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Frank A. La Sorte

Myla F.J. Aronson

Nicholas S.G. Williams

Laura Celesti-Grapow

Sarel Cilliers

See next page for additional authors

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Authors

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RESEARCH PAPER

Beta diversity of urban floras among European and non-European cities

Frank A. La Sorte[1]*, Myla F. J. Aronson[2], Nicholas S. G. Williams[3,4], Laura Celesti-Grapow[5], Sarel Cilliers[6], Bruce D. Clarkson[7], Rebecca W. Dolan[8], Andrew Hipp[9], Stefan Klotz[10,11], Ingolf Kühn[10,11], Petr Pyšek[12,13,14], Stefan Siebert[6] and Marten Winter[11]

[1]*Cornell Lab of Ornithology, Ithaca, NY 14850, USA,* [2]*Department of Ecology, Evolution, and Natural Resources, Rutgers, The State University of New Jersey, New Brunswick, NJ 08901, USA,* [3]*Department of Resource Management and Geography, The University of Melbourne, 500 Yarra Blvd, Richmond, VIC 3070, Australia,* [4]*Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne, c/o School of Botany, The University of Melbourne, Melbourne, VIC 3010, Australia,* [5]*Environmental Biology Department, Sapienza University, Piazzale Moro 5, I-00185 Rome, Italy,* [6]*Unit of Environmental Sciences and Development, North-West University, Potchefstroom, South Africa,* [7]*Centre for Biodiversity and Ecology Research, Department of Biological Sciences, The University of Waikato, Hamilton 3240, New Zealand,* [8]*Friesner Herbarium and Center for Urban Ecology, Butler University, Indianapolis, IN 46208, USA,* [9]*The Morton Arboretum, Lisle, IL 60532, USA,* [10]*Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Strasse 4, 06120 Halle, Germany,* [11]*German Centre for Integrative Biodiversity Research (iDiv) Halle–Jena–Leipzig, Deutscher Platz 5d, 04103 Leipzig, Germany,* [12]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic,* [13]*Department of Ecology, Faculty of Science, Charles University Prague, Viničná 7, CZ-12843 Praha 2, Czech Republic,* [14]*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa*

ABSTRACT

Aim Cities represent an ideal study system for assessing how intensive land-use change and biotic interchange have altered beta diversity at broad geographic extents. Here we test the hypothesis that floras in cities located in disparate regions of the globe are being homogenized by species classified as invasive (naturalized species that have spread over a large area) or as a European archaeophyte (species introduced into Europe before AD 1500 from the Mediterranean Basin). We also test the prediction that the global influences of European activities (colonization, agriculture, commerce) have supported this outcome.

Location One hundred and ten cities world-wide.

Methods We examined the richness and composition of urban floras among European ($n = 85$) and non-European cities ($n = 25$) for species classified as native or non-native, or further classified as European archaeophyte or invasive. We modelled how geographic, climatic and anthropogenic factors were related to compositional similarity between European and non-European cities.

Results We found that most plants in the cities we examined, particularly non-European cities, were native and unique to each city. Non-native species were similarly unique, but occurred in much lower proportions relative to natives. Although European archaeophytes and invasive species also occurred in lower proportions, they had similar compositions among cities. European archaeophytes were most prevalent in European cities, but were most similar among non-European cities. Contrasting European and non-European cities, geography and climate were most relevant for native and invasive species, whereas climate and agriculture were most relevant for European archaeophytes.

Main conclusions Cities in disparate regions of the globe retain regionally distinct native and non-native plant assemblages, while invasive species, and especially European archaeophytes, were associated with lower beta diversity among cities. These findings suggest that intensive land-use change and biotic interchange, shaped through European influences, have had a world-wide effect on the beta diversity of urban plant assemblages.

Keywords

Agriculture, archaeophytes, beta diversity, biological invasions, biotic homogenization, extra-regional residence time, introduction pathways, non-native species, plants, urbanization.

*Correspondence: Frank A. La Sorte, Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.
E-mail: fal42@cornell.edu*

INTRODUCTION

Human activities reduce beta diversity, resulting in more similar ecological communities across space, or lower spatial turnover in species composition (McKinney & Lockwood, 1999; Baiser *et al.*, 2012). This process, often termed biotic homogenization, is characterized by a decline in regional distinctiveness through the loss of specialized native species and the increasing dominance of common and often non-native species (McKinney & Lockwood, 1999). Here, non-native species are species not indigenous to an area the presence of which is due to direct or indirect consequences of human activities (Pyšek *et al.*, 2004). Biotic homogenization has been investigated from taxonomic, functional and phylogenetic perspectives, and has been demonstrated across spatial extents and grains based primarily on occurrence data for a range of taxonomic groups (Baiser *et al.*, 2012). Nevertheless, some investigators have suggested that global homogenization is unlikely (Collins *et al.*, 2002) and the few spatially explicit taxonomic studies conducted at intercontinental or global spatial extents indicate that global biotic homogenization is not fully established (La Sorte *et al.*, 2007; Winter *et al.*, 2010; Villéger *et al.*, 2011). However, biotic homogenization has become a dominant ecological paradigm and, in many cases, is assumed to be a global phenomenon despite a lack of empirical evidence at global scales for many taxa. To determine the quality of these assumptions, and to better inform current research, intercontinental and global-scale investigations are needed.

