



Dispersal limitation is stronger in communities of microorganisms than macroorganisms across Central European cities

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ABSTRACT

Aim It is generally believed that communities of small organisms, or those with small propagules, are structured mainly by local niche-based processes, and less by dispersal limitation. Conversely, weaker environmental and stronger spatial structure, indicating dispersal limitation, are expected to occur more frequently in communities of large organisms. However, this hypothesis has rarely been tested by comparing spatial and environmental effects across groups of organisms of different size (or with different size of propagules) sampled at the same set of sites. Here, we test it in urban environments.

Location Thirty-two cities in 10 countries of Central Europe and Benelux.

Methods We compared effects of spatial location and climate on species composition of different groups of organisms sampled in corresponding types of urban habitats. The studied groups were: (1) subaerial cyanobacteria and algae, (2) vascular plants, (3) land snails; and subgroups of vascular plants with different life form and dispersal mode, namely: (4) herbs, (5) animal-dispersed trees and shrubs, and (6) wind-dispersed trees and shrubs. Data were analysed by variation partitioning based on redundancy analysis (RDA) with principal coordinates of neighbour matrices (PCNM). Eighteen PCNM eigenvectors (expressing spatial effects) and mean annual temperature, July–January temperature difference and annual precipitation sum (expressing environmental effects) were used as explanatory variables.

Results Pure effects of climate on species composition, indicating niche-based processes, were not significant for any group or subgroup of the studied organisms. In contrast, pure effects of space, indicating dispersal limitation, were significant for all groups and subgroups except herbs. Surprisingly, the community of cyanobacteria/algae possessed much stronger spatial structure independent of climate than communities of larger organisms, although cyanobacteria/algae had the lowest beta diversity among the studied cities.

Main conclusions We hypothesize that the community of subaerial cyanobacteria/algae is structured by natural processes which involve dispersal limitation, whereas communities of urban plants and snails are influenced by human-assisted dispersal of their propagules between cities, which results in weaker dispersal limitation. Our study indicates that dispersal vectors can be more important for community structure than size of organisms or of their propagules.

Keywords

Algae, body size, community structure, cyanobacteria, environmental filtering, land snails, spatial structure, urban ecology, variation partitioning, vascular plants.

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INTRODUCTION

The current theory of community ecology understands the species composition of local communities to be an outcome of both local niche-based processes (Hutchinson, 1957; Chase & Leibold, 2003) and regional processes such as speciation, extinction, migration and dispersal (Ricklefs & Schluter, 1993; Zobel, 1997), but their relative importance in different contexts is still poorly known. The key concept for understanding these processes is that of the metacommunity, defined as a set of local communities connected by the dispersal of multiple species (Hubbell, 2001). In the metacommunity framework, mechanisms underlying niche-based versus dispersal-limited community structures are described respectively by the species-sorting model and the neutral model (Leibold *et al.*, 2004). The species-sorting model is derived from the theory of species composition change along environmental gradients (Whittaker, 1967). It assumes that environment is heterogeneous across landscapes, and local species composition is an outcome of the adaptation of different species to particular environmental qualities and local interspecific interactions. Thus, beta diversity is generated by environmental heterogeneity and environmental control of species distributions (Legendre *et al.*, 2005). In contrast, the neutral model assumes spatially homogeneous environments and equivalence of species with respect to their environmental requirements (Bell, 2001; Hubbell, 2001); under this model, dispersal limitation is the only factor responsible for variation in species composition among local communities.

The role of dispersal limitation has traditionally been inferred from the observation of decreasing similarity in species composition with geographical distance, known as the distance decay of similarity (Qian *et al.*, 1998; Nekola & White, 1999; McKinney, 2004, 2006; Soininen *et al.*, 2007; La Sorte *et al.*, 2008; Leng *et al.*, 2010). However, not only species composition, but also environment, can become less similar with increasing distance, and in such cases, distance decay can result from niche-based processes rather than from dispersal limitation. It is therefore necessary to measure environmental variables relevant to the studied community, and partition variation in its species composition into fractions explained by the effect of spatial distance, the effect of environment, and the shared effect of both, the latter of which is sometimes called spatially structured environmental variation (Borcard *et al.*, 1992).

Spatial effects can operate on various scales, including migration and range extension on large scales and mass effect or sink–source dynamics on smaller scales. Any of these processes can be important at some scales but insignificant at others (Verleyen *et al.*, 2009). Recently developed methods such as principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2002) or Moran's eigenvector maps (Dray *et al.*, 2006) enable spatial structure to be described across multiple scales through a series of eigenvector-based variables, which are used as predictors in variation partitioning models, e.g. using redundancy analysis (RDA). Cottenie (2005)

suggested that a combination of significant pure effects of environmental variables and non-significant pure effects of spatial variables in variation partitioning indicates a community structure based on the species-sorting model, while the opposite pattern indicates the neutral or patch-dynamics model. However, the shared effect of environmental and spatial variables can also be very important in these considerations (Smith & Lundholm, 2010).

