

Effects of alien species on homogenization of urban floras across continents: a tale of two mediterranean cities on two different continents

Pedro P. Garcillán^{1,*}, Elías D. Dana², Jon P. Rebman³ & Julio Peñas⁴

¹Centro de Investigaciones Biológicas del Noroeste, Instituto Politécnico Nacional 195, Col. Playa Palo de Santa Rita; La Paz, Baja California Sur 23096, Mexico

²Grupo de Investigación Transferencia de I+D en Recursos Naturales, Universidad de Almería, ES-04120, Almería, Spain

³San Diego Natural History Museum, P.O. Box 121390, San Diego, CA 92112, USA

⁴Departamento de Botánica, Universidad de Granada, ES-18071 Granada, Spain

*Author for correspondence: ppgarcillan@cibnor.mx

Background and aims – Biotic homogenization, i.e. increasing similarity between communities through time, is promoted by alien species exchange. Biotic homogenization can occur at several spatial scales. Urban environments, with their deep and convergent anthropogenic transformation worldwide, are nodes of intense species exchange. Our objective was to explore biotic homogenization at a global scale, and to achieve this goal we analyzed the effect of alien species on homogenization of two urban floras at an intercontinental scale.

Methods – We sampled the spontaneous flora of two mediterranean cities located on two different continents: Almería (Europe) and Ensenada (North America) and analyzed the effect of alien species on the similarity between both urban floras.

Key results – Floristic similarity between both cities increased significantly due to alien species establishment. Alien species corresponded mainly to biotic exchanges occurring between both mediterranean regions, especially from Mediterranean Basin to California. Native species from the Mediterranean Basin are the principal group of total exchanged species, and therefore of increased similarity, with very little weight to archaeophytes. Alien species coming from third regions have a minor impact on floristic homogenization between these two cities, and they apparently even have a differentiating effect.

Conclusions – The trend of biotic homogenization increasing as a result of biotic exchange at different scales does not seem to be temporally or spatially uniform. It reflects, at least partially, the path of footprints following human expansion history on Earth.

Keywords – Alien species, homogenization, mediterranean regions, urban floras.

INTRODUCTION

The increasing impacts and geographical expansion of human land use during the last centuries have transformed natural systems worldwide (Haberl et al. 2007, Ellis et al. 2010, Steffen et al. 2011). One of the global changes caused by this anthropogenic modification of the biosphere is the growing biotic exchange that occurs at different geographical scales (Drake et al. 1989, Mack et al. 2000, Kowarik 2003, Perrings et al. 2005). The establishment of alien species (i.e. species translocated intentionally or unintentionally by human activities beyond their native biogeographical regions, Richardson et al. 2000, Pyšek et al. 2004), influences diversity patterns and dynamics of ecological systems (Mack et al. 2000, Godefroid 2001, Ellis & Ramankutty 2008, La Sorte et al. 2008, Vilà et al. 2009).

One of the potential effects of alien species on biodiversity is biotic homogenization, defined as the increase in biological similarity between communities through time (McKinney & Lockwood 1999, Olden & Poff 2004). However, the spread of alien species does not necessarily always lead to increasing similarity (Olden & Poff 2003). Biotic homogenization is a process of multidimensional factors that can occur at several levels of biological organization: taxonomic, genetic or functional (Olden & Rooney 2006), and across different geographical scales and time frames (Ricotta et al. 2012, Campos et al. 2013).

Biotic homogenization can occur not only due to geographic expansion of some alien species ('winners'), but can also be caused by the range reduction of others, normally native species ('losers') (McKinney & Lockwood 1999). Some

mechanisms that can change species ranges are environmental disturbance and transportation of alien species (Vitousek et al. 1996). Probably, no other human land use such as urbanization contains a stronger combination of these two potential mechanisms responsible for biotic homogenization. Urbanization is an intense anthropogenic modification of the environment to fit the ecological requirements of only one species, human beings, that results in an ecological convergence of urban habitats worldwide (McKinney 2006). On the other hand, cities are nodes where human activities of surrounding regions are anchored to form a complex geographical network across different scales based on the movement of people and products. Therefore, urban areas are places where local extirpation of native species and the introduction of new species occur intensively (Celesti-Grapow & Blasi 1998, Godefroid 2001, Wittig 2004, McKinney 2006). Urban populations and urbanization processes are estimated to continue increasing into the future (United Nations 2012). Therefore, we can think of urbanized areas as a growing and scattered forefront of biotic homogenization worldwide (McKinney 2006). In this way, urban areas are unintentional experiments where dynamics of worldwide species exchange can be explored to understand some of the long-term consequences of the globalization of the Earth's biota (Vitousek et al. 1997).