Cities are considered to be centres of loss in regional distinctiveness due to their extremely high levels of human activity and land-use change, as well as human-mediated extirpations of native species and introductions of new species (Pyšek, 1998; Kühn & Klotz, 2006; McKinney, 2006; Aronson *et al.*, 2014). Cities world-wide share very similar environmental characteristics, such as high disturbance frequencies, heat island effects, a high density of built structures and impervious surfaces, and fragmentation of native land cover (Rebele, 1994; Pickett *et al.*, 2001; Faeth *et al.*, 2005). These features are expected to result in a common suite of urban-adapted biota world-wide (Williams *et al.*, 2009).

Due to their role as centres for transport, cities have a long history as foci of species introductions. In countries colonized by Europeans, the development of new cities or the expansion of existing cities was often the first form of large-scale land-cover change. This would be expected to leave cities with a long biological legacy of introduced species that continues to increase through globalization and the intensification of human-mediated biotic interchange (Hulme, 2009). Cities are therefore an ideal study system to improve our understanding of the continental and intercontinental patterns, drivers and implications of the effects of intensive human-mediated biotic interchange and land-use change on the structure and composition of ecological communities.

The composition of non-native species within ecological communities is often used to assess the impacts of human activities on beta diversity. Non-native species can affect composi-tional patterns among localities to differing degrees, depending on the time since first introduction into a non-native region (residence time; Rejmánek, 2000; Richardson & Pyšek, 2006) and their native place of origin (La Sorte & McKinney, 2006; La Sorte & Pyšek, 2009; Winter *et al.*, 2009). An additional facet to residence time is extra-regional residence time, which is defined as the residence time of a species in a region outside its native range whose propagules are then introduced into a new region (La Sorte & Pyšek, 2009). The primary example of extra-regional residence time is that of European archaeophytes, plant species introduced into regions of Europe between the initiation of agricultural activities during the Neolithic period (*c.* 4000 BC) and the European exploration of the Americas (*c.* AD 1500; Preston *et al.*, 2004; Pyšek *et al.*, 2004). During their residence time in Europe, European archaeophytes developed an association with early agricultural activities that remains evident today (Pyšek *et al.*, 2005), an association that is likely to have promoted the transport, introduction and establishment of archaeophytes in regions outside Europe (La Sorte & Pyšek, 2009), including introductions through agricultural activities in regions that were later urbanized. European archaeophytes have been implicated in the homogenization of floras within Europe (La Sorte *et al.*, 2008; Ricotta *et al.*, 2012), North America (La Sorte & Pyšek, 2009) and between the two continents (La Sorte *et al.*, 2007).

Invasiveness, defined here as the ability of a non-native species to become naturalized and spread over a large geographic area (Pyšek *et al.*, 2004), is also likely to be an important factor in determining how plant species affect compositional patterns among cities. Invasive species are more likely to be transported between cities through human activities due to their high prevalence and, once introduced, are often pre-adapted to the high disturbance levels and early successional stages found in urban areas (Catford *et al.*, 2012). The introduction pathway of an invasive species may also be important (Pyšek *et al.*, 2011). Species that have been intentionally introduced by humans are likely to have increased propagule pressure, which may support their establishment and spread (Křivánek *et al.*, 2006). In addition, place of origin and its level of invasiveness are not necessarily independent. For example, plant introductions have primarily been unidirectional from Europe to North America (La Sorte *et al.*, 2007; Winter *et al.*, 2010) with a large proportion of European archaeophytes identified as invasive in North America (La Sorte & Pyšek, 2009), indicating the importance of European agriculture, human settlement, trade and commerce in defining patterns of biotic interchange (Crosby, 1986; di Castri, 1989).

Using the largest global database of urban plant occurrences, compiled from 110 globally distributed cities (Aronson *et al.*, 2014), we examine the continental and intercontinental patterns and associations of urban plant diversity. We test the hypothesis that floras in cities from disparate regions of the globe are taxonomically homogenized and investigate the contribution of invasive species, European archaeophytes and other non-native species to this pattern. Our goal is to determine how the combination of urbanization and human-mediated biotic

interchange driven by European influences may have altered geographic patterns of urban plant diversity.

METHODS

Data compilation

We compiled vascular plant floras of species occurrence for 110 cities, distributed globally but with the majority (77%) located in Europe (Fig. 1a; see Appendix S1 in Supporting Information). We merged all varieties and subspecies identified in each flora into the species rank and standardized taxonomic nomenclature using the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/; accessed July 2011). The 110 floras contained a total of 14,240 plant species.

The 110 floras are a result of intentional surveys of spontaneous vegetation (i.e. species that grow and reproduce outside cultivation) within each city. The floras were compiled using a variety of different field survey techniques, herbarium records or a combination of both, and the floras estimate the composition of species within individual cities for a range of time intervals, occurring after 1900 but primarily between 1950 and 2009 (Appendix S1). Sampling effort was therefore highly variable among the 110 cities; however, there is no indication that this variation contained geographic biases that would influence our results (Appendix S1).

