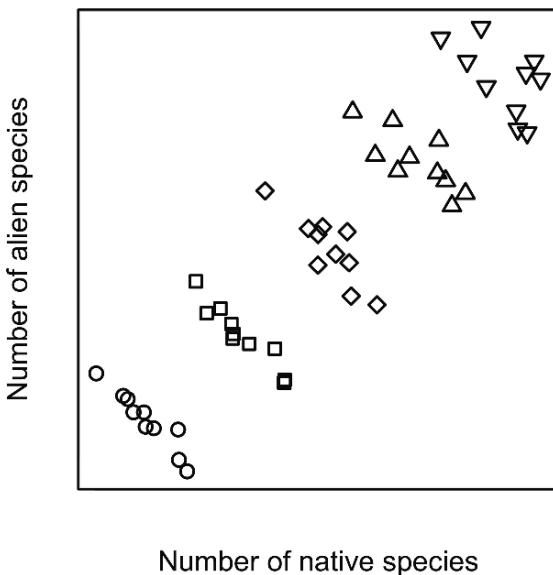


Fig. 11.1 Hypothesised relationship between native and alien species richness at different scales. At a local scale with little environmental variation within communities, a negative relationship between alien and native species richness can be observed due to small-scale neighbourhood processes such as competition. Across these communities, environmental heterogeneity increases and affects alien and native species richness in similar ways, through covarying factors (after Shea and Chesson 2002, using randomly generated data)

biological invasions. However, this could also be a consequence of small-scale ecological processes such as competition (even if it were simply competition for space). The positive correlation between diversity and invasion success across communities would result from the combined effects of these local factors and additional covarying factors (Levine et al. 2002). The latter may act at larger scales, such as gradients in disturbance regime, climate, soil properties, and dispersal (propagule pressure). Therefore, such larger-scale processes drive not only native species richness but, to a large extent, also alien species richness (Kühn et al. 2003), and can dominate over small-scale species interactions or neighbourhood effects. In Fig. 11.2, we present a causal framework to summarise these different scale-dependent processes, acting in the same direction on both alien and native species richness at larger scales but in opposite directions through well-documented local-scale neighbourhood processes such as competition.

Within the framework, we combine ideas of Brandl et al. (2001), Levine et al. (2002) and Shea and Chesson (2002) which can reconcile the niche concepts of Grinnell (1928) and Hutchinson (1957) discussed above, and the seemingly contrasting patterns of alien and native species richness on local and larger scales. Large-scale geographic gradients act mainly on more regional processes, especially as constraints for specific climates, soils, habitats, etc. Due to biogeographic constraints, however, there are direct influences of large-scale gradients on species distributions, e.g. through individual

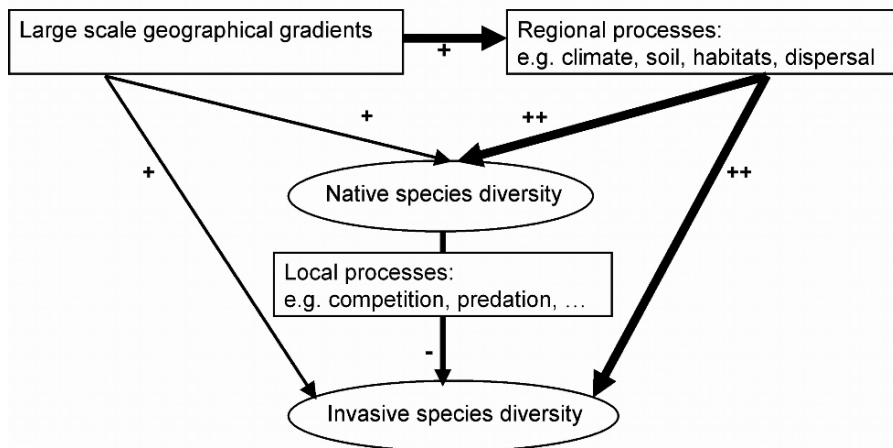


Fig. 11.2 A conceptual framework to reconcile small-scale neighbourhood processes (as explained by Hutchinson’s (1928) niche concept) and large-scale environmental processes (as explained by Grinnell’s (1957) niche concept). *Thick arrows* represent strong effects, *thin arrows* weak effects. *Plus symbols* indicate effects in the same direction (either both positive or both negative), and the *minus symbol* indicates effects in opposite directions

