Journal of Vegetation Science **27** (2016) 452–459

Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences

Zdeňka Lososová, Milan Chytrý, Jiří Danihelka, Lubomír Tichý & Carlo Ricotta

Keywords
Archaeophyte; Environmental filter; Habitat; Neophyte; Richness difference; Turnover; Urban ecology; β-diversity

Received 21 August 2015
Accepted 25 November 2015
Co-ordinating Editor: Ingolf Kühn

Lososová, Z. (corresponding author, lososova@sci.muni.cz)[1],
Chytrý, M. (chytry@sci.muni.cz)[1],
Danihelka, J. (danihel@sci.muni.cz)[1,2],
Tichý, L. (tichy@sci.muni.cz)[1],
Ricotta, C. (carlo.ricotta@uniroma1.it)[3]

[1]Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic;
[2]Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-657 20 Brno, Czech Republic;
[3]Department of Environmental Biology, University of Rome 'La Sapienza', Piazzale Aldo Moro 5, IT-00185 Rome, Italy

Abstract

Question: The spread of alien species has been changing the diversity of plant communities all over the world, perhaps most notably in urban habitats. It has been shown that alien species with different residence times have different impacts on the β-diversity of urban plant communities: archaeophytes tend to contribute to homogenization, while neophytes tend to increase differentiation among sites. However, it has not been determined whether these processes result from changes in species turnover or from differences in species richness. Here, we use an additive partitioning framework to disentangle the contribution of species turnover and richness difference to β-diversity patterns in invaded urban plant communities.

Location: Thirty-two cities in ten countries of Central Europe and Benelux.

Methods: We analysed the effects of alien species on β-diversity of urban plant communities separately for archaeophytes and neophytes to assess whether the observed patterns differ between these two groups of species with different residence times in the invaded region. We used additive as well as non-additive measures of species turnover and richness difference. For this purpose, we proposed a new index that complements the recently proposed Podani-Schmera index of richness difference.

Results: We confirmed the results of earlier studies that neophytes tend to differentiate the urban plant communities, while archaeophytes tend to homogenize, although in some specific habitats they can also contribute to differentiation. The observed changes in β-diversity were related to the turnover component of β-diversity in most cases, especially for neophytes. In contrast, the richness difference component was not significantly different between neophytes and native species. The trends for archaeophytes were less consistent, but in most habitats their turnover and richness difference were not significantly different from native species.

Conclusions: Changes in β-diversity of urban plant communities induced by the establishment of alien species reflect mainly species turnover, whereas the richness difference component has small effects restricted to certain habitats only.

Introduction

Biological invasions strongly contribute to biodiversity changes throughout the world (Vilà et al. 2011; Pyšek et al. 2012; Simberloff et al. 2013), but our knowledge of the effects of alien plant species on the diversity of recipient communities is still insufficient. In this study, we focus on diversity changes due to the invasion of urban plant communities by alien species. The detailed knowledge of invasion processes in urban environments is important because of the accelerating rate of urbanization throughout the world and associated increase in biotic invasions, which may impact health and wellbeing of urban dwellers (Maller et al. 2009). In addition to these applied issues, urban plant communities are very good models for fundamental studies of biological invasions. Floras of large cities are rich

Doi: 10.1111/jvs.12381

in both native and alien species (Kühn et al. 2004; Kühn & Klotz 2006; Wania et al. 2006; Pyšek et al. 2010; Lososová et al. 2012a), which co-exist in a variety of distinct habitats, such as squares, streets, parks, residential or industrial areas, each with different environmental conditions and specific species pools (Roy et al. 1999). These urban habitats are similar among cities from different regions (Savard et al. 2000), which makes it possible to apply a comparative approach involving multiple cities across large geographic areas.

In their seminal paper, McKinney & Lockwood (1999) hypothesized that alien species tend to homogenize the invaded biotas, making their species composition more similar among different sites. Since then, it has been repeatedly shown that the introduction of alien species changes the β-diversity of urban plant communities (e.g. McKinney 2004, 2006; Kühn & Klotz 2006; La Sorte & McKinney 2006; La Sorte et al. 2007, 2014; Ricotta et al. 2010, 2012; Lososová et al. 2012b). However, alien species with different residence times in the invaded area tend to have contrasting effects on β-diversity (Lososová et al. 2012b; Ricotta et al. 2014). In cities, archaeophytes (species introduced before AD 1500; Pyšek et al. 2002) tend to increase floristic homogenization, whereas neophytes (species introduced after AD 1500) usually have the opposite effect (Lososová et al. 2012b).

Although several studies on biotic homogenization due to establishment of alien species have been conducted, some aspects of β-diversity change in invaded communities have generally been neglected. Variation in β-diversity caused by alien species may be either due to species turnover (also called replacement) or due to species loss (or gain), leading to richness differences and nestedness in community structure (Lennon et al. 2001; Legendre 2014). These two processes might have different ecological and biogeographic causes (Baselga 2010; Leprieur et al. 2011). Therefore, disentangling species turnover from richness differences is important for complete understanding of effects of alien species on plant community diversity.