To provide a standard classification system for species that would support compositional analysis across multiple floras, we used methods consistent with those developed in similar studies (La Sorte *et al.*, 2007, 2008). In non-European cities, species were classified as either native or non-native based on classifications in the original floras (Appendix S1). In European cities, species were classified as native or, if non-native, as either archaeophyte or neophyte based on classifications in the original floras (Appendix S1): these are non-native species introduced to Europe before and after *c.* AD 1500, respectively (Pyšek *et al.*, 2004). Classification systems used in the original floras relied on a variety of different approaches to identify non-native species, which were typically identified as non-native to the region where the city was located or non-native to the broader floristic region. Among the European cities, 538 species were identified as European archaeophytes. We used this list of 538 species to identify European archaeophytes in all European and non-European cities. From the total of 14,240 species in our floras, we identified 634 invasive species from a list of 830 invasive plant species of the world (E. Weber, University of Potsdam, unpublished updated database based on Weber, 2003). Of the 538 European archaeophytes, 66 were identified as invasive (12%). These species were classified as both European archaeophytes and invasive in our analysis. The species in each city were categorized as European archaeophyte and/or invasive; species that were not identified in these categories retained their original classification as either native or non-native.

We identified introduction pathways for the 634 invasive species based on 10 non-mutually exclusive classes: (1) ornamental; (2) boundary or barrier; (3) wood; (4) building
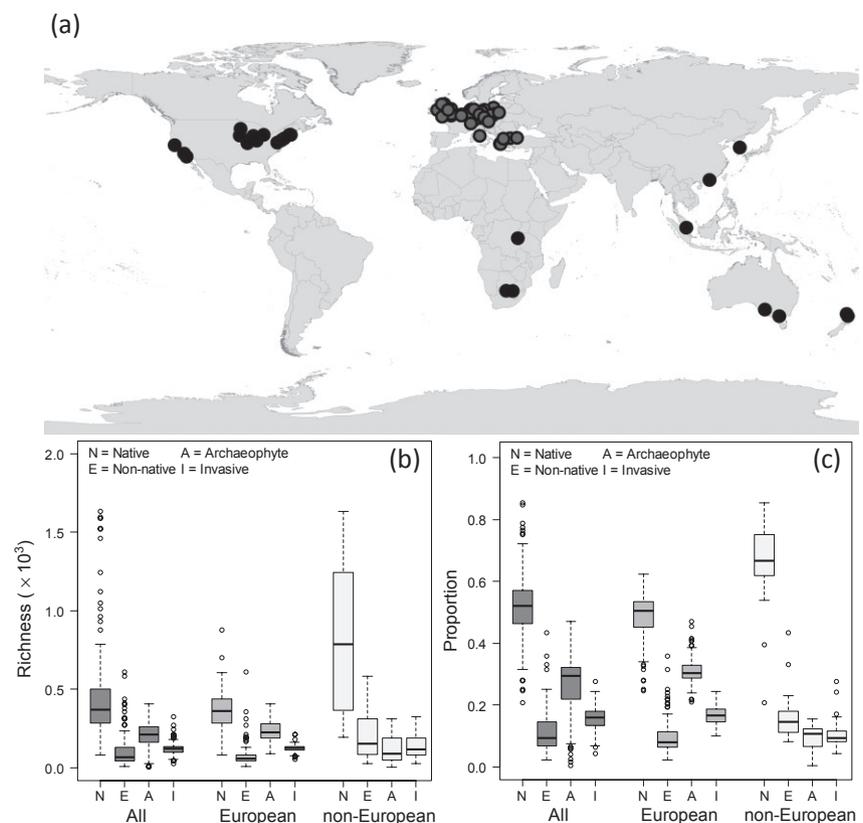
(a)

Figure 1 (a) The location of the 85 European cities (light gray points) and the 25 non-European cities (dark gray points) considered in the analysis. Box-plots of (b) species richness and (c) the proportion of (N) native species, (E) non-native species, (A) European archaeophytes and (I) invasive species for all cities combined (All) and for the 85 European and 25 non-European cities.

materials; (5) re-vegetation, shelter or soil improvement; (6) erosion control; (7) fuelwood; (8) human food; (9) animal food or forage; and (10) unknown (for details see Weber, 2003). The 634 invasive species were allocated up to five introduction pathways, with 74% having one class, 18% two, 7% three, 1% four and < 1% five classes. We analysed the distribution of introduction pathways among the 634 invasive species using chi-square goodness-of-fit tests, and the distribution of introduction pathways within cities using one-way ANOVA.

Compositional analysis

We examined the floristic dissimilarity between cities using the Simpson multiple site dissimilarity index (M_{Sim}; Baselga *et al.*, 2007). This index is in the range [0,1] with values approaching one indicating greater dissimilarity. This index has conceptual and methodological advantages over traditional pairwise approaches, and provides an estimate of overall compositional heterogeneity among sites independent of differences in species richness (Baselga, 2013). We applied the index to three geographic classifications of cities: (1) all 110 cities combined, (2) 85 European cities, and (3) 25 non-European cities (see Fig. 1a). We considered four classifications of species as defined above: (1) native species, (2) non-native species, (3) species identified as European archaeophytes, and (4) species identified as invasive.

