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Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types

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ABSTRACT

Spread of alien species may result in biotic homogenization, i.e. increasing similarity between biotas of different areas. We examined whether the flora of Central European cities is becoming homogenized because of the spread of alien species, whether the contribution of aliens to homogenization depends on residence time, and whether habitats under more intense human pressure are more homogenized. Using floristic composition data from a standardized sample of 1-ha plots located in seven habitat types in 32 cities in Central Europe, Belgium and the Netherlands, we compared homogenization effects of archaeophytes (pre-AD 1500 aliens) and neophytes (post-AD 1500 aliens) using rarefaction curves, Jaccard dissimilarity index, Mantel tests and homogenization index. We found that archaeophytes contributed to homogenization and neophytes to differentiation of floras among cities, but generally the spread of alien species caused differentiation. Differentiation was low in the most disturbed urban habitats, such as city squares, boulevards or early successional sites, but was strongest in moderately disturbed habitats, such as city parks and residential areas with an open building pattern. We conclude that biotic homogenization depends on alien plants' residence time. Aliens introduced within the past five centuries are often rare, not yet having achieved their potential range; they therefore increase floristic differentiation. Conversely, species introduced more than five centuries ago have had sufficient time to disperse into most suitable habitats, and consequently contribute to homogenization. Although invasions may therefore initially increase biodiversity, they could ultimately lead to homogenization. These processes are faster and stronger in more disturbed habitats.

1. Introduction

Human activities promote the introduction of alien species to new areas and cause changes in biodiversity. Locally, the spread of aliens may increase biodiversity (McKinney and Lockwood, 1999; Sax and Gaines, 2003; McKinney, 2006), but a large-scale introduction of generalist cosmopolitan species, sometimes associated with a decline in native species, may lead to increasing similarity in species composition between regions, called "biotic homogenization" (McKinney and Lockwood, 1999; Olden et al., 2004).

Olden and Poff (2003) pointed out that introduction of alien species need not necessarily result in biotic homogenization. On the contrary, it may increase dissimilarity between communities, especially on the local scale, because different alien species may establish in different areas and invasions are often not accompanied by extinctions of native species, or these extinctions are only local.

The degree of biotic homogenization varies among taxa, habitat types and regions (Smart et al., 2006; van Turnhout et al., 2007; Lambdon et al., 2008; Qian et al., 2008; Qian and Guo, 2010; Shaw et al., 2010) and depends on the history of invasions. Rejmánek (2000) introduced the concept of residence time to describe the period of time that a species has been present as an alien in a new region. Where residence time is long, alien species will tend to occupy the majority of suitable habitats and sites across larger areas, and thus contribute to biotic homogenization. Conversely, recently introduced species were able to establish only in some of the suitable habitats and sites within their potential distribution range, but are still absent in others; thus, they temporally

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contribute to biotic differentiation among regions (Olden and Poff, 2003; Pyšek and Jarošík, 2005; La Sorte and McKinney, 2006; Williamson et al., 2009).

The studies mentioned above have significantly improved our understanding of how biotic homogenization depends on the spatial and temporal scales. However, there is still very little understanding of biotic homogenization across different habitats. Given that habitat types differ considerably in the number of alien species they sustain (Chytrý et al., 2008a,b; Gassó et al., 2011), it is possible that they will also differ in the degree of biotic homogenization associated with invasions.

Here we focus on biotic homogenization of flora in Central European cities and how it varies across urban habitat types. Cities are suitable models for a study of this type, because urban flora is richer in alien species than the flora of open landscapes, while at the same time it does not tend to be poorer in native species (Pyšek, 1998; Kühn et al., 2004; Wania et al., 2006). Previous studies have examined the effect of urbanization on biotic homogenization in North America and Europe (Kühn and Klotz, 2006; McKinney, 2006; La Sorte et al., 2008), but all of them were based on the complete urban floras without considering differences between habitat types. Every large city contains a variety of distinct urban habitats, but corresponding habitat types such as squares, streets, residential areas, parks or recently disturbed and abandoned sites are very similar among cities across large areas (Savard et al., 2000). A few previous studies of urban habitats have explored how species composition and richness of their flora changes with urbanization (e.g. McKinney, 2008). The biota of these habitats depends mainly on their specific management, and is less influenced by large-scale environmental variables, such as climate (Lososová et al., 2011b). Therefore, a comparison of the degree of biotic homogenization across urban habitat types can reveal how different types and intensity of human management affect the homogenization of flora resulting from the spread of alien species.