In one of the first studies on intercontinental homogenization, La Sorte et al. (2007) found that alien species increased homogenization between urban floras of Central Europe and Eastern United States of America (USA) and that this process was driven primarily by the shared archaeophytes (i.e. alien species that arrived to Europe associated with human activities from the beginning of the Neolithic period to the

year 1500). Furthermore, homogenization was due mainly to unidirectional flow from Central Europe to North American cities. These patterns of biotic exchange do reflect the geographical print of human history between the two regions, that is to say the intense and prolonged relationship between the USA and Western Europe during the last two centuries (La Sorte et al. 2007).

The pioneering work of La Sorte et al. (2007) was done using long-time established cities of medium size (979,000 inhabitants on average), and well interconnected inside their respective temperate biomes found in Central Europe and Eastern USA. In our present study, we were interested to explore to what extent these patterns of intercontinental homogenization have occurred in other types of cities and biomes, i.e. with a different biogeography and human history. More specifically, we evaluate the taxonomic level of homogenization, as the basis for taxonomic similarity (i.e. taxonomic homogenization) between two or more biotas over a specified time interval (Olden & Rooney 2006). To this aim, we chose two cities, Almería (Spain) and Ensenada (Mexico), located in the mediterranean-type regions of Europe and North America, respectively. These cities share important common features: they are relatively small in size (< 300,000 inhabitants), historically poorly interconnected cities inside their respective regions, and both are subjected to semiarid-type climate conditions.

We analyzed the urban floras of Almería and Ensenada to explore these hypotheses: (1) alien species increase the floristic similarity between the two cities, (2) the legacy of human history between both mediterranean regions will affect the directionality of species exchange shown by their urban floras, and (3) the residence time of alien species influences

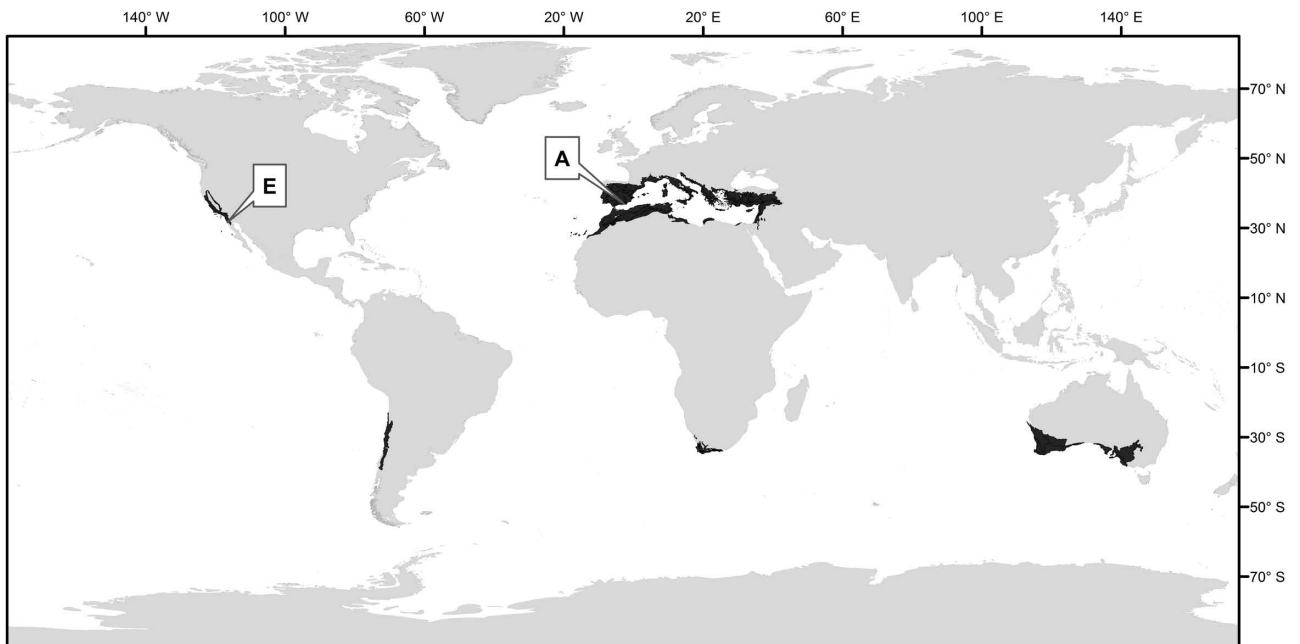


Figure 1 – Mediterranean-type regions of the world, showing the geographic location of the cities of Almería, Spain (A), and Ensenada, Mexico (E), inside the California and Mediterranean Basin regions, respectively. Modified from Olson et al. (2001).