We used permutation tests to estimate the likelihood of observed differences in compositional dissimilarity among cities occurring by chance alone between: (1) native species and non-native species, (2) native species and European archaeophytes, and (3) native species and invasive species. The difference between the Simpson multiple site dissimilarity index calculated for native species and for each of the three categories of species provided our test statistic for each permutation procedure. For non-native species, we permuted native and non-native classifications among species within each city's flora independently for species that were not classified as archaeophyte or invasive. For European archaeophytes, we classified 538 randomly selected species as European archaeophytes from the full list of 14,240 species, whose presence was then determined in all the floras. For invasive species, we classified 634 randomly selected species as invasive from the full list of 14,240 species, which were then identified in all the floras. Native species thus provided an ecological baseline for estimating the compositional effects of the other three categories of species.

After each permutation procedure was implemented for each category of species, the Simpson multiple site dissimilarity index was recalculated for that category and for native species. The difference between these two estimates was then extracted. The permutation procedure was implemented 999 times for each of the three categories of species. Where the observed test statistic occurred within the distribution of 999 permutation-derived test statistics was then used to estimate one-sided *P*-values. For each category, the *P*-value is the estimated probability of getting a difference in compositional dissimilarity from native species as extreme as, or more extreme than, the observed difference. One-

sided tests were used because the permutation procedures did not result in distributions that included zero (i.e. native species always retained greater dissimilarity) and we were not interested in testing if the differences in compositional dissimilarity were smaller than expected by chance.

European versus non-European cities

We examined patterns of floristic dissimilarity between European and non-European cities using the β_{sim} dissimilarity index (Lennon *et al.*, 2001; Koleff *et al.*, 2003). This index is in the range [0,1] with values approaching one indicating greater dissimilarity. We calculated the index between each of the 25 non-European cities and each of the 85 European cities for: (1) native species, (2) European archaeophytes, and (3) invasive species. We then averaged the 85 values for each of the three classes of species to give one measure of floristic dissimilarity between each of the 25 non-European cities and all European cities combined.

We used generalized additive models (GAMs) to test the influence of five predictor variables hypothesized to correlate with floristic dissimilarity between European and non-European cities. A GAM was applied separately to native species, European archaeophytes and invasive species. The predictors include: (1) the establishment date of the non-European city based on the year the city was founded, (2) the average geodesic distance of the non-European city from European cities, (3) the average climatic distance of the non-European city from European cities, and (4) the proportion of cropland within a 15-km radius of the city centre before urbanization of the non-European city. Although a city's founding date is not universally defined, this information is readily available and is used here to estimate on a relative scale when urbanization was initiated in each city. The fifth predictor is the population size of each non-European city, which was included to control for possible species–area effects. Population size was based on the most recent estimates compiled by the United Nations (UN) Statistics Division for 2011. We used population size because, unlike city area, it is based on national estimates that are compiled by the UN in a consistent and systematic fashion. Since the majority of the cities we examined have experienced population growth over the past 60 years, the 2011 population estimates are likely to be larger than the population size that existed when the city's flora were compiled.

Climatic similarity was estimated using the Malahanobis distance between the non-European city's climate vector and the centroid of the climate of all European cities. Four climate variables were used in these calculations: annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality (BIOCLIM variables BIO1, BIO4, BIO12 and BIO15, respectively). These variables are gridded at a 30 arcsec resolution (*c.* 1 km at the equator) and summarize climatic conditions for the period 1950–2000 (WorldClim; Hijmans *et al.*, 2005). Temperature seasonality was estimated using the standard deviation of monthly temperature values and precipitation seasonality using the coefficient of variation of monthly precipita-

tion values. We summarized these measures for each city based on their mean values calculated within a circle of radius 15 km centred on each city.

The proportion of cropland was estimated using the HYDE 3.1 historical land-cover inventory data set (Klein Goldewijk *et al.*, 2011) that includes global cropland cover from 10,000 BC to AD 2005 at a resolution of 5 arcmin (*c.* 10 km at the equator). For each of the 25 non-European cities, we calculated the maximum proportion of cropland that occurred within a circle of radius 15 km centred on each city during the period from the city's date of establishment to 2005. The proportion of cropland peaked for the majority of the non-European cities during the 1800s, and dropped in association with increasing urbanization during the 1900s (Fig. S1 in Appendix S2). Our measure therefore represents the maximum degree of land-use change before urbanization, and distinguishes cities where urbanization occurred on agricultural lands from those where urbanization removed intact native vegetation.

GAM variable selection was implemented using a multistep approach (Wood, 2006). Initially we started with a full model containing all five predictors with smoothing parameters having a basis dimension (*k*) equal to four. We then dropped predictors following three criteria. First, we checked whether the estimated degrees of freedom for each smoothing parameter were close to one, indicating that the relationship was linear. Second, we checked whether after fitting the GAM, zero was included in the confidence band throughout the range of the predictor. Third, we checked whether there was a drop in the general cross-validation score after removing the predictor. If all three criteria applied, we dropped the predictor from the model. If the estimated degrees of freedom were close to one but the other two criteria did not apply, we replaced the smoothing parameter with a linear term for the predictor. All analyses were conducted in R version 2.15.1 (R Development Core Team, 2014). The GAM was implemented using the mgcv library (Wood, 2006).