It is generally believed that small organisms (especially microorganisms) or those with small propagules are widespread over large areas, and their occurrence at particular sites is explained mainly or entirely by environmental qualities (Finlay *et al.*, 1996; Fenchel & Finlay, 2004; Green & Bohannan, 2006; Van der Gucht *et al.*, 2007). Consequently, their community structure would be determined by species sorting. The reasoning behind this assumption is that the small size of individuals or propagules can facilitate long-distance passive dispersal, and that the large population sizes and short generation times typical of small organisms result in high dispersal rates. In contrast, larger organisms, or those with large propagules, are supposed to be dispersal-limited, and therefore, besides environmental qualities, their current distribution is also strongly dependent on the history of their evolution and migration.

Contrary to the common belief that for microorganisms 'everything is everywhere, but, the environment selects' (de Wit & Bouvier, 2006), some recent studies demonstrate that communities of unicellular organisms can possess a notable spatial structure (Martiny *et al.*, 2006; Telford *et al.*, 2006; Pommier *et al.*, 2007; Vyverman *et al.*, 2007; Verleyen *et al.*, 2009; Heino *et al.*, 2010). To date, there have been few comparative studies of communities of organisms of different size (e.g. Hillebrand *et al.*, 2001; Cottenie, 2005), and even fewer studies based on a set of samples of differently-sized organisms from the same set of sites, which would enable a comparison of the relative effects of spatial and environmental variables on community structure. Of these, Beisner *et al.* (2006) have demonstrated that communities of bacteria, plankton and fish in Canadian lakes tend to be less environmentally and more spatially structured with increasing size of organism. Hájek *et al.* (2011) found a stronger spatial structure for organisms with large propagules (vascular plants and molluscs) than for those with small propagules (diatoms and bryophytes) in Carpathian fens. Astorga *et al.* (2011) revealed much stronger environmental than spatial structure in diatoms, bryophytes and macroinvertebrates in Finnish streams. Sattler *et al.* (2010) also observed a weak spatial structure in a study of spiders, bees and birds within Swiss cities, but this could be due to the restricted spatial extent of their study. Generally, these studies support the notion that communities of larger organisms or those with larger propagules tend to have a stronger spatial structure, but distinct spatial structures are often also present in communities of organisms with small propagules.

Here, we compare the relative effects of spatial and environmental factors on the community structure of three

groups of organisms possessing different sized individuals and propagules: (1) subaerial cyanobacteria and algae, (2) vascular plants, and (3) land snails, each of which were consistently sampled in 32 cities of Central Europe and Benelux. Cities are very suitable for a study such as this, because urban habitats are created and strongly influenced by humans, and are therefore very similar across large geographical distances (McKinney, 2006). Given that we sampled corresponding habitats in each city and merged the samples from individual habitats for each city, the main environmental differences between samples from different cities were climatic. We hypothesized that, due to their smaller propagule size, the community of cyanobacteria and algae would be mainly structured by climate, without any purely spatial effects, thus conforming to the species-sorting model of the metacommunity with no dispersal limitation. In contrast, the communities of plants and snails would be partly structured by purely spatial effects not associated with climatic differences, indicating dispersal limitation.

MATERIALS AND METHODS

Species data

We sampled 32 cities, each with more than 100,000 inhabitants, in Belgium, the Netherlands, Germany, Poland, the Czech

Republic, Slovakia, Switzerland, Austria, Slovenia and Hungary (for simplicity, this region is referred to as Central Europe throughout this paper; Fig. 1). The ranges of climatic characteristics across these cities were as follows: mean annual temperature 7.9–11.2 °C, January–July temperature difference 14.2–23.0 °C, and annual precipitation sum 544–1312 mm. Sampling was performed from June to August in 2007–2009.