their impact on the homogenization process. Thus, if these hypotheses are correct we would expect that (1) floristic similarity between cities will be higher after alien species establishment, (2) species exchange will be mostly between both mediterranean regions, concretely from Almería to Ensenada, and species from outside regions will be low in number and scarcely shared, and (3) archaeophytes will be the main group of shared species.

MATERIAL AND METHODS

Study areas

The study was carried out in two coastal cities, Almería (Spain) and Ensenada (Mexico), located in the mediterranean regions of Europe and North America, respectively, which correspond to two biodiversity hotspots with high numbers of endemics and fast habitat transformation (Myers et al. 2000) (fig. 1). Both cities have arid mediterranean-type climates, with annual precipitation around 250 mm (Almería: 231 mm; Ensenada: 283 mm), mean monthly temperature between 16 and 20°C, and they are essentially frost-free.

These two cities are small-size (Almería: 189,000 inhab. in 2009, Dana et al. 2011; Ensenada: 280,000 inhab. in 2010, INEGI, 2011), and poorly interconnected. Almería was founded in 955 and enjoyed a fluent marine trade inside the Mediterranean Basin until the 12th century. After that, its relative status in trade interchange has been gradually decreasing, with a period of moderate trade relationships with South America between the 19th century and the first decades of 20th century (Dana et al. 2011). Conversely, Ensenada is a very young city founded in 1882 (Piñera-Ramírez 2006) that has been poorly interconnected with the rest of Mexico until recently. Similarly to other parts of the world, both cities have grown significantly after the 1940s, but while Almería “only” doubled its size, Ensenada has multiplied it by 60 (1940: 4,616 inhab., 2010: 280,000 inhab.; Dirección General de Estadística 1942, INEGI 2011). Therefore, Ensenada represents a paradigmatic example of a young and fast-growing city which is frequently observed in developing countries (Pauchard et al. 2006).

Data analysis

We sampled the spontaneous vascular flora of Almería in different urban habitats during a five-year period (1994–1999; see sampling details in Dana et al. 2002) and in vacant lots and ephemeral-flowing arroyos inside the city of Ensenada for two years (2006–2007; see sampling details in Garcillán et al. 2009). We identified plant taxa at the species level. Plant species of each city were categorized into two types: native and alien (non-native) species. Only alien species outside of cultivation were included, i.e. casual and naturalized alien species (Richardson et al. 2000, Pyšek et al. 2004), and their biogeographical origin was assigned based on available sources such as the Global Compendium of Weeds (www.hear.org/gcw/), the Germplasm Resources Information Network (www.grin.org), www.efloras.org, Malezas de Mexico (<http://www.conabio.gob.mx/malezasdemexico/2inicio/home-malezas-mexico.htm>), and CalFlora www.calflora.org. As suggested by Pyšek et al. (2002), we categorized the

geographical origin of the species approximately at the continental scale (Eurasia, Asia, Europe (Ural Mountains - Caspian Sea - Caucasus Mountains as the eastern limit), Mediterranean Basin, Africa, North America, South America, and Australia). We further divided alien species in respect to their residence time into two types: archaeophytes, those species introduced in Almería region before year 1500, and neophytes, which were introduced after that date.

We analyzed the floristic similarity between the two cities using the Jaccard index (J), widely used in homogenization studies (McKinney 2005, Olden & Rooney 2006). It calculates the proportion of shared species between two sites with respect to the total species. Later, we estimated the homogenization impact of alien species using the homogenization index (H), defined as the difference between the similarity index considering the total number of species (J) and the index obtained from using only native species (J_n) (Rahel 2000). Values of H above zero represent a homogenization effect, and negative values indicate a differentiation effect.

Based on their biogeographical origin we defined two groups of alien species: (a) species with bidirectional exchange (be), those alien species of one city which come from the biogeographical region where the other city is located; (b) species from external exchange (ee), those alien species present in one or both cities whose native ranges are in a third and yet different region (i.e. not Mediterranean Basin or California Floristic Province). We estimated the homogenization effect of each of the two groups of alien species through the homogenization index: (a) species resultant from bidirectional exchange (be): $H_{be} = J_{n+be} - J_n$, and (b) species coming from external exchange (ee) with other regions: $H_{ee} = J_{n+ee} - J_n$. Finally, we estimated the role that archaeophytes and natives had on the homogenization impact of bidirectional exchange species.