RESULTS

The 110 cities considered in this study contained a median of 766 species with a median of 373 native, 69 non-native, 214 European archaeophyte and 124 invasive species (Fig. 1b). The 110 cities had a median proportion of 52% native, 9% non-native, 29% archaeophytes and 16% invasive species (Fig. 1c). European cities had a greater proportion of archaeophyte (Welch two-sample *t*-test, $t = 21.63$, d.f. $= 42.9$, $P < 0.001$) and invasive species ($t = 5.02$, d.f. $= 27.8$, $P < 0.001$) relative to non-European cities (Fig. 1c). Non-European cities had a greater proportion of native species (Welch two sample *t*-test, $t = 6.17$, d.f. $= 29.3$, $P < 0.001$) and non-native species ($t = 3.58$, d.f. $= 33.7$, $P = 0.001$) relative to European cities (Fig. 1c).

All 10 introduction pathways were identified among the 634 invasive species. When examined among the 634 invasive species, introduction pathways were not distributed uniformly (goodness-of-fit $\chi^2 = 862.5$, d.f. $= 9$, $P < 0.001$) with the majority of species classified as ornamental (38%) or unknown (23%).
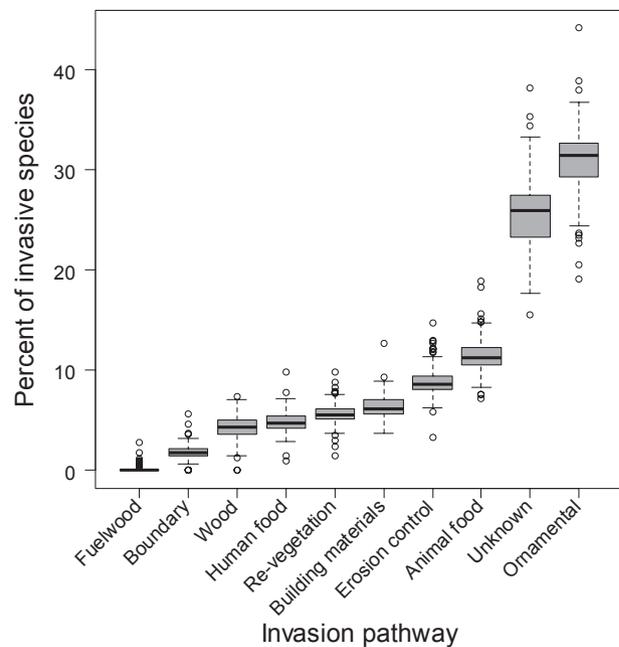

Figure 2 The percentage of invasive species ($n = 634$) classified into 10 introduction pathways within the floras of 110 cities ordered by increasing values. See Methods for details about introduction pathways.

When examined among the 110 cities, introduction pathways were not distributed uniformly among invasive species (one-way ANOVA, $F_{9,1090} = 2968.8$, $P < 0.001$) with the majority classified as ornamental (mean = 31%) or unknown (mean = 26%; Fig. 2).

Compositional analysis

Dissimilarity in species composition was generally high among the 110 cities, with native species having the greatest dissimilarity ($M_{Sim} = 0.964$; Fig. 3). Dissimilarity in species composition for non-native species did not differ from that observed for native species ($M_{Sim} = 0.955$, $P = 1.00$), but was significantly lower for European archaeophytes ($M_{Sim} = 0.915$, $P < 0.001$) and invasive species ($M_{Sim} = 0.934$, $P < 0.001$; Fig. 3). Results were analogous when European and non-European cities were considered separately; however, dissimilarity was particularly low for archaeophytes in non-European cities ($M_{Sim} = 0.681$, $P < 0.001$; Fig. 3), i.e. there were similar suites of European archaeophytes in non-European cities. Thus, European archaeophytes and invasive species increased compositional similarity among cities world-wide and also among European and non-European cities. Because the compositional dissimilarity of non-native species did not differ from native species, non-native species were not considered further in our analysis.

European versus non-European cities

Native species assemblages between non-European and European cities were strongly dissimilar. The relationship between

dissimilarity and our five predictors was weak overall for native species, but all differed statistically from zero (Fig. 4, Table 1, Fig. S2 in Appendix S2). After controlling for population size, the best combination of predictors for native species suggested similarity decreased with geodesic and climatic distance from European cities, with geodesic distance having a slightly unimodal relationship (Fig. 4, Table 2). Non-European cities therefore shared very few native species with European cities, and this dissimilarity increased with increasing geographic and climatic separation.