evolutionary histories, dispersal, movements or recolonisation after the last glaciation. These processes, of course, work at more local scales but nevertheless are constrained by large-scale processes which may hinder natural new species occurrences far outside a species' range. On a regional scale, those processes determining native species richness, such as resource availability (e.g. temperature, water, nutrients, habitats) act also on alien species diversity, these being the ones relevant in Grinnell's (1928) niche concept. It can therefore be expected that species richness patterns of native and alien species are positively correlated at larger scales. It is only at a very local scale that neighbourhood effects and other local-scale processes, inferred by Hutchinson (1957), come into play, so that native species richness can increase resistance to biotic invasions. These local patterns, however, are often much more weakly expressed than are the larger-scale patterns.

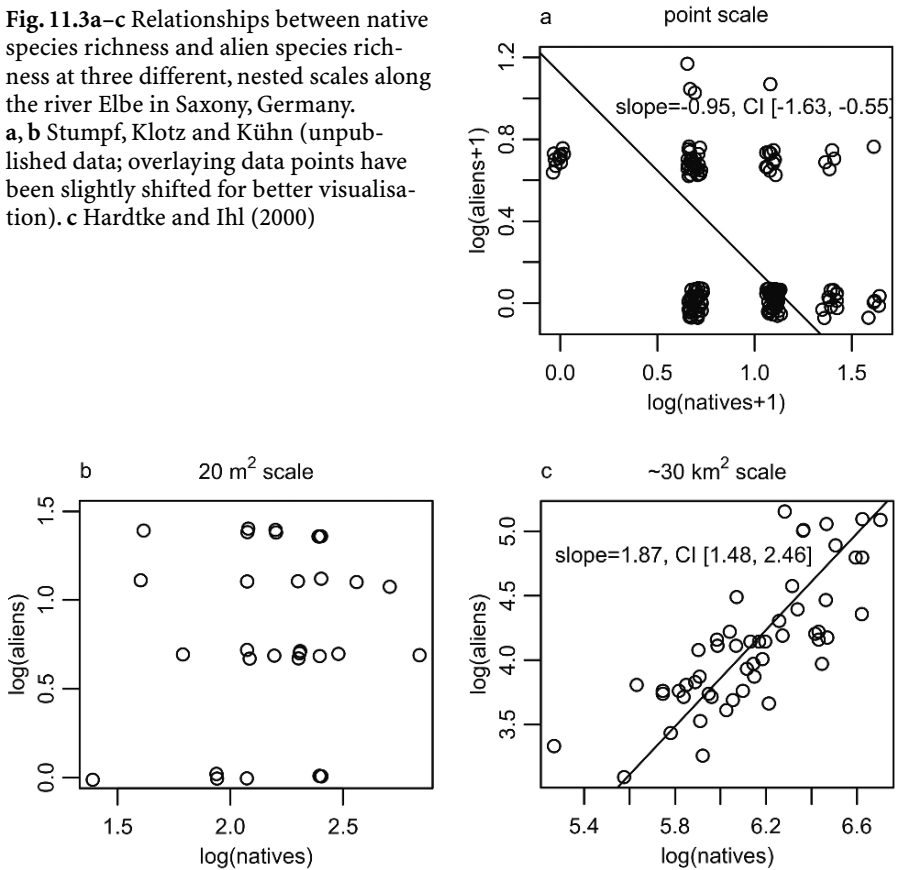
11.5 Local, Regional and Global Patterns