In a previous study based on floristic data collected in seven habitat types in 32 cities in Northwestern and Central Europe, Lososová et al. (2012b) showed that alien species with different residence times have different effects on the β-diversity of urban plant communities. Using the same data set, the objective of this study is to test whether alien plant species affect β-diversity of urban plant communities in terms of species turnover or richness differences, and how these patterns vary across urban habitats.

Assuming that invasion of neophytes leads to differentiation of urban floras (as detected by Lososová et al. 2012b), we ask whether such differentiation is due to higher species turnover within neophytes than within native species (Fig. 1a). An alternative possibility would be that the differentiation is due to larger differences in species richness within neophytes than within native species (Fig. 1b). In contrast, invasion of archaeophytes leads to homogenization of urban floras (Lososová et al. 2012b). This process can result either from a lower turnover within archaeophytes than within native species (Fig. 1c), or from lower differences in species richness within archaeophytes than within native species (Fig. 1d).

Methods

Data set

We used a data set on vascular plant species sampled in 32 cities with more than 100 000 inhabitants in Belgium, the Netherlands, Germany, Poland, the Czech Republic,

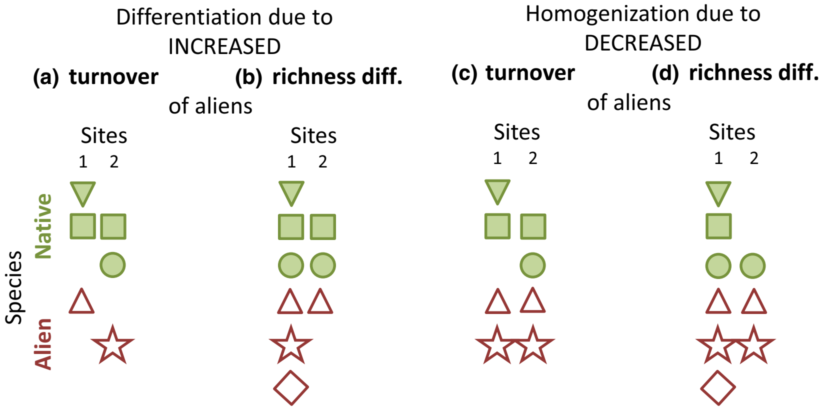

Fig. 1. Conceptual representation of the changes in β-diversity due to invasion of alien species into communities of native species. These changes can result in either increased differentiation among sites or contribute to homogenization among sites. Differentiation can be due to either larger turnover (**a**) or larger differences in species richness (**b**) among sites within the group of aliens than within the group of native species. Homogenization can be due to either smaller turnover (**c**) or smaller richness difference (**d**) of aliens than of native species. Potential effects of outcompeting of some native species by invading aliens are not considered here.

Slovakia, Hungary, Slovenia, Austria and Switzerland (Fig. 2). We selected seven urban habitats differing in their degree of human impact, which are usually present in each large European city: city square, boulevard, residential area with compact building pattern, residential area with open building pattern, park, early successional site and mid-successional site. We recorded all spontaneously established vascular plant species in one square plot of 1-ha size in each habitat of each city in 2007–2009. Due to restricted access to private gardens in residential areas with compact building patterns, street sections of 500 m in length were sampled instead of 1-ha plots in this habitat. Planted individuals were not recorded. For a detailed description of the sampling protocol, see Lososová et al. (2011, 2012a).

Species were classified according to their status as native or alien; alien species were further divided according to their residence time into archaeophytes and neophytes. The classification followed the national lists of alien plants and information obtained from the DAISIE database (www.europe-aliens.org, accessed 2010). The classification into native plant species, archaeophytes and neophytes is not always consistent across Europe. A few species that are native to one region of Europe could be considered as aliens in other regions, such as *Primula vulgaris*, which is native to Western and Southern Europe, but introduced as an ornamental plant and spreading from cultivation in some parts of Central and Eastern Europe. To provide a consistent classification scheme in which each species is assigned to only one category, species that were considered native in at least one flora were classified as native in the whole database. Likewise, species were classified as archaeophytes if they were not considered as native in any flora and designated as archaeophyte in at least one flora. In this conservative approach to alien status assessment, native status was given a higher priority than alien status, and archaeophyte status was given a higher priority than neophyte status (Ricotta et al. 2012).