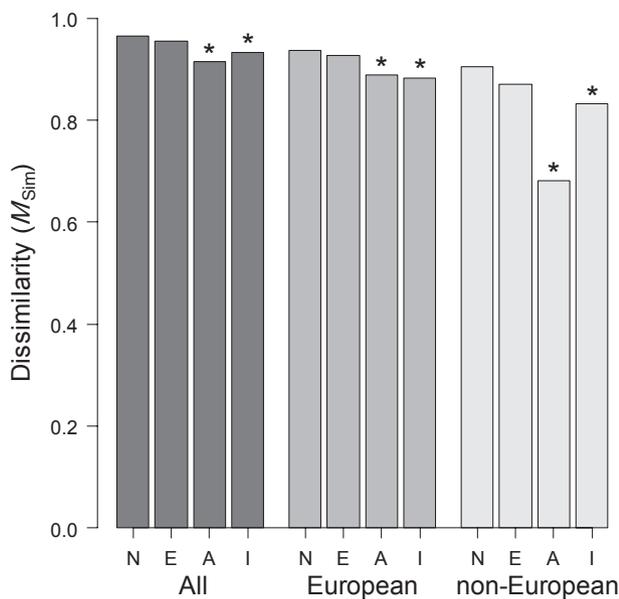The results for invasive species and European archaeophytes differed substantially from native species (Fig. 4, Table 1, Fig. S2 in Appendix S2). When the five predictors were examined individually, invasive species had weaker associations with broader confidence bands but with steeper slopes that differed statistically from zero for all but population size. European archaeophytes, in contrast, had stronger associations with lower variance and narrower confidence bands but shallower slopes that did not consistently differ from zero. Specifically, compositional dissimilarity of invasive species and European archaeophytes was positively correlated with the establishment date of non-European cities, with younger cities having greater compositional dissimilarity (Fig. 4a). Invasive species and European archaeophytes also had positive correlations with climatic similarity to European cities (Fig. 4c) and inverse correlations with the proportion of cropland before urbanization (Fig. 4d). Geographic distance was slightly unimodal for archaeophytes and strongly so for invasive species, patterns driven by cities in New Zealand and Australia that had the greatest geographic separation from Europe, and lower than expected levels of dissimilarity overall, especially with invasive species (Fig. 4b).

After controlling for population size, the best combination of predictors of invasive species compositional dissimilarity was geodesic and climatic distance from European cities (Table 2, Fig. 4). For European archaeophytes, the best combination of predictors after controlling for population size was climatic distance from European cities and the proportion of cropland before urbanization (Table 2, Fig. 4). In total, these results indicate that the processes associated with the distribution of native species between European and non-European cities differ substantially from those that define the distributions of European archaeophytes and invasive species.

DISCUSSION

Our results suggest that human-mediated biotic interchange has resulted in lower compositional dissimilarity (lower beta diversity) among urban floras located in disparate regions of the globe. Invasive species and European archaeophytes strongly influenced these patterns, with European archaeophytes having a larger effect, particularly for cities outside Europe.

Native species made up the largest proportion of species in urban floras, especially outside Europe, and were defined by

Figure 3 The Simpson multiple site dissimilarity index for (N) native species, (E) non-native species, (A) European archaeophytes and (I) invasive species for all cities combined (All) and for European ($n = 85$) and non-European cities ($n = 25$). Asterisks indicate levels of compositional dissimilarity that, when compared with that observed with native species, were unlikely to have occurred by chance alone ($P < 0.001$ based on 999 permutations).

Table 1 Summary of smooth terms with the approximate F statistic, estimated degrees of freedom (e.d.f.), P-value and adjusted R^2 for single-predictor generalized additive models examining the relationship between the compositional dissimilarity of native species, European archaeophytes and invasive species between European ($n = 85$) and non-European cities ($n = 25$). See Methods for details on predictors and models.

Predictor	Native				Archaeophyte				Invasive			
	F	e.d.f.	P	R^2	F	e.d.f.	P	R^2	F	e.d.f.	P	R^2
Establishment date	23.18	1.00	< 0.001	0.48	9.08	1.00	0.006	0.25	9.48	1.00	0.005	0.26
Geodesic distance	12.06	1.98	< 0.001	0.53	1.83	1.84	0.180	0.12	8.46	2.40	0.001	0.51
Climatic distance	5.41	1.00	0.029	0.16	11.50	1.00	0.002	0.30	26.94	1.00	< 0.001	0.52
Cropland	10.33	1.08	0.003	0.33	5.68	1.00	0.026	0.16	20.61	1.00	< 0.001	0.45
Population size	0.54	1.00	0.471	0.02	0.08	1.00	0.783	0.04	0.04	1.19	0.909	0.03