Samples of subaerial cyanobacteria and algae were collected on building stone (preferably sandstone) and tree bark, each of these two substrates being both sampled in the city centre (usually on a historical square) and in a city park. Sampled surfaces were 1 cm² large, located at a height of 120–150 cm on a building wall or a tree trunk. Sampling sites on buildings in the city centre were selected from both north-facing and south-facing walls, while sites on stones in parks and trees were selected from the north-facing side. Five samples from each city were sampled (centre–stone–north-facing, centre–stone–south-facing, centre–tree, park–stone, park–tree). Samples were cultivated in Petri dishes and tubes containing the culture medium BBM (Smith & Bold, 1966) under controlled conditions (temperature 21 °C, humidity 60%, irradiance 10.3 μmol s⁻¹ m⁻², light 660 lx, PhAR 2.14 W m⁻² and a photoperiod of 12:12 h light : dark). The initial sample incubation in Petri dishes (7–21 days) was followed by isolation of clones. The morphometric data were measured from both natural populations and isolates maintained in



Figure 1 Map of Central Europe showing the 32 cities studied.

cultures. Samples were observed and documented using the Olympus BX 50 light microscope equipped with Lucia Image Analysis and the Olympus SZH stereomicroscope.

Species composition (presence/absence) of vascular plants and land snails was recorded in seven 1-ha plots in each city, each of them representing one urban habitat type: (1) square in the historical city centre, (2) 19th-century boulevard, (3) residential area with closed building pattern of family houses and private gardens, (4) residential area with open building pattern with blocks of flats, (5) city park, (6) unmanaged mid-successional site with perennial herbaceous vegetation and scattered shrubs or trees, and (7) recently disturbed site (see Lososová *et al.*, 2011a for details). At each site, all land snails and all spontaneously established vascular plant species were recorded, including garden escapes and seedlings of spontaneously regenerating planted trees and shrubs. Plant species represented only by deliberately planted individuals were not recorded. Plants were classified according to their life form and dispersal mode as (1) herbs, (2) animal-dispersed trees and shrubs, and (3) wind-dispersed trees and shrubs. Snails were searched for by eye in all appropriate microhabitats within each site. All live snail individuals, as well as empty shells with intact periostracum, were considered. For each city and each group of organisms, a pooled list of all species recorded in all the studied habitats was prepared and analyses were based on these pooled species lists. For all species groups, presence/absence data were analysed.

Explanatory variables

Variables analysed for their effects on species composition were: (1) geographical distance between cities, and (2) climatic data (from Hijmans *et al.*, 2005), including mean annual temperature (°C), annual temperature range expressed as the difference between July and January mean temperature (°C) and annual precipitation sum (mm). To quantify the effects of the spatial component on species composition, we produced a matrix of between-city geographical distances (truncated at a distance determined by the minimum spanning tree technique), which we analysed using principal coordinates of neighbour matrices (PCNM; Borcard & Legendre, 2002). The calculations were done in the R program (<http://www.r-project.org>), using the 'PCNM' package (https://r-forge.r-project.org/R/?group_id=195). The 18 eigenvectors corresponding to positive eigenvalues obtained in this analysis were used as independent variables to explain the effect of spatial distance between cities on changes in species composition.

Statistical analysis

We calculated alpha (α), beta (β) and gamma (γ) diversity of all the studied groups of organisms in Central European cities, where α -diversity was defined as the mean number of species recorded in single cities, β -diversity as the mean dissimilarity in species composition between cities, and γ -diversity as the cumulative number of all species found in the 32 studied cities.

We used the mean Jaccard dissimilarity index as a measure of β -diversity (Koleff *et al.*, 2003). Sample-based rarefaction curves (Gotelli & Colwell, 2001), calculated according to the analytical formula published by Colwell *et al.* (2004), were used to compare species richness of the studied species groups. This calculation was performed using the JUICE program, version 7 (Tichý, 2002).

To visualize the main patterns in species composition among the studied cities, we used principal components analysis (PCA) with Hellinger-transformed presence/absence species data (Legendre & Gallagher, 2001) in the CANOCO program, version 4.5 (ter Braak & Šmilauer, 2002). We then determined relative effects of climate and space on species composition of each group of organisms using variation partitioning based on the above-mentioned climatic and spatial variables. Three climatic variables and 18 spatial variables with positive eigenvalues obtained from the PCNM analysis were included in redundancy analyses (RDA) with the Hellinger-transformed presence/absence species data. The variation partitioning algorithm proposed by Peres-Neto *et al.* (2006) was used to balance the possible bias in estimation of the variation explained by climate and space, which might occur because of different number of explanatory variables for these two groups (Kromrey & Hines, 1995). The significance of the pure effects of climatic variables and spatial distance was tested by Monte Carlo tests with 999 permutations. These calculations were done in the R program, using the 'vegan' package, version 1.17-2 (https://r-forge.r-project.org/R/?group_id=68).