RESULTS

We found a total of 312 different plant species from both cities, 124 of them are alien species at least for one city. Ensenada showed a higher proportion of exotic species (61% of its 157 species) than Almería (19% of its 211 species). Native species of Almería were dominated by Poaceae, Asteraceae, Brassicaceae and Chenopodiaceae (54%). In Ensenada, the majority of native species are concentrated in three families, Poaceae and Asteraceae (46%) and Euphorbiaceae (6%). The majority of the alien flora of Almería belongs to four families, Poaceae, Asteraceae, Amaranthaceae (47%) and Chenopodiaceae (7.5%). Ensenada's alien species are dominated by only three families, Poaceae, Asteraceae and Brassicaceae (51%). In Ensenada the majority of the alien species (64%) come from the Mediterranean Basin (28%), Eurasia (27%), and Europe (9%); in contrast with Almería, where the high proportion (55%) of the forty alien species are from North America or South America. The proportion of alien species coming from the rest of regions (Africa, Asia, Australia and South Africa) is moderate and similar for both cities (fig. 2).

The similarity value using only native species was $J_n = 0.0087$, resultant from only two shared species (*Plantago ovata* Forssk. and *Xanthium strumarium* L.) of the total

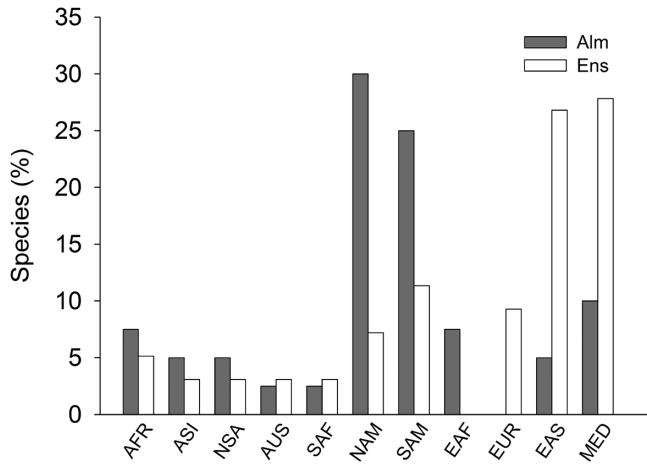


Figure 2 – Distribution of alien plant species in relation to their geographic origin: AFR, Africa; ASI, Asia; AUS, Australia; EAS, Eurasia; EUR, Europe; EAF, Europe-Africa; MED, Mediterranean Basin; NAM, North America; SAM, South America; NSA, North and South America; and SAF, South Africa.

230 native species from the two cities. Although *P. ovata* was considered in the past as non-native to the New World, there are Pleistocene packrat midden fossils (Anderson & Van Devender 1995) and recent molecular data (Meyers & Liston 2008) showing it as a New World native. However, this widespread species contains several infra-specific taxa (Meyers & Liston 2008), and the New World and Old World varieties are different between our two cities studied. In the case of *Xanthium strumarium*, it is a species so closely associated with people that its native status could be questionable. When we added alien species, the number of shared species increased to 56 and the total species to 312, giving a total similarity index $J_t = 0.1795$ (fig. 3). Therefore, the homogenization index resultant was $H = 0.1708$. If we consider the geographic origin, the total number of species introduced from third regions (*ee*, external exchange) was slightly greater than those species coming from bidirectional exchange, 63 vs. 61 species, respectively. However, the proportion of shared species from external exchange was distinctly lower, only six of the total 63 species (9%), than among bidirectional exchange species, 48 shared species of the total 61 (79%). Therefore, the homogenization impact of bidirectional exchange on native similarity ($H_{be} = J_{n+be} - J_n = 0.2008 - 0.0087 = 0.1921$) was higher than the resultant of external exchange ($H_{ee} = J_{n+ee} - J_n = 0.0273 - 0.0087 = 0.0186$). Furthermore, when we considered all the alien species, we observed that the external exchange group diminished the homogenization effect caused by the bidirectional exchange group ($H_{ee-(n+be)} = J_t - J_{n+be} = 0.1795 - 0.2008 = -0.0213$) (fig. 3). Finally, the bidirectional exchange of species was indeed strongly unidirectional from the Almería biogeographical region (Mediterranean Basin) to Ensenada, which included 57 of the total 61 species, in contrast with only four species coming from the opposite direction. The 57 species coming from the Almería region were dominated by native species (45 species; 38 of them shared by both cities), and only twelve archaeophytes (six of them shared by both cities).