Data analysis

To test whether the introduction of alien species affects β-diversity of the urban floras, we first calculated for each species group (natives, archaeophytes and neophytes) a

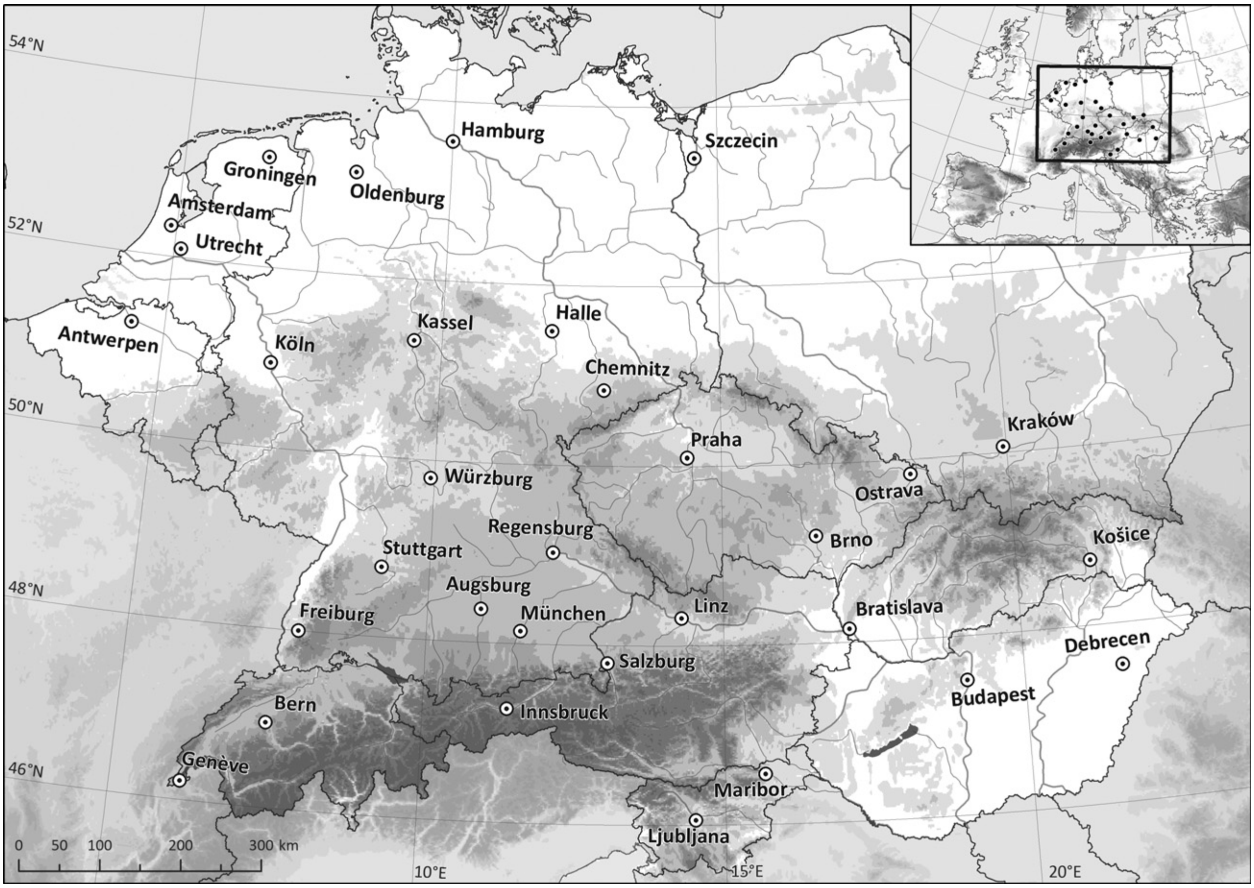

Fig. 2. Map of the studied cities in Central Europe.

Doi: 10.1111/jvs.12381

pair-wise dissimilarity matrix among all individual urban floras using the Jaccard dissimilarity $J = (b + c)/(a + b + c)$, where a is the number of species present in both floras, b is the number of species in the first flora but not in the second, and c is the number of species in the second flora but not in the first. Next, to compare the Jaccard dissimilarity matrices of the native species with those of the alien species groups, we tested for differences in the mean dissimilarity of individual cities from their group centroid in ordination space following Anderson (2006). We used the R function *betadisper* of the *vegan* package (R Foundation for Statistical Computing, Vienna, AT; v 2.2-1, http://cran.r-project.org) to generate the dissimilarities of each urban flora from the corresponding group centroid in principal coordinate space. We then tested for differences in mean dissimilarity from the group centroid between archaeophytes and natives and between neophytes and natives with a *t*-test. *P*-values were obtained using 999 pair-wise permutations of the dissimilarities of individual cities from group centroids. To emphasize potential differences between urban habitats, all analyses were performed separately for each habitat and for the pooled set of species across all seven habitats from each city.

To separate species turnover between assemblages from richness differences (Baselga 2010; Baiser et al. 2012), we used the method of Podani & Schmera (2011; see also Carvalho et al. 2013) to partition the Jaccard dissimilarity into two additive terms: the dissimilarity due to species turnover (J_T) and the dissimilarity due to richness differences (J_R) such that $J = J_T + J_R$. The dissimilarity fraction J_T computes how many species in the first assemblage are substituted by a different species in the second assemblage, divided by the total number of species in both assemblages ($a + b + c$). As one replacement always involves two species, the total number of replaced species equals 2 min$\{b, c\}$, hence:

$$J_T = \frac{2\min\{b, c\}}{a + b + c} \qquad (1)$$

In contrast, the fraction J_R quantifies the relative difference in species richness between the first and the second assemblage normalized by the total number of species in both assemblages and is calculated as:

$$J_R = \frac{|b - c|}{a + b + c} \qquad (2)$$

Based on Equations (1) and (2), we also tested for differences in mean dissimilarity from the group centroid in the principal coordinate space between native and alien species separately for both additive terms J_T and J_R. Finally, as Baselga (2012) criticized the additive partition of the Jaccard index proposed by Podani & Schmera (2011) from a technical viewpoint, arguing that species turnover 2 min$\{b, c\}$ and richness difference $|b - c|$ cannot be normalized by the same quantity ($a + b + c$), we also used two additional, non-additive measures of richness difference and turnover: the Simpson index $S = \min\{b, c\}/(a + \min\{b, c\}$, which is a classical measure of species turnover that relates the observed turnover $\min\{b, c\}$ to its maximum possible value (i.e. the number of species in the more species-poor flora; see Baselga 2012), and a new index $R = |b - c|/(a + \max\{b, c\})$, which relates the richness difference between two floras $|b - c|$ to the number of species in the richer flora.

Results

We recorded 1136 species (562 native, 188 archaeophytes and 386 neophytes) in 224 plots (32 cities × 7 habitats; Table 1). For each urban habitat, the mean dissimilarities of individual cities from the centroid of each species group (natives, archaeophytes and neophytes) are shown in Table 2, while the dissimilarities of the pooled city floras (cumulative species lists across seven habitats) from the corresponding group centroids are in Fig. 3. For the pooled set of species, neophytes increased differentiation among the urban floras (i.e. their dissimilarities from group centroids in the principal coordinate space were all significantly higher than those for the native species), whereas archaeophytes contributed to homogenization. In both cases, the observed changes in β-diversity caused by the alien species were related to the turnover component, whereas the richness difference component was not significantly different between alien and native species.

A similar pattern was also observed for single urban habitats: neophytes always increased β-diversity within habitats among cities, while archaeophytes had no effect in most habitats, although in some habitats they increased

Table 1. Mean numbers of native and alien species per habitat or city and total numbers of species found in all habitats across all cities. NAT = native species, ARC = archaeophytes, NEO = neophytes.

	All species	NAT	ARC	NEO
Square	47	23	14	10
Boulevard	89	47	26	16
Residential compact	120	65	29	26
Residential open	118	66	31	21
Park	91	60	18	13
Early successional site	114	58	40	16
Mid-successional site	120	77	26	17
City	303	162	74	62
Total (all habitats across all cities)	1136	562	188	386

Table 2. Mean dissimilarity of individual cities from the centroid of each species group in the principal coordinate space calculated for each urban habitat and for the pooled set of species from all habitats within single cities. The statistical significances of the pair-wise comparisons (two-tailed permutation-based *t*-test; 999 permutations) of native species vs archaeophytes and neophytes are shown. NAT = native species, ARC = archaeophytes, NEO = neophytes.

	Jaccard Dissimilarity $(b + c)/(a + b + c)$			Species turnover $2\min\{b,c\}/(a + b + c)$			Richness difference $\lvert b - c\rvert/(a + b + c)$			Simpson dissimilarity $\min\{b,c\}/(a + \min\{b,c\})$			New dissimilarity index $\lvert b - c\rvert/(a + \max\{b,c\})$		
	NAT	ARC	NEO	NAT	ARC	NEO	NAT	ARC	NEO	NAT	ARC	NEO	NAT	ARC	NEO
Square	0.525	0.517	0.565**	0.356	0.338	0.418*	0.200	0.215	0.175	0.350	0.328	0.428**	0.250	0.263	0.228
Boulevard	0.492	0.494	0.542**	0.340	0.339	0.400*	0.172	0.162	0.145	0.316	0.307	0.393**	0.215	0.205	0.198
Residential compact	0.470	0.474	0.563**	0.339	0.340	0.449**	0.131	0.137	0.118	0.295	0.302	0.438**	0.169	0.178	0.170
Residential open	0.466	0.492*	0.587**	0.359	0.340	0.437**	0.129	0.166	0.159	0.284	0.313	0.466**	0.160	0.211	0.222
Park	0.468	0.545**	0.592**	0.340	0.374	0.458**	0.140	0.211*	0.148	0.288	0.372**	0.483**	0.178	0.263*	0.212
Early successional site	0.509	0.486	0.574**	0.372	0.350	0.394	0.158	0.149	0.193	0.334	0.311	0.422**	0.202	0.190	0.256
Mid-successional site	0.500	0.506	0.579**	0.385	0.332*	0.433*	0.114	0.193**	0.169	0.347	0.321	0.448**	0.155	0.241**	0.228*
Total (all Habitats)	0.393	0.351**	0.493**	0.319	0.263**	0.413**	0.072	0.092	0.077	0.241	0.191**	0.352**	0.092	0.112	0.106

The significance levels are: $^{**}P < 0.01$ (dark grey); $^{*}P < 0.05$ (light grey).

and in others decreased β-diversity. Neophytes also showed significantly higher species turnover than native species. At the same time, the richness difference of neophytes was generally not significantly different from that of the native species. Archaeophytes showed a less consistent pattern. Overall, they were not very different from native species, and in a few cases they had a significantly higher richness difference and lower species turnover than the native species.

