# Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient

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*Abstract.* Urban areas are among the most heavily managed landscapes in the world, yet they harbor a remarkable richness of species. Private yards are common habitats in urban areas and are places where cultivated species manage to escape cultivation and become part of the spontaneous species pool. Yards are novel ecosystems where community assembly is driven by both natural and anthropogenic processes. Phylogenetic diversity and functional traits are increasingly recognized as critical to understanding processes of community assembly. Recent evidence indicates that urban areas may select more closely related plant species from the pool of regionally occurring species than do nonurban areas, and that exotic species are phylogenetically clustered within communities. We tested whether phylogenetic diversity and functional trait composition in privately managed yards change along a gradient of housing density in the Minneapolis-Saint Paul metropolis, Minnesota, USA, in accordance with these predictions. We also identified characteristics of the spontaneous yard flora by comparing its phylogenetic diversity and functional composition with the "natural-areas" species pool represented by the flora of nearby Cedar Creek Ecosystem Science Reserve. Along the urbanization gradient, yards had more species per hectare in densely built regions than in lower-density regions, but phylogenetic diversity and functional composition did not change with housing density. In contrast, in comparison to species in natural areas, yard species were more closely related to each other and functionally distinct: They were more often short-lived, self-compatible, and had higher specific leaf area than species of Cedar Creek. The high number of exotic yard species increased the yard flora's phylogenetic relatedness in comparison to species of Cedar Creek, causing a degree of phylogenetic homogenization within yards. The urban environment and homeowners' preferences select for trait attributes and phylogenetic lineages that can colonize and persist in yards. As yard species disperse beyond household boundaries, their functional attributes will affect ecosystem processes in urban environments and beyond, such as accelerating decomposition rates. Limited phylogenetic diversity may reduce the potential of ecosystems to respond to environmental changes. As cities continue to expand globally, understanding the impacts of yard management for biodiversity and ecosystem services becomes increasingly important.

Key words: Cedar Creek Ecosystem Science Reserve; community assembly; domestic gardens; exotic species; functional traits; land use; novel ecosystems; phylogenetic distinctness; phylogenetic diversity; urban ecology; vascular plants.

### INTRODUCTION

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Urban areas harbor considerable vascular plant diversity, often with increasing numbers of both native and exotic species with increasing urbanization (e.g., Dobson et al. 2001, Hope et al. 2003). Urban environmental conditions and human activities influence species diversity and composition in several fundamental ways. Humans introduce (intentionally and unintentionally) large numbers of species that would not otherwise occur in a region. Once introduced, many of these species persist spontaneously (i.e., not having been planted, but not necessarily being naturalized, yet). Thus, urban areas are the starting point of colonization for many exotic species and drive the global homogenization of floras (Olden et al. 2006), such that urban biodiversity also affects nonurban biodiversity (i.e., cities export their biodiversity together with its functional and phylogenetic characteristics; see von der Lippe and Kowarik 2008). Urban environments have altered environmental conditions relative to rural areas. For example, increasing air temperatures and decreasing atmospheric moisture are often associated with increasing urbanization (urban heat island; Landsberg 1981), particularly in temperate regions (as opposed to, e.g., desert cities; Brazel et al. 2000). Urbanization is also accompanied by high levels of fragmentation, altered biogeochemical cycles, intensive and irregular disturbances by human activities, and pollution of air, water, and soil (e.g., Grimm et al. 2008).

Household yards, found worldwide throughout urban areas, are crucial habitats where humans directly influence biodiversity and composition through culture, values, and lifestyles (Grove et al. 2006). Yards contribute high numbers of species to urban biodiversity (see Gaston et al. 2005 and references therein), which can even exceed species numbers of seminatural habitats (Loram et al. 2008). They are centers of species cultivation, especially for ornamental species. Ornamental horticulture is a major pathway for the introduction of exotic species and the main pathway for the introduction of invasive species (Dehnen-Schmutz et al. 2007). As yards are the places where exotic species that escaped cultivation often occur first, spontaneous yard floras are highly interesting with respect to potential future shifts in biodiversity: Given the high rates of species exchanges between yards and their surroundings (Hanspach et al. 2008, Hulme 2011), the characteristics of yard biodiversity partly anticipate characteristics of a future biodiversity beyond the yard.

The conditions present in urban areas act as environmental filters, which affect the functional and phylogenetic components of biodiversity and, in turn, community assembly, ecosystem functions, and ecosystem services (Williams et al. 2009). In natural systems, community assembly is driven by biogeographic processes, the regional species pool, dispersal, environmental filtering, and density-dependent species interactions (Cavender-Bares et al. 2009). In managed systems, such as urban areas, anthropogenic effects add to these drivers of community assembly (Donoghue 2008) or manipulate them, for example, by anthropogenic selection of species or the creation of novel habitats, such as yards (Kowarik 2011). In this context, it becomes clear that by global change "we are rapidly creating genuinely unparalleled circumstances in which it is becoming difficult to apply our expanding knowledge of the past to predict the future" (Donoghue 2008:11 554).

Urban areas are a key to understanding anthropogenic effects on community assembly and ecosystem functions because they combine the two main components of global change: land-use change and climate change. The urban heat island, by increasing urban temperatures beyond rural temperatures, anticipates future temperatures of nonurban areas (Grimm et al. 2008). Thus, understanding today's urban biodiversity will help us to predict future biodiversity, and "phylogenetic diversity may be a useful biodiversity metric for predicting the ecological consequences of modern diversity change" (Cadotte et al. 2008:17 015). Both functional and phylogenetic diversity have been shown to predict ecosystem properties and functions better than species richness does (Díaz and Cabido 2001, Cadotte et al. 2008). However, until now only a small number of studies have combined function and phylogeny to elucidate community assembly in urban areas. Knapp et al. (2008a) found that urban land use can decrease the phylogenetic distinctness of floras by filtering out phylogenetic lineages from the pool of regionally available species that are poorly adapted to urban environmental conditions. These tend to be lineages dominated by long-lived species poorly adapted to frequent disturbances or species adapted to humid habitats. Accordingly, the lack of specific niches in urban areas restricts the occurrence and phylogenetic diversity of these species. Moreover, rare species are taxonomically more diverse than common species in urban floras (Ricotta et al. 2008), and at the same time, common plant species have a higher affinity to urban areas than rare plant species (Knapp et al. 2009). Thus, the high proportion of common and closely related species in cities decreases total urban lineage diversity. Cadotte et al. (2010) found that exotic species are phylogenetically clustered within communities and consequently reduce total phylogenetic diversity in comparison to native species. Thus, the high number of exotic species in urban areas should reduce the phylogenetic diversity of urban floras. Nevertheless, changes in species richness across urban-to-rural gradients are scale dependent (Pautasso 2007), and also phylogenetic urban-to-rural changes might differ across scales.

We studied species richness and phylogenetic characteristics of household yard biodiversity and their changes along an urbanization gradient in the Minneapolis–Saint Paul metropolitan area, Minnesota, USA. Our objectives were to test whether species richness and phylogenetic diversity vary as predicted by the results of Knapp et al. (2008*a*) and Cadotte et al. (2010), i.e., increasing richness but decreasing phylogenetic diversity with increasing urbanization, and