As described above, the relationship between species richness and ecosystem invasibility is scale-dependent. It should therefore be possible to recognise these patterns, and some possible turning point, in a nested analysis. We analyzed 30 plots, each 1×20 m in size, in tall herb communities along the river Elbe in Saxony, Germany, in 2002. Within each of these randomly selected plots, we used five point estimates by counting the number of native and alien species which touched a stake regularly put to the ground. We also noted all species present within each of the 30 plots. A species inventory at a landscape scale for the Elbe River region was available from the atlas of Hardtke and Ihl (2000), with a resolution of 5' longitude and 3' latitude (i.e. ca. 30 km^2). A major axis regression on log-transformed species numbers clearly exhibited a negative relationship at the point scale, no relationship at the 20 m^2 scale, and a positive relationship at the ca. 30 km^2 scale (Fig. 11.3). Thus, we were able to demonstrate the scale dependence of the relationship between native and alien species number for a single observatory frame within a restricted region.

Our study did not show any clear relationship at a resolution of 20 m^2 . However, other studies have reported significant positive relationships at even smaller scales. Plots with sizes of 1 m^2 showed weak positive relationships (Stohlgren et al. 2003) or significant positive and negative relationships between alien and native plant species richness in grasslands of the USA (Stohlgren et al. 1999) whereas only positive correlations were observed by, for example, Sax (2002) at all scales between 1 and 400 m^2 in scrub communities of Chile and California.

Within Germany, we were able to show that the positive relationship between alien and native plant species was caused by a similar set of environmental factors, thus corroborating the notion of common large-scale

Fig. 11.3a–c Relationships between native species richness and alien species richness at three different, nested scales along the river Elbe in Saxony, Germany. **a, b** Stumpf, Klotz and Kühn (unpublished data; overlaying data points have been slightly shifted for better visualisation). **c** Hardtke and Ihl (2000)



environmental factors driving both native as well as alien plant species richness at all but neighbourhood scales. Analysing 40 randomly selected plots of size 250×250 m in an urban and an agricultural landscape near Halle, Wania et al. (2006) confirmed the expected positive correlation, and showed that especially habitat diversity was able to explain both native and alien plant species richness. At a slightly larger scale, 5' longitude and 3' latitude in the district of Dessau (central Germany), Deutschewitz et al. (2003) explained increases in native and alien plant richness in terms of moderate levels of natural and/or anthropogenic disturbances, coupled with high levels of habitat and structural heterogeneity in these urban, riverine, and small-scale rural ecosystems. For Germany (at a scale of 10' longitude and 6' latitude, i.e. ca. 130 km^2), the diversity of geological substrates proved to be the best predictor for both alien and native plant species richness (Kühn et al. 2003). Nevertheless, native plant species richness was further explained by other natural parameters whereas alien plant species richness was additionally explained by urban land cover.

Similarly, environmental heterogeneity was able to account for species richness of natives and aliens in the USA (Stohlgren et al. 2006). Although this pattern of positive correlation between native and exotic species was also observed at a global scale (Lonsdale 1999), we are not aware of any analysis demonstrating a set of common drivers behind this relationship. Nevertheless, it is very likely that the same variables, i.e. energy (temperature) and water availability (Francis and Currie 2003), are able to at least largely explain this pattern for both alien and native plant species.

11.6 Scale-Dependent Consequences for Biodiversity of Invaded Ecosystems

We showed that patterns of ecosystem invasibility changed with spatial scale, especially resolution. What will the consequences of this be for biodiversity? It seems short-sighted to focus simply on biodiversity and disregard other well-documented impacts of biological invasions involving nutrient cycling (especially by nitrogen fixers such as *Acacia* or *Myrica faya*, the fayatree, Chap. 10), water table depletion (*Acacia* or *Tamarix ramosissima*, the salt cedar), alteration of soil structure through salt accumulation (*Mesembryanthemum crystallinum*, the ice plant) or soil perturbation by digging (the feral pig *Sus scrofa domestica*), which additionally disperse seeds of alien plant species and fertilise the soil (Williamson 1996). However, it is biodiversity or rather, its elements (i.e. species) which largely drive ecosystem processes. Still, most conservation actions are concerned with species as such, not with the goods and services they provide as integral parts of an ecosystem.