Discussion

Species turnover and richness differences in invaded urban plant communities

Several studies have shown that the introduction of alien species affects the β-diversity of urban plant communities (McKinney 2004, 2006; Kühn & Klotz 2006; Qian et al. 2008; La Sorte et al. 2014) and that alien species with different residence times have different effects: in European cities, archaeophytes tend to cause floristic homogenization of urban floras, whereas neophytes usually have the opposite effect (Lososová et al. 2012b; Ricotta et al. 2014). The aim of the present study was to show the relative importance of turnover and richness differences associated with the invasion of alien species. We found that the changes in β-diversity due to alien plant invasion reflect mainly species turnover, whereas richness differences are non-significant or occur only in specific cases. This finding means that if there are differences in native species richness between urban floras, in most cases there are also parallel differences in alien species richness, indicating that the richness patterns of native and alien species are largely shaped by the same environmental filters (Stohlgren et al. 1999; Kühn et al. 2003; Chytrý et al. 2005; Ricotta et al. 2014).

The relative importance of the turnover component of β-diversity depends on the group of alien species. In the studied urban floras, neophytes had a significantly higher turnover than native species in nearly all habitats, but, with one exception, they did not have higher or lower richness differences than native species. In contrast, differences in turnover within archaeophytes were different from those in native species only in some habitats; in two habitats (parks and mid-successional sites), archaeophytes also had higher richness difference than native species. This comparison of neophytes and archaeophytes indicates that the time since introduction plays a major role in shaping the structure of invaded plant communities. Nevertheless, the residence time is not the only difference between Central European archaeophytes and neophytes. There are differences between these groups in spectra of life forms and reproduction strategies (Pyšek et al. 2011), although on average, archaeophytes and

Doi: 10.1111/jvs.12381 © 2016 International Association for Vegetation Science

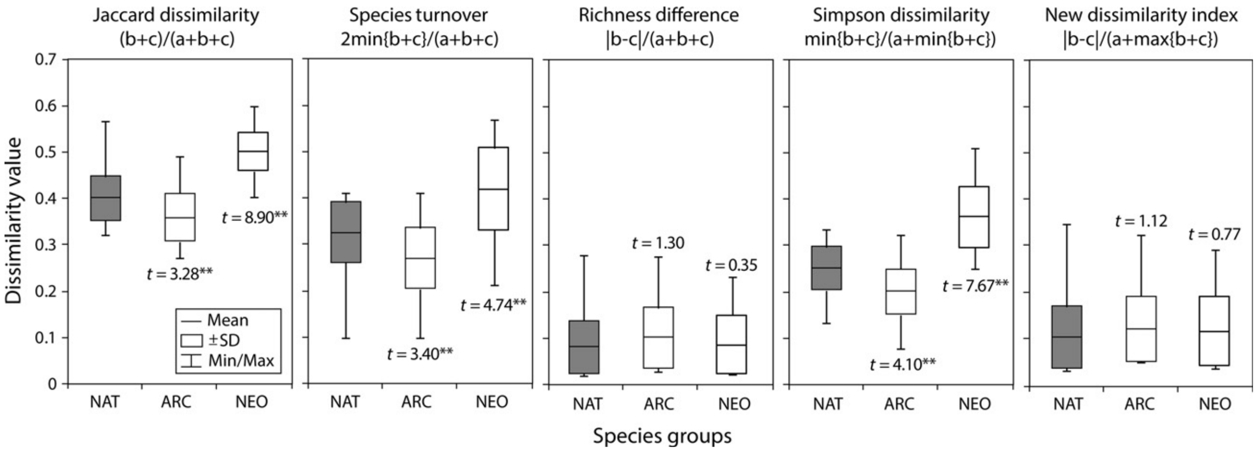

Fig. 3. Box plots of all dissimilarity values of the total urban floras (pooled species lists from seven habitats) from the centroids of each species group in the principal coordinate space. NAT = native species (in grey), ARC = archaeophytes, NEO = neophytes. The values of the permutation-based *t*-tests (999 permutations, two-tailed test) of native species vs archaeophytes and neophytes are also shown. The significance levels are: ** $P < 0.01$; *$P < 0.05$.

neophytes possess similar dispersal abilities, types of reproduction or mortality rates: species in both groups have nonspecific dispersal modes, tend to produce large amounts of easily germinable seeds and show a combination of both short and long dispersal strategies (Pyšek & Richardson 2007; Simonová & Lososová 2008). These traits enable them to pass through several environmental filters during their invasion. It is likely that these filters select a specific set of alien species with similar traits. Therefore, it seems that the main difference between these two species groups is that archaeophytes have had more time for the colonization of suitable habitats, whereas the introduction and spread of neophytes is still continuing (Kühn et al. 2004; Pyšek & Jarošík 2005; Wilson et al. 2007; Williamson et al. 2009). Accordingly, neophytes tend to differentiate urban floras (i.e. their dissimilarities from group centroids in the principal coordinate space are significantly higher than those for the native species; see Table 2, first three columns), whereas archaeophytes often tend to homogenize, although their effects on the β-diversity of urban communities are less consistent.