DISCUSSION

Our results show that alien species increased homogenization between both cities, although the geographical origin of exchanged species influenced the magnitude of their homogenization effect.

The city of Ensenada showed a noticeably higher percentage of alien species (61%) than observed in Almería (20%). The proportion of alien plants in Almería is similar to the value found in other urban floras of the Mediterranean Basin, e.g. 12–26% for five Italian cities (Celesti-Grappo & Blasi 1998), 14% in Podgorica, Montenegro (Stešević et al. 2009), 12–14% in three cities of Greece (Chronopoulos & Christodoulakis 1996, 2000, Tsioutsiou & Christodoulakis 2004, Krigas & Kokkini 2004). Urban floras of the Mediterranean Basin show a rather low composition of alien species in contrast to that found for Central European cities which comprise in average 35–40% (Pyšek 1998). Contrastingly to the pattern observed in Central Europe, in the cities of the Mediterranean Basin there are many extralimital native species or apophytes, i.e. native species from surrounding areas that have established in urban environments (Kornas 1982). In addition, the Mediterranean Basin cities are, in general, of oldest origin, smaller foundation sizes, and of slower growth rates than cities in most others regions. In this way, one would expect high numbers of native species in urban cities of the Mediterranean Basin. On the contrary, although we have no specific data on alien species proportions in urban floras of the mediterranean region of California, due to the short history of agriculture in the California region (< 200 years) it seems that the native flora of mediterranean California has low numbers of apophytes. Besides that, and contrasting to the multi-century growth of Almería, Ensenada became a real urban settlement barely after the 1940s. Since

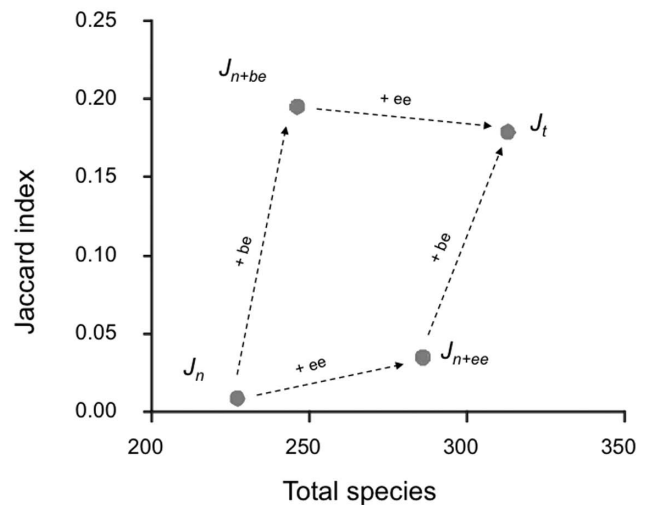


Figure 3 – Floristic similarity between urban floras of Almería and Ensenada with respect to only native species (J_n), native species and alien species from bidirectional exchange (J_{n+be}), native species and alien species from external exchange (J_{n+ee}), and all species combined (J_t).

that time, Ensenada grew fast (its population multiplied by sixty in this period), and through a *tabula rasa* type of urbanization process that did not leave many remaining patches of natural vegetation within the city's boundaries (Garcillán et al. 2009). This extensive disturbance probably yielded the local extirpation of many native species. We strictly collected inside those urban limits of Ensenada and various more natural areas located in the edge transition of the city were not included in the research. Finally, invasion patterns among the five mediterranean regions of the world show California as the region with the highest invasion degree and the Mediterranean Basin with the lowest one (Fox 1990). In this way, the mediterranean region of California, north of Ensenada, would potentially have worked as a source of alien plant propagules, contrasting with the Almería region that despite its long history of anthropic use shows only a moderate proportion of alien species (Sanz-Elorza et al. 2004). This explanation is supported by the results found by Stohlgren et al. (2011), that Europe had only 1% alien species among the most widespread species of the flora, in contrast with the 51.3% in North America.