We discussed several studies showing an increase of alien species at higher native species levels at larger spatial scales. At the global scale, however, alien species are considered to be among the major causes of species extinctions (e.g. Diamond 1989; Sala et al. 2000; Chaps. 13, 15, 16). This impact seems inevitable, given that global extinction rates cannot be compensated by speciation rates. At a global scale, the introduction of species into a new habitat or biogeographical region does not add to biodiversity but the loss of a single species due to this introduction decreases biodiversity. Within regions (i.e. areas which are intermediate in size between those of the globe and small study plots), Sax and Gaines (2003) show for a variety of groups of organisms and across many different parts of the world that the net gain of species due to biological invasions is higher than the loss of species. As an example from Europe, the German Red List of endangered vascular plant species (Korneck et al. 1996) lists 47 taxa as extinct and 118 as threatened. On the other hand, 470 vascular plant species are considered to be naturalised aliens (neophytes; Klotz et al. 2002), and alien species are not among the major causes for species extinctions in Germany (Korneck et

al. 1998). Indeed, theoretical approaches (Rosenzweig 2001) and palaeontological records (Vermeij 1991) suggest that diversity increases after faunal mixing of formerly separated biota.

At the local scale, extirpations of rare native species have been observed. More common, however, are shifts in abundance. Sax and Gaines (2003) reported that the diversity of intact systems has often increased locally but can decrease or remain unchanged as well.

What are the consequences for formerly distinct biota? The introduction of alien species across biogeographical barriers into previously isolated regions was termed a 'new Pangaea' (Rosenzweig 2001). The idea is that formerly distinct biota become more similar, a process termed biotic homogenisation (McKinney and Lockwood 1999). Again, at a global scale, biotic homogenisation is the predictable result in the short term. At local or regional scales, however, patterns of homogenisation but also of differentiation can be observed. Which of these patterns predominates is again scale-dependent: at a local scale, differentiation seems predominant whereas, at a more regional scale, homogenisation can become important. Also, it seems that alien species from less-distant areas tend to promote homogenisation whereas species from more-distant areas tend to promote differentiation (Kühn et al. 2003; McKinney 2004; 2005; Kühn and Klotz 2006).

To better understand the consequences of biological invasions, and to be able to provide plausible scenarios for the future, it is not only necessary to study the problem at an appropriate scale. It is also necessary to use appropriate assumptions of future biodiversity in modelling ecosystem responses. However, most concepts postulate a decrease in biodiversity at all scales – actually, it would be meaningful to also examine the effects of biodiversity increase on ecosystems.

11.7 Conclusions

Patterns of ecosystem invasibility are scale-dependent. Though it seems obvious, we showed that it is indeed necessary to use the appropriate scale to analyse invasibility. This choice of scale, however, is crucial not only in investigating relationships between biotic and abiotic factors but also for the selection of an appropriate theoretical framework and, hence, to understand a system correctly. We discussed that, at smallest scales, high native species richness enhances the invasion resistance of ecosystems through various neighbourhood interactions and processes, consistent with Hutchinson's (1957) niche concept. At larger scales, environmental heterogeneity increases and native as well as alien species richness is determined by largely the same environmental factors, and therefore covary. These larger-scale relationships can be explained by Grinnell's (1928) niche concept.

To increase the quality of future scenarios for invasive species, it is essential to fully comprehend the exact causal relationship between native and invasive species richness at relevant scales. For this, it is also crucial to use correct assumptions about the direction of future (native and invasive) species richness in a system which is also scale-dependent. To date, many analyses of invasibility have been too descriptive or correlative, and lack a true mechanistic understanding of processes at different scales. This gap in our knowledge can probably be minimised by joint research programmes combining observational, experimental and mechanistic approaches across spatial scales.

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