There is an ongoing debate on the relative effectiveness of various methods that have been proposed to disentangle the environmental and spatial effects on community composition, namely the raw-data approach, such as canonical ordination with spatial explanatory variables (e.g. PCNM eigenvectors) versus the distance-based approach, such as correlation between distance matrices (Legendre *et al.*, 2005, 2008; Tuomisto & Ruokolainen, 2006, 2008). Here we use the raw-data approach, because it is more appropriate for the question that we ask, i.e. whether the variation in community composition among sites is due to variation in environmental conditions or to neutral community dynamics (Legendre *et al.*, 2008). However, recent comparisons of different methods based on simulated data (Gilbert & Bennett, 2010; Smith & Lundholm, 2010) have demonstrated that raw-data approaches tend to underestimate the environmental component of community variation, whereas distance-based approaches consistently underestimate the spatial component. Therefore we additionally analysed our data following a distance-based approach, namely Mantel statistic of matrix correlation and partial matrix correlation. We used matrices of Jaccard dissimilarities in species composition between cities, a matrix of geographical distances between cities and a matrix of Euclidean distances calculated based on the three climatic variables. Significances of matrix correlations were tested using Monte Carlo permutation test with 999 permutations (using the 'vegan' package in the R program).

In addition to the RDA-based variation partitioning, we visualized the relationships between Jaccard dissimilarities in species composition and geographical distances between the cities using scatter plots (an opposite pattern to the plots of distance decay of similarity; Nekola & White, 1999). Because the observations in dissimilarity or distance matrices are not independent, the significance of this relationship could not be tested using traditional regression techniques. Therefore, we computed Mantel permutation tests using the ‘vegan’ package of the R program. Following Baselga (2010), we compared the slopes of this relationship among different organism groups by bootstrapping, using a case resampling approach with 10,000 iterations. The *P*-value of the null hypothesis of no difference between the slopes was estimated from the proportion of iterations for which the slope of one group was smaller than the slope of the other group.

RESULTS

Species lists from the 32 studied cities contained on average 59 species of cyanobacteria/algae, 303 vascular plants (among them 250 herbs, 31 animal-dispersed trees and shrubs, and 21 wind-dispersed trees and shrubs), and 22 land snails (Table 1). Numbers of species found in each city were not correlated between the studied groups of organisms; for example, cities with many snail species were not particularly rich in species of cyanobacteria/algae or plants (correlation coefficients: cyanobacteria/algae–plants -0.14 n.s.; cyanobacteria/algae–snails 0.20 n.s.; plants–snails -0.07 n.s.). β -diversity, calculated as the mean dissimilarity in species composition between cities, was largest for land snails, followed by plants and cyanobacteria/algae (Table 1). This means that Central European urban communities of cyanobacteria/algae shared a larger proportion of widespread species than plant communities, and snail communities had the lowest proportion of species shared between different cities. For subgroups of vascular plants, the largest β -diversity was in animal-dispersed trees and shrubs, followed by herbs and wind-dispersed trees and shrubs.

Like the mean species richness of the cities, the cumulative species richness across all cities (γ -diversity) was also highest for plants and lowest for snails (Table 1). The shape of the rarefaction curves (Fig. 2) differed among the studied groups. For cyanobacteria/algae, a steep increase followed by a levelling of the rarefaction curve indicated the lowest β -diversity of their communities. However, PCA ordination revealed a distinct geographical gradient associated with changes in species

composition of cyanobacteria/algae, beginning with Hungarian and Slovak cities near the top of the scatter plot and ending with Dutch and Belgian cities on the right side (Fig. 3a). Very similar but less pronounced geographical gradients were found for the other species groups (Fig. 3b–f).

Dissimilarity in species composition within all the studied groups of organisms increased with geographical distance between the cities (Fig. 4, Mantel test, $P < 0.001$). This increase was significantly higher for cyanobacteria/algae and snails than for plants. There were no differences in the slopes for the subgroups of plants.

For all the studied groups of organisms, spatial distribution of the cities explained a larger proportion of variation in

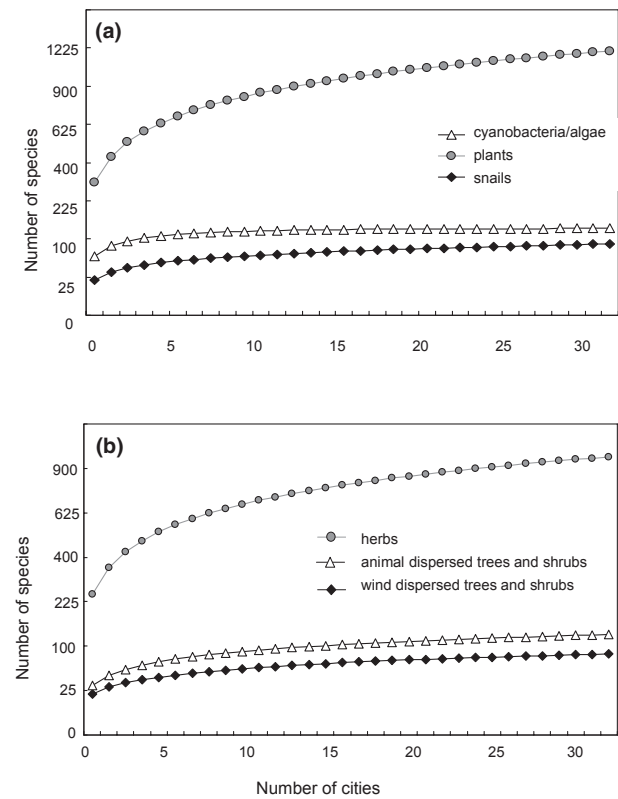


Figure 2 Sample-based rarefaction curves showing an increase in the total number of species of (a) cyanobacteria/algae, plants and snails; (b) herbs, animal-dispersed trees and shrubs, and wind-dispersed trees and shrubs recorded in Central European cities with increasing number of cities sampled. Note the square-root transformation of the vertical axis.

Table 1 Mean numbers of species (\pm standard deviation) found in single Central European cities (α -diversity), mean Jaccard dissimilarities between species lists from individual cities (β -diversity), and total numbers of species found in all the studied cities (γ -diversity).

	Cyanobacteria/algae	Plants	Land snails	Herbs	Animal-dispersed trees and shrubs	Wind-dispersed trees and shrubs
No. of species per city	59 \pm 11	303 \pm 25	22 \pm 5	250 \pm 21	31 \pm 6	21 \pm 0.2
Mean Jaccard dissimilarity	0.55	0.59	0.64	0.59	0.63	0.56
Total no. of species	129	1196	87	979	120	87

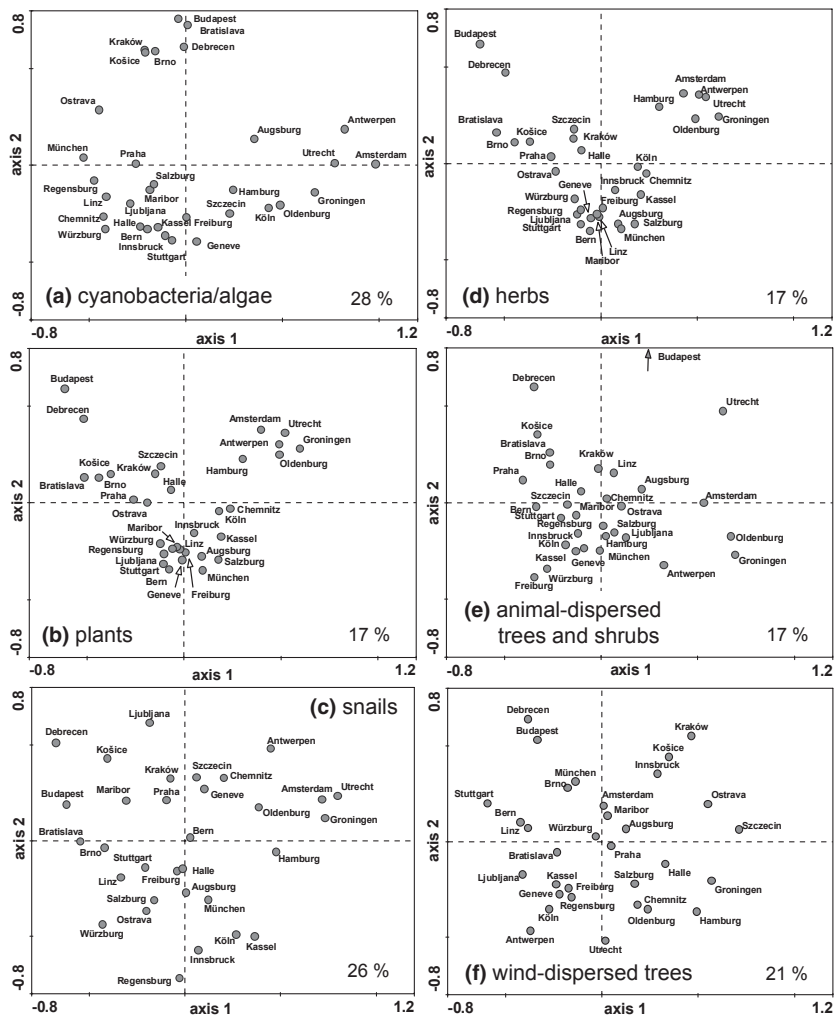


Figure 3 Ordination diagrams of the 32 Central European cities studied based on species composition of individual groups of organisms (principal components analysis; PCA). Variations explained cumulatively by the first and second ordination axes are given in percentages of total inertia.

species composition than did climate. Redundancy analysis (RDA) detected significant gross effects of climate on species composition of each of the studied groups, but these effects were shared with spatial effects, whereas pure effects of climate were non-significant (Fig. 5). The total variation in species composition jointly explained by both climate and space, as well as the variation explained by the pure effects of space, were highest for cyanobacteria/algae, followed by snails and plants. For subgroups of vascular plants, the pure effects of space were only significant for trees and shrubs, but not for herbs. The distance-based approach (Mantel tests, not shown) gave the same results as the raw-data approach (RDA): pure effects of climate were non-significant, while pure effects of distance were significant for all the studied organism groups and subgroups.

DISCUSSION

We demonstrated that the community of subaerial cyanobacteria and algae in Central European cities has a strong spatial structure, with a considerable spatial component of variation in species composition that is independent of the variation in climate. This is consistent with recent studies showing that not

only communities of macroorganisms, but also those of microorganisms, such as bacteria (Martiny *et al.*, 2006; Pommer *et al.*, 2007) or diatoms (Telford *et al.*, 2006; Vyverman *et al.*, 2007; Verleyen *et al.*, 2009; Heino *et al.*, 2010; Hájek *et al.*, 2011), are spatially structured, at least at larger spatial scales (Verleyen *et al.*, 2009). This pattern suggests that although microscopic cyanobacteria and algae are believed to have generally better dispersal abilities, as may be deduced from their large distribution ranges and small propagules (Rindi & Guiry, 2004; Neustupa & Škaloud, 2008; but see Jenkins *et al.*, 2007), their community composition and β -diversity is still structured by dispersal limitation.

Moreover, spatial structure of the community of cyanobacteria and algae was found to be much stronger than that of the communities of vascular plants and land snails across the studied cities. Redundancy analyses with PCNM-based spatial variables identified a weaker pure effect of space on plants and snails than on cyanobacteria/algae. This is surprising given that many vascular plant species possess heavy seeds with poor dispersal abilities (Klotz *et al.*, 2002), and land snails are traditionally believed to have low dispersal rates (Baur & Baur, 1995), especially those with body size larger than *c.* 10 mm (McClain & Nekola, 2008; Cameron *et al.*, 2010). The entire

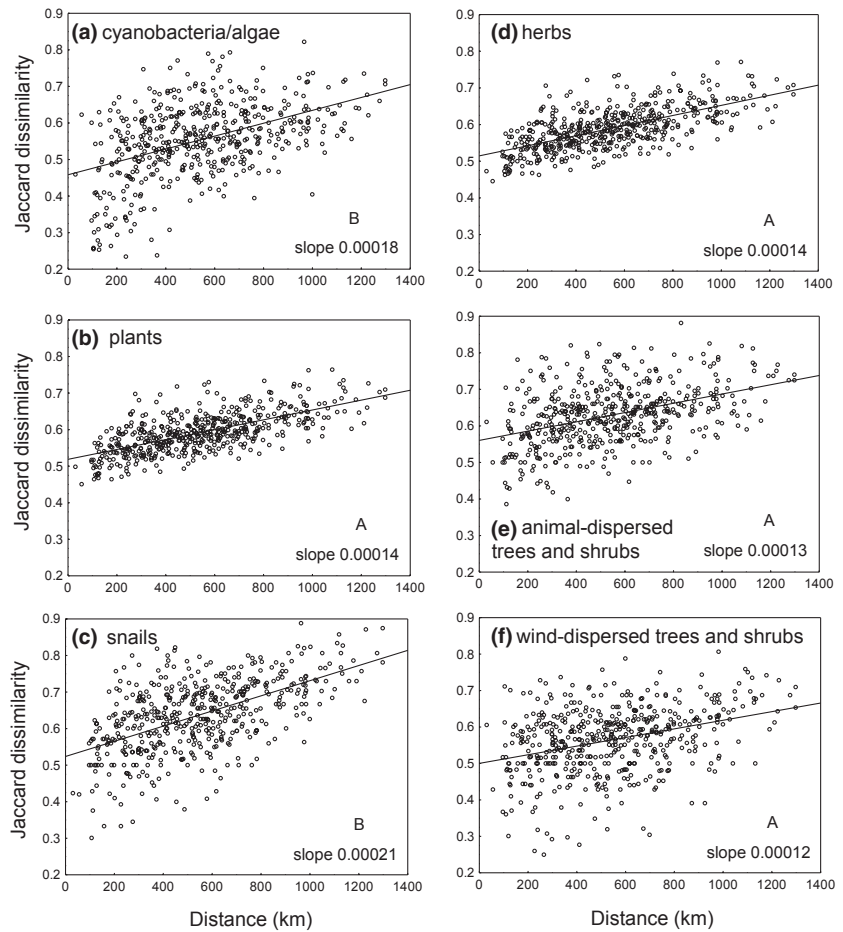


Figure 4 Relationships between the Jaccard indices of dissimilarity in species composition and geographical distance. Dissimilarity values resulting from 496 pairwise comparisons among the 32 Central European cities studied are plotted against between-city geographical distances. All relationships are significantly positive (Mantel test, $P < 0.001$); they are illustrated by the lines fitted by the least-square method. Differences in the slopes among the organism groups were tested by bootstrapping; the same letters indicate no differences between groups ($P < 0.05$).

snail body acts as a propagule, and their long-distance dispersal can be only passive, mostly on the surface or in guts of highly mobile animals such as birds (Gittenberger *et al.*, 2006; Kawakami *et al.*, 2008; Wada *et al.*, 2012). This is true for minute land snail species, and particularly for freshwater molluscs and their development stages (Piechocki, 1979). In contrast, most subaerial cyanobacteria and algae are adapted for wind dispersal. Their spores are very small, ranging from 2.5 to 25 μm in diameter, and in particular those smaller than 20 μm are easily dispersed (Nienow, 1996). Although most spores land within a few centimetres to 1 m from the parent, some are carried by air currents to more remote places. Thus, our finding of strong spatial structure within the community of subaerial cyanobacteria and algae sharply contradicts the results of other studies that compared the spatial and environmental components of variation in communities of organisms with large and small propagules sampled at the same set of sites (Beisner *et al.*, 2006; Hájek *et al.*, 2011), and found a stronger spatial structure in the former.

Thus we reject our initial hypothesis that in the studied urban environments communities of smaller organisms are structured by local niche-based processes consistent with the species-sorting model, as opposed to communities of larger organisms (or those with larger propagules) that are more strongly structured by dispersal limitation. This unexpected

finding can probably be explained by the fact that dispersal of subaerial cyanobacteria and algae is not directly affected by humans, although they were partly sampled on human-made substrates, such as buildings. In contrast, seeds and vegetative propagules of plants, as well as whole individuals of snails, are passively dispersed by humans through traffic, transport of commodities and the horticultural market, and such dispersal events are particularly frequent between cities and other densely populated areas (Hodkinson & Thompson, 1997; Cowie & Robinson, 2003; Aubry *et al.*, 2006). Therefore, we suggest that, unlike the case for subaerial cyanobacteria and algae, the spatial structure of plant and snail communities among cities is influenced by human-mediated dispersal of these organisms, and that this has a stronger effect than the passive dispersal of small propagules.

The larger proportion of the explained variation in species composition of subaerial cyanobacteria/algae than of the two groups of larger organisms is coupled with a lower β -diversity of the former. In this study we recorded 129 species of subaerial cyanobacteria/algae, 1196 species of vascular plants and 87 species of snails, which in turn represent *c.* 64%, 23.5% and 28%, respectively, of the total number of species within these groups known to occur in Central Europe (Tutin *et al.*, 1968-1993; Kerney *et al.*, 1983; Nienow, 1996). This indicates that, although the community of subaerial cyanobacteria/algae

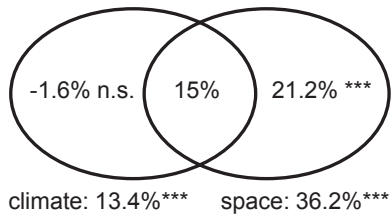
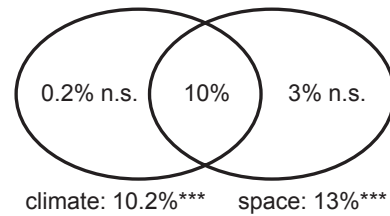
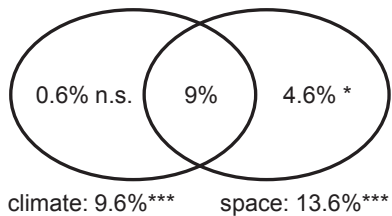
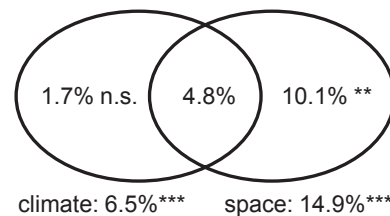
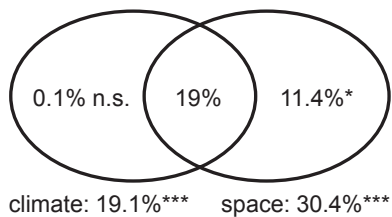
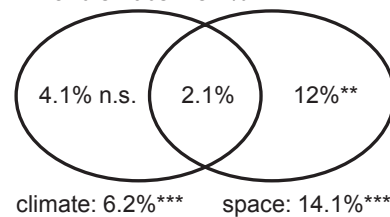
(a) cyanobacteria/algae: 34.6%**(d)** herbs: 13.2%**(b)** plants: 14.2%**(e)** animal-dispersed trees and shrubs: 16.6%**(c)** snails: 30.5%**(f)** wind-dispersed trees and shrubs: 18.2%

Figure 5 Partitioning the variation in species composition explained by climatic and spatial variables. Proportions of explained variation were calculated using redundancy analysis. The adjusted values of R^2 are given. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; n.s., not significant.

is very similar among cities, its structure is more deterministic with respect to space and inter-city distances, whereas more dissimilar communities of plants and snails are structured more stochastically. We hypothesize that the higher degree of stochasticity is partly due to human-mediated dispersal of plants and snails, but that other unknown factors can also be involved.

We detected no pure effects of climate on species composition of any of the studied groups of organisms. Climatic effects were included in the component of explained variation shared with spatial effects, but given that we sampled a transect of over 1200 km in length, from oceanic Belgium and the Netherlands to continental Hungary, this shared component was still rather low (19% for snails, and even lower for the other two groups). This indicates that human activities cause urban floras and faunas to be relatively homogeneous among cities in spite of climatic differences (McKinney, 2006). In plants, this interpretation is supported by the fact that the mean between-city similarity in species composition is larger within the group of archaeophytes (alien plants introduced before AD 1500) than within the group of native species (La Sorte *et al.*, 2007, 2008). The former, supported by human activities, have probably had enough time to disperse widely among cities, whereas many of the latter are rarely dispersed by

humans. However, this is not valid for neophytes (post-AD 1500 aliens), which are also supported by human activities, but are still spreading; therefore the dissimilarity in species composition among cities is large within this group. Nevertheless, neophytes are less numerous in our studied plots (Lososová *et al.*, 2011b), and their effect on the dissimilarity of total floras is therefore weaker. Similarly, alien snail species of large body size are restricted to the cities in the study area and are rather common there (see also Horsák *et al.*, 2009).

We would like to add two methodological remarks. First, the results of variation partitioning between environmental and spatial factors are critically dependent on whether or not the key environmental variables had been correctly measured and included in the analysis. We did not include any environmental variables other than climate in our analyses, because we sampled the same set of representative habitats for each group of organisms in each city, and used cumulative species lists across all studied habitats for each city. By using this methodology, we removed the effect of urban habitats (e.g. Sattler *et al.*, 2010; Lososová *et al.*, 2011a) and we assumed that the share of variation potentially explained by other environmental variables than climate would be very low in our data set. Bedrock types may have affected between-city differences in composition of plant and snail communities,

but most of the sampled sites were either on deep soil or had a large proportion of paved or asphalted areas, which alleviated the effect of different bedrocks.

Second, it might be argued that the large variation explained by the spatial component and small variation explained by climate in this study is due to the tendency of RDA with PCNM to inflate the variation explained by spatial variables (Gilbert & Bennett, 2010; Smith & Lundholm, 2010). However, Mantel tests, which tend to underestimate spatial component, but may provide evidence for environmental control where RDA does not, confirmed the results of the RDA–PCNM analysis. Moreover, our main result (i.e. spatial structure of cyanobacterial/algal community is stronger than that of the plant and snail communities) would be hardly affected by similar artefacts, because they would probably influence the results for each of these groups to a similar degree.

We conclude that communities of microscopic organisms, such as subaerial cyanobacteria and algae, can exhibit a distinct spatial structure and dispersal limitation, even though they mostly have large geographical ranges that result in low β -diversity. Their spatial structure can be even stronger than that in communities of organisms with larger propagules, provided that dispersal of larger propagules is facilitated by human activities.

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Author contributions: M.C. and Z.L. conceived the ideas and led the writing; M.C., Z.L., J.D., K.F., D.L., Z.O. and L.T. collected botanical data in the field; J.D. and V.Ř. identified and revised the herbarium specimens; M.H., T.Č. and L.J. collected and identified the land snails; B.U. cultivated and identified the cyanobacteria and algae; Z.L., K.K. and L.T. analysed the data; O.H. processed spatial data and prepared the map; all authors commented on the manuscript.

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