Unlike previous studies, which compiled data from earlier surveys undertaken for various purposes, and used different sampling schemes, we collected an original data set following a standardized sampling protocol for floras of seven urban habitat types in 32 cities of Central Europe, Belgium and the Netherlands. Using this data set, we test the following hypotheses: (1) The urban floras are being homogenized due to the spread of alien species; (2) Alien species with a longer residence time in the target area contribute to biotic homogenization, while those with shorter residence time have the opposite effect, causing an increased differentiation in floristic composition among sites; (3) The degree of homogenization is stronger in habitats that are under more intense human pressure.

2. Methods

2.1. Data set

We sampled floras in 32 cities with more than 100,000 inhabitants across different climatic regions in Belgium, the Netherlands, Germany, Poland, the Czech Republic, Slovakia, Switzerland, Austria, Slovenia and Hungary (hereafter we refer this region to as Central Europe for simplicity; Fig. 1). The threshold size of 100,000 inhabitants was selected to ensure the sample included cities that are similar in degree of disturbance, alien propagule pressure associated with the intensity of traffic and trade, and with limited dispersal of plant species from semi-natural vegetation in the city surroundings to the city centres. Sampling was performed from June to August in 2007–2009. Vascular plant species were recorded in seven 1-ha plots in each city, each plot representing one of the following urban habitat types:

(1) *Historical city square*, usually with pre-19th century houses, and with paved or sealed area > 90%.
(2) *Boulevard* with 19th-century houses, lines of trees, small lawns, and paved or sealed area > 70%.
(3) *Residential area with compact building pattern*, consisting of family houses at least 50 years old and private gardens.
(4) *Residential area with open building pattern*, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs.
(5) *City park* with old deciduous trees (tree cover 10–50%) and frequently mown lawns.
(6) *Early successional site*, strongly disturbed 1–3 years ago, with prevailing bare ground and scarce vegetation cover, usually within or around construction sites.
(7) *Mid-successional site*, abandoned for 5–15 years, dominated by perennial grassland, with scattered shrubs and young trees.

Because of restricted access to private gardens in residential areas with compact building pattern, 500 m of streets instead of a 1-ha plot were sampled in this habitat type, recording plants growing in accessible public areas as well as plants in private gardens that were visible from the street. At each site, all spontaneously established vascular plant species were recorded, including garden escapes and seedlings of spontaneously regenerating planted trees and shrubs. Species represented only by deliberately planted individuals were not recorded. The species were classified according to their status as either native or alien and, additionally, alien species were divided according to their residence time into archaeophytes (introduced before approximately AD 1500, i.e. the European discovery of America and beginning of introductions of plant species from the New World), and neophytes (introduced after AD 1500). The classification was consistent with national lists of alien plants and specialized databases (Klotz et al., 2002; Pyšek et al., 2002; DAISIE, 2009). Species considered native in one part of a country but alien in another were considered native in the whole country. Species data sets were edited using the JUICE program (version 9; Tichý, 2002). Besides species lists from individual 1-ha plots, a pooled species list across all the seven sampled plots was prepared for each city. For more detailed information on sampling and data editing, see Lososová et al. (2011a,b).

2.2. Data analysis

We compared the numbers of native species, archaeophytes and neophytes using sample-based rarefaction curves (Gotelli and Colwell, 2001), calculated according to the analytical formula published by Colwell et al. (2004). These curves were computed for each of the three groups of species. This calculation was done using the JUICE program (version 9; Tichý, 2002).

We measured disimilarity in species composition (beta diversity) among the sites representing the same habitat type and among whole cities for three classes of species origin and residence time (native species, archaeophytes and neophytes) by taking the mean of pairwise Jaccard dissimilarity indices (Whittaker, 1975; Koleff et al., 2003). The Jaccard dissimilarity index between two species assemblages is defined as:

$$J = 1 - a/(a + b + c)$$

where a is the number of species shared, b is the number of species unique to the first assemblage and c is the number of species unique to the second assemblage. J ranges between 0 and 1, where a result of 1 means that the two assemblages have no species in common, and a result of 0 means that the assemblages are identical.

To examine the relationships between dissimilarity of urban floras and geographical distance, we calculated Mantel correlations