Figure 4 The fit of generalized additive models (GAM) with 95% confidence bands examining the individual relationship between average dissimilarity in species composition between European ($n = 85$) and non-European cities ($n = 25$) based on four predictors and three categories of species. The categories include native species (dotted line, squares), European archaeophytes (dashed line, triangles) and invasive species (solid line, circles). Each category contains 25 points for the 25 non-European cities. The predictors include (a) the establishment date of the non-European city (small values represent older establishment dates and older cities), (b) average geodesic distance between each non-European city and all European cities, (c) the climatic distance between each non-European city and all European cities based on four climate measures, and (d) and percentage of cropland within the region of the non-European city before urbanization. Asterisks in the plot legends indicate categories where the GAM smoothing term differed from zero ($P < 0.05$; see Table 1). See Methods for additional details on models, categories and predictors.
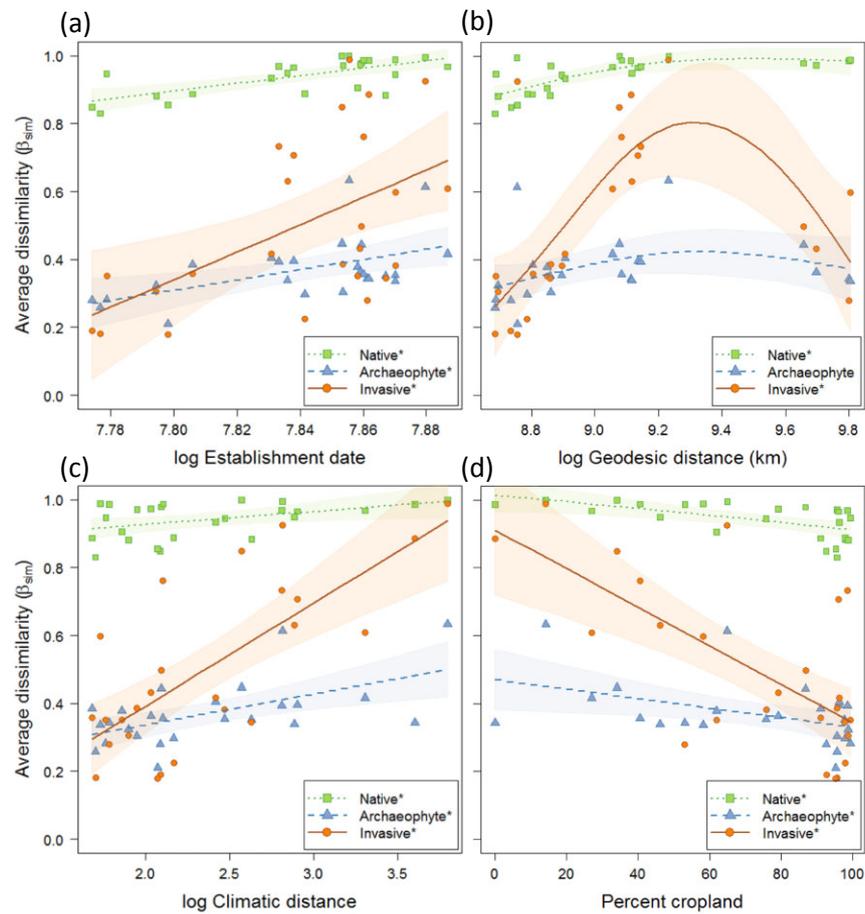

Table 2 Summary of smooth terms with the approximate F statistic, estimated degrees of freedom (e.d.f.), P-value and adjusted R^2 for predictors selected by generalized additive models examining the relationship between the compositional dissimilarity of native species, European archaeophytes and invasive species between European ($n = 85$) and non-European cities ($n = 25$). In each reduced model, e.d.f. values greater than one are smooth terms and e.d.f. values equal to one are parametric linear terms. See Methods for details on predictors, models and the variable selection procedure.

Predictor	Native			Archaeophyte			Invasive		
	F	e.d.f.	P	F	e.d.f.	P	F	e.d.f.	P
Geodesic distance	20.81	1.36	< 0.001				3.25	1.70	0.058
Climatic distance	11.11	1	0.003	5.58	1.73	0.011	15.69	1	< 0.001
Cropland				2.69	2.23	0.079			
Population size	11.06	1.00	0.003				4.20	1	0.054
R^2		0.68			0.44			0.64	

distinct species assemblages that were strongly dissimilar among cities. However, our approach for classifying native species is not necessarily comprehensive. First, our approach for providing a consistent classification of invasive species and European archaeophytes among floras may result in lower proportions of native species. This is especially the case with European archaeophytes where the distinction between native and archaeophyte within individual cities is often uncertain; this can

result in discrepancies among classifications of species in floras (Chytrý *et al.*, 2008a). Another consideration are species that are not native to the local floristic province where the city is located but are native elsewhere within the broader floristic region (extra-limital native; La Sorte & McKinney, 2006). Our data lacked this distinction, which may have over-emphasized the proportion of native species in our floras. For example, urban floras in the north-eastern USA were composed of *c.* 13%

extra-limital natives, which when compared with native species were associated with limited differentiation of species composition (La Sorte & McKinney, 2006).

Despite the limitations in how native species were classified in our analysis, our findings still indicate that the level of geographic separation among cities is substantial enough to result in unique assemblages of native species, even among the highly aggregated cities of Europe. However, compositions of native floras have been significantly simplified by urbanization (Aronson *et al.*, 2014). Thus, through local extinctions and the non-random geographic locations of cities, our findings suggest cities retain regionally distinct remnants of native floras. We believe these findings highlight the need for additional and more focused evaluations of these native floras to better understanding their ecology, which in turn can be used to maintain or promote this unique form of plant diversity.