Our results show evidence for hypothesis 1), that alien species have increased similarity between both cities. Homogenization impacts of alien species ($H = 0.1708$) was higher than the values between -0.080 and 0.067 found by Qian & Ricklefs (2006) for state and provincial floras in North America north of Mexico, or for the values of H along the Chilean flora ranging from -0.072 to 0.075 (Castro & Jaksic 2008). Olden (2006) reviewed several studies which reported quantitative change of similarity and found for plants a value between -0.6 and 2.6. In this context, the elevated value of our homogenization index may be related to the smaller size and more extensively disturbed characteristics of the urban areas in comparison to larger geographic units such as counties, regions or states used in other studies. Local extirpations of native species are high in urban areas due to extensive disturbance, and simultaneously, to the arrival of large numbers of alien species produce intense temporal species turnover. However, it is remarkable that the proportion of shared species between Ensenada and Almería (18%), which are cities separated by the Atlantic Ocean plus the North American continent, was greater than the maximum value of 11% found for Italian cities (Celesti-Grappo & Blasi 1998) or even to the average of 15% for Central European cities (Kunick 1982).

The results we found also support our hypothesis 2), that human relationship between both mediterranean regions affected the flux of species exchange between the two cities.

The homogenization effect of the alien species caused by bidirectional exchange was higher (19.2%) than that resulting from external exchange (1.9%). Species exchange between both cities was markedly unidirectional, from the Almería biogeographical region (Mediterranean Basin) to Ensenada (mediterranean California) (93% of the total 61 bidirectional exchange species), in agreement with the pattern found by La Sorte et al. (2007) for urban floras of the temperate region of Europe and North America. It also agrees with the observed trend of species interchange between mediterranean regions of the world (Fox 1990). Ensenada and Almería have not maintained significant direct interchanges

of trade or people; therefore, the arrival of the majority of alien species from the Mediterranean Basin to North America must have occurred secondarily through the transformation of California after European colonization (Mack & Erneberg 2002). However, it is possible that some species have arrived previously to Ensenada during the European colonization of the Baja California peninsula and California during the 17th and 18th centuries. In this sense, the true footprint of human history through European expansion and colonization would still be present in the biota.

Finally, our results suggest that hypothesis 3), the influence of residence time on the homogenization impact of alien species, could be extended beyond archaeophytes. Bidirectional exchange of plant species is the major factor responsible for homogenization between both cities and is dominated by native species in the total numbers (84% of 61 species) and in the shared species (87% of 48 species), with only moderate roles pertaining to archaeophytes. Contrasting to the dominance by archaeophytes found by La Sorte et al. (2007), our results show a very dominant role for the group of native species originating in the Mediterranean Basin that were transported to Ensenada. Regions with a long history of land usage like the Mediterranean Basin, besides its own archaeophytes, harbor many native species adapted to human activities, expanding their ranges and abundances into humanized landscapes. We could consider that these extralimital natives or apophytes, similarly to archaeophytes, have been able to “build biological and geographical potential for invasions” (La Sorte & Pyšek 2009), but inside their own regions of origin. Therefore, if we are correct, colonizing capacity of apophytes as alien species should be considered as a complementary variant of the residence time hypothesis.

On the other hand, the alien species coming from external exchange reduce the homogenization effect of bidirectional exchange species because the majority of outside species (90%) are not shared between both cities. This is in agreement with the differentiation effect (reducing similarity), that alien species from different regions can have on the receiving communities (McKinney 2004, Kühn & Klotz 2006, Ricotta et al. 2012). Thus, biotic exchange, even between remote places, does not seem to be a geographically nor temporally uniform process for increasing homogenization. Instead, it better reflects the temporal and geographical history of human expansion and colonization of Earth.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of: (1) list of plant species found from sampling spontaneous urban flora of Almería (Spain) and Ensenada (Mexico) (Excel file); and (2) pictures of some representative species found from sampling urban floras of Almería (Spain) and Ensenada (Mexico) (pdf file).

ACKNOWLEDGMENTS

We are grateful to Francisco Casillas and Eulogio López-Reyes for their help in the field work, and to Charlotte E.

González-Abraham for her assistance with figures. We really appreciate the comments of Richard Felger and of an anonymous reviewer that improved our manuscript. We are in debt to Rutger Barendse (Balen, Belgium) and Enrique Sánchez Gullón (Huelva, Spain) for sharing plant pictures. The financial support that facilitated fieldwork in Ensenada was provided by Instituto Nacional de Ecología (INE), México.

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Manuscript received 13 Nov. 2013; accepted in revised version 31 Jan. 2014.

Communicating Editor: Elmar Robbrecht.