Measuring species turnover and richness difference: technical issues

All measures of species turnover and richness difference used in this study are consistent in the sign and strength of the obtained results, supporting the interpretation that the observed patterns are ecologically meaningful and not mere statistical artifacts. However, the best way of computing and interpreting these measures is currently a matter of active debate (Baselga 2010, 2012; Podani & Schmera 2011; Carvalho et al. 2013). While all authors agree that the 'operational portion' (*sensu* Legendre 2014) of the measures summarizing species replacement and richness difference are min $\{b, c\}$ (or 2 min$\{b, c\}$) and $|b - c|$ used as the numerator of indices for presence–absence data, a discussion is ongoing concerning the choice of an appropriate denominator. However, a perfect index that would be able to condense all of the relevant information contained in multivariate ecological data into a single measure simply does not exist, and none of the denominators proposed up to now has all the desired properties. Therefore, we developed a new index $|b - c|/(a + \max\{b, c\})$ that complements the richness difference index $|b - c|/(a + b + c)$ proposed by Podani & Schmera (2011). Likewise, another measure of richness difference, $|b - c|/\max\{b, c\}$, which relates the component $|b - c|$ to its maximum possible value $\max\{b, c\}$ would be equally adequate. However, as the results obtained with this additional measure are nearly identical to the results obtained with the previous two indices, they are not shown here.

The same disagreement exists for the calculation of a proper index of species turnover. For instance, the turnover index $2\min\{b, c\}/(a + b + c)$ is generally considered as an appropriate component of the additive partition of the Jaccard dissimilarity (Carvalho et al. 2013). However, in this measure, the operational portion 2 min$\{b, c\}$ used for summarizing species turnover is 'over-diluted' by the presence of both dissimilarity components *b* and *c* in the index denominator. Accordingly, the higher species turnover of neophytes compared to native species is more pronounced if turnover is measured with the Simpson index (see Table 2). Overall, irrespective of the index used, we hope our work has contributed to clarification of the patterns of β-diversity in plant communities due to alien species invasions.

Acknowledgements

We thank Karel Fajmon, Deana Láníková and Zdenka Preislerová for participation in field data sampling, Tomáš Čejka, Michal Horsák, Tomáš Juřička, Lucie Juřičková and Stanislav Němejc for logistic help in the field, Vladimír Řehořek for identification of some taxa, David Zelený for comments on the manuscript and Ondřej Hájek for preparing the map of the studied cities. This work was supported by the Czech Science Foundation (project 14-10723S).

References

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245–253.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L. & McKinney, M.L. 2012. Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society of London. Series B* 279: 4772–4777.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134–143.

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* 21: 1223–1232.

Carvalho, J.C., Cardoso, P., Borges, P.A.V., Schmera, D. & Podani, J. 2013. Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos* 122: 825–834.

Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. 2005. Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia* 77: 339–354.

Kühn, I. & Klotz, S. 2006. Urbanization and homogenization – comparing the floras of urban and rural areas in Germany. *Biological Conservation* 127: 292–300.

Kühn, I., Brandl, R., May, R. & Klotz, S. 2003. Plant distribution patterns in Germany – Will aliens match natives? *Feddes Repertorium* 114: 559–573.

Kühn, I., Brandl, R. & Klotz, S. 2004. The flora of German cities is naturally species rich. *Evolutionary Ecology Research* 6: 749–764.

La Sorte, F.A. & McKinney, M.L. 2006. Compositional similarity and the distribution of geographic range size for native and alien species in urban floras. *Diversity and Distributions* 12: 679–686.

La Sorte, F.A., McKinney, M.L. & Pyšek, P. 2007. Compositional similarity among urban floras within and across continents: biogeographical consequences of human-mediated biotic interchange. *Global Change Biology* 13: 913–921.

La Sorte, F.A., Aronson, M.F.J., Williams, N.S.G., Celesti-Grapow, L., Cilliers, S., Clarkson, B.D., Dolan, R.W., Hipp, A., Klotz, S., (...) & Winter, M. 2014. Beta diversity of urban floras among European and non-European cities. *Global Ecology and Biogeography* 23: 769–779.

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography* 23: 1324–1334.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70: 966–979.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & Oberdorff, T. 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters* 14: 325–334.

Lososová, Z., Horsák, M., Chytrý, M., Čejka, T., Danihelka, J., Fajmon, K., Hájek, O., Juřičková, L., Kintrová, K., (...) & Řehořek, V. 2011. Diversity of Central European biota: effects of human-made habitat types on plants and land snails. *Journal of Biogeography* 38: 1152–1163.

Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Kühn, I., Láníková, D., (...) & Řehořek, V. 2012a. Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. *Global Ecology and Biogeography* 21: 545–555.

Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O., Kintrová, K., Láníková, D., Otýpková, Z. & Řehořek, V. 2012b. Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation* 145: 179–184.