Our findings show that European cities and European colonization history more generally may have influenced the composition of urban floras outside Europe. The greater the climatic distance from European cities, the less similar the composition of native species, European archaeophytes and especially invasive species. Geographic distance from European cities had a similar association with native species, but a slightly different one with European archaeophytes that was weakly supported, and a dramatically different relationship with invasive species. The presence in New Zealand and Australia of the suite of European archaeophytes, and especially invasive species found in European cities, resulted in a strong nonlinear relationship with geographic distance. Deliberate introductions of European species into New Zealand and Australia are likely to be partly responsible, as is the long history of European immigration and commerce resulting in land-use changes replicating the agricultural activities and urban environments found in Europe (Crosby, 1986). New Zealand, the most isolated island system examined in our study, is more invaded than its mainland counterparts (Pyšek & Richardson, 2006) and has lower native species richness, with many introduced plants able to fill ecological niches due to the lack of many functional groups within the native flora (Atkinson & Cameron, 1993).

The presence of cropland before urbanization was most strongly associated with European archaeophytes, suggesting that agricultural activities have assisted in the spread and establishment of European archaeophytes outside Europe. Extending the findings of La Sorte & Pyšek (2009), these results suggest that European archaeophytes represent a global example of the combined consequences of extra-regional residence time and human-mediated biotic interchange. Geographic distance from source populations in Europe and city age had limited influence on the patterns of occurrence for European archaeophytes, but their association with climatic distance suggests that, even though broadly distributed among urban areas, these species are still constrained, albeit to a limited degree, by climate (see Fig. 3c). The lack of a strong influence of city age suggests that European archaeophytes can quickly become established within non-European cities due to early introductions, high propagule pressure and a strong affinity to anthropogenic environments

and activities developed through residence time in Europe (Chytrý *et al.*, 2008b). European archaeophytes represents a fixed species pool and the role of these species as a global homogenizing influence, at least in urban areas, is likely to decline. This is due in large part to the increasing importance of invasive species, the growth of global commerce and the decline in the size and frequency of patches of arable habitats in urban areas (Pyšek *et al.*, 2005).

The variables associated with European archaeophytes are in strong contrast to those identified for invasive species. By definition, invasive species are locally abundant and geographically widespread, and homogenization is therefore a logical consequence of the invasion process (McKinney & La Sorte, 2007). Unlike European archaeophytes, the majority of invasive species represent more recent introductions with shorter residence times, probably no extra-regional residence time in Europe or other regions and more limited associations with pre-urban agricultural activities. The primary driver underlying the invasion process for these species is therefore the direct and indirect consequences of modern anthropogenic activities (Pyšek *et al.*, 2010). While agricultural activities have probably decreased as a key driver for new invasions in urban areas, our findings are consistent with other studies suggesting that the ornamental introduction pathway has increased in importance (Dolan *et al.*, 2011).

In contrast to invasive species and European archaeophytes, the introductions of non-native species that do not fall into these two categories tend to be more stochastic (Qian & Ricklefs, 2006). This less directed process has resulted in compositional patterns among cities that, as documented in this study, are more similar to that observed with native species. In some regions, such as Europe, the variability in recent non-native introductions has resulted in the differentiation of species composition among cities (La Sorte *et al.*, 2008).

The generally high dissimilarity among cities identified in our analysis suggests that any patterns of homogenization may have limited ecological effects, especially for cities outside Europe, which currently have very low proportions of invasive species and European archaeophytes. Nevertheless, we were unable to account for variation in species abundance as only occurrence data were available. Compositional patterns based on species occurrence have been found to be associated with more pronounced homogenization trends when abundance information is included in the assessment (La Sorte & McKinney, 2007). It is likely the distribution of abundances among plant species in cities is substantially skewed towards invasive species (McKinney & La Sorte, 2007). In addition, native species are likely to be functioning under an extinction debt (Hahs *et al.*, 2009; Gilbert & Levine, 2013) while invasive species are experiencing an invasion debt (Essl *et al.*, 2011), defined as time lags in the cause–effect relationship leading to extinction or invasion. Invasive species and European archaeophytes may therefore fulfil a larger ecological role within cities than suggested by occurrence information alone. Specifically, these species may more readily fill functional niches that are unique to urban environments or were vacated through the loss of native species.

In summary, our findings suggest that invasive species and European archaeophytes have promoted the homogenization of urban floras across disparate regions of the globe. Our findings indicate that introduction pathways for European archaeophytes may be due to historical agricultural activities within the region, and for invasive species the human preference for non-native ornamentals within cultivated areas. We conclude then that biotic homogenization of urban plant communities is a developing phenomenon that is likely to increase in intensity and extent into the future with invasive species probably taking on a more significant role. However, it must be noted that this conclusion is limited to urban systems, and the implications of our findings for the surrounding areas are not well understood and represent an important topic for further study. Additionally, not all regions were fully represented in our analysis. To add much needed international breadth to current research, and to expand and refine upon our conclusions, ecological data are needed from more non-European cities, in particular cities in the Afrotropics, Neotropics and the western portion of the Palaearctic.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 The 110 cities considered in the analysis and the total number of species, native species, non-native species, invasive species and European archaeophytes identified in each flora and the data source.

Appendix S2 Supporting figures of the percentage of cropland and urban land cover from HYDE 3.1; the percentage of invasive species classified into 10 introduction pathways; and the relationship between dissimilarity in species composition between European and non-European cities and human population size.

BIOSKETCH

Our research team is interested in exploring, from a global perspective, the patterns of urban biota and the physical, biological and social processes that have shaped them in order to better understand the impacts of urbanization and its implications for biodiversity conservation and sustainability within cities.

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