Maller, C.J., Henderson-Wilson, C. & Townsend, M. 2009. Rediscovering nature in everyday settings: or how to create healthy environments and healthy people. *EcoHealth* 6: 553–556.

McKinney, M.L. 2004. Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions* 6: 495–504.

McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247–260.

McKinney, M.L. & Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14: 450–453.

Podani, J. & Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. *Oikos* 120: 1625–1638.

Pyšek, P. & Jarošík, V. 2005. Residence time determines the distribution of alien plants. In: Inderjit, (ed.), *Invasive plants: ecological and agricultural aspects*, pp. 77–96. Birkhäuser, Basel, CH.

Pyšek, P. & Richardson, D.M. 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (ed.), *Biological invasions*, pp. 97–125. Springer, New York, NY, US.

Pyšek, P., Sádlo, J. & Mandák, B. 2002. Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186.

Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., Gassó, N., Kenis, M., Lambdon, P.W., (...) & Hulme, P.E. 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography* 19: 317–331.

Pyšek, P., Jarošík, V., Chytrý, M., Danihelka, J., Kühn, I., Pergl, J., Tichý, L., Biesmeijer, J.C., Ellis, W.N., (. . .) & Settele, J. 2011. Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. *Ecological Monographs* 81: 277–293.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725–1737.

Qian, H., McKinney, M.L. & Kühn, I. 2008. Effects of introduced species on floristic similarity: comparing two US states. *Basic and Applied Ecology* 9: 617–625.

Ricotta, C., Godefroid, S. & Rocchini, D. 2010. Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. *Biological Invasions* 12: 233–240.

Ricotta, C., La Sorte, F.A., Pyšek, P., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. 2012. Phylogenetic beta diversity of native and alien species in European urban floras. *Global Ecology and Biogeography* 21: 751–759.

Ricotta, C., Celesti-Grapow, L., Kühn, I., Rapson, G., Pyšek, P., La Sorte, F.A. & Thompson, K. 2014. Geographical constraints are stronger than invasion pattern for European urban floras. *PLoS ONE* 9: e85661.

Roy, D.B., Hill, M.O. & Rothery, P. 1999. Effects of urban land cover on the local species pool in Britain. *Ecography* 22: 507–515.

Savard, J.P.L., Clergeau, P. & Mennechez, G. 2000. Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning* 4: 131–142.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., (. . .) & Vilà, M. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66.

Simonová, D. & Lososová, Z. 2008. Which factors determine plant invasions in man-made habitats in the Czech Republic? *Perspectives in Plant Ecology, Evolution and Systematics* 10: 89–100.

Stohlgren, T.J., Binkley, D.T., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69: 25–46.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.

Wania, A., Kühn, I. & Klotz, S. 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning* 75: 97–110.

Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., Stout, J. & Pyšek, P. 2009. The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions* 15: 158–166.

Wilson, J.R.U., Richardson, D.M., Rouget, M., Proches, S., Amis, M.A., Henderson, L. & Thuiller, W. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions* 13: 11–22.

Journal of Vegetation Science **27** (2016) 439–440

COMMENTARY

Moving beyond biotic homogenization: searching for new insights into vegetation dynamics

Amy K. Hahs & Mark J. McDonnell

Hahs, A.K. (corresponding author, hahsa@unimelb.edu.au)[1,2],
McDonnell, M.J.
(markmc@unimelb.edu.au)[1,2]

[1]Australian Research Centre for Urban Ecology (ARCUE), Royal Botanic Gardens Victoria, Private Bag 2000, South Yarra, Vic. 3141, Australia;
[2]School of BioSciences, The University of Melbourne, Melbourne, Vic. 3010, Australia

Abstract

Biotic homogenization has been predicted to occur in cities across the world. However, the empirical evidence has been less than convincing. Lososová et al. explore the middle ground between these two points of view in this issue of *Journal of Vegetation Science*. They take a more sophisticated approach, linking homogenization to bigger questions of vegetation assembly in urban environments.

Biotic homogenization is the term that has been used to describe the perceived increasing similarity in the plants and animals observed in cities around the world. The concept emerged from the idea that humans are deliberately and accidentally contributing to much higher rates of biotic exchange due to their rapid and extensive mobility. In addition, homogenization could also be driven by the harsh environmental conditions of cities, which would be expected to limit the potential species pool. However, recent global studies have found limited evidence in support of homogenization (Aronson et al. 2014). Yet we know that there are now very many cosmopolitan species found in cities around the world (Pyšek 1998), and many native species are being lost from cities (Hahs et al. 2009). So how can we reconcile the loss of native biodiversity, and gain of cosmopolitan plants, with the lack of observable homogenization?

Lososová et al. (2016) explore this issue by looking at differences in species richness and turnover in archaeophytes, neophytes and native plants between 32 cities in Europe. While the categorization of neophytes, archaeophytes and native plants is well recognized in Europe, its applicability to other continents is less clear.

Europe has a long history of human movements and anthropogenic exchange of plant materials between different continents. To account for the different lengths of residence time for introduced (alien) species, distinctions are made between 'Old World' alien plants (archaeophytes) and modern alien plants (neophytes), with a cut-off year of AD 1492 used to distinguish the two groups of aliens in Europe (Preston et al. 2004). This year was selected as it is the year in which Christopher Columbus first set off to sail to the 'New World'. Archaeophytes have therefore been present in the local plant communities for long enough that they can be considered 'almost native'. Yet in other ways, they also retain characteristics of alien species, as these traits potentially explain how they were able to arrive and colonize new areas prior to the surge in human mobility. Therefore, they represent an interesting group of organisms in the context of European and other Old World cities. However, what this mean for our understanding of vegetation dynamics for cities outside of Europe is less clear.

To explore how the concept of archaeophyte and neophytes may apply in different contexts, it is useful to consider our understanding of the invasion process. Invasion is generally explained as a seed or propagule arriving at a safe site, where it is able to germinate, establish and grow. Based on how well the species performs in the landscape, it is subsequently able to establish a source population from which seeds and propagules can disperse and the species begins to spread. Over time, the dispersal effectiveness of a population increases as the invasion process proceeds (Fig. 1b), until it reaches some species-specific optimum, similar to that observed within native species (Fig. 1a). Based on performance, the rate of increase may be relatively rapid (Fig. 1c), or if the environment remains stable, the species may remain in relatively discrete locations in the landscape for a long period of time (Fig. 1d). As archaeophytes have been in the system for at least 400 yrs, most of them have already passed through the dispersal phase (Fig. 1b), and they are now distributed fairly widely across Central Europe. This is essentially the pattern reported by Lososová et al., who found there is relatively

Doi: 10.1111/jvs.12415

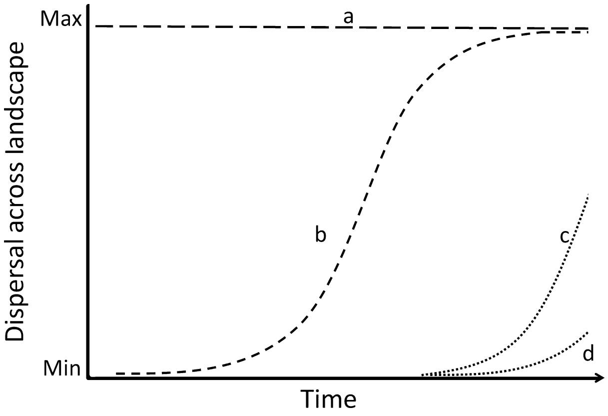

Fig. 1. Conceptual drawing illustrating how dispersal across a landscape may change over time as a species remains in the system. Curves represent (a) natives, (b) archaeophytes, (c) neophytes with rapid establishment and spread, and (d) neophytes with slower establishment and spread.

low turnover and relatively consistent species richness of archaeophytes between their 32 cities. However, for neophytes, the invasion process has begun relatively recently, and species may not yet have reached their maximum dispersal across a landscape (Fig. 1c, d). Therefore, they will be observed in more discrete locations, and their presence may more strongly reflect stochastic dispersal and population dynamics rather than niche availability. The high rates of turnover between cities for neophytes observed by Lososová et al. also support this pattern of more random distributions of species.

Here we present some fundamental questions that arise from the research presented by Lososová et al., all of which have implications for understanding the dynamics of vegetation assembly in cities: (1) what is the nature of disturbance regimes in cities and how does this translate into the availability of safe sites for organisms; (2) what is the pool of available propagules, are there some neophytes in the seed bank, and what might break their dormancy; (3) what are the competitive interactions between species, particularly different combinations of natives, archaeophytes and neophytes; (4) are there particular plant traits that influence arrival and performance under historical conditions (e.g. archaeophytes; Pyšek et al. 2009) or existing conditions (e.g. neophytes); (5) are there particular plant traits that influence species performance under predicted future conditions and altered disturbance regimes, or which might confer an ability to outcompete and dominate plant assemblages in urban environments; (6) how do these new dynamics affect the extinction debt of native plants in urban environments; and (7) how can we use this fuller understanding of plant community assembly processes to feed back into our broader understanding of vegetation dynamics? These questions are all critical for informing our understanding of how to maintain resilient vegetation in cities, which is predicted to change rapidly with urban development and global climate change. Lososová et al. present an interesting assessment. It is now up to the broader research community to see where this path takes us.

Acknowledgements

This paper was produced with financial support from The Baker Foundation.

References

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S. (...) & Winter, M. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 281: 20133330.

Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W. & Williams, N.S. 2009. A global synthesis of plant extinction rates in urban areas. *Ecology Letters* 12: 1165–1173.

Lososová, Z., Chytrý, M., Danihelka, J., Tichý, L. & Ricotta, C. 2016. Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences. *Journal of Vegetation Science* 27: 452–459.

Preston, D., Pearman, D.A. & Hall, A.R. 2004. Archaeophytes in Britain. *Botanical Journal of the Linnean Society* 145: 257–294.

Pyšek, P. 1998. Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography* 25: 155–163.

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J. & Sádlo, J. 2009. The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions* 15: 891–903.

Doi: 10.1111/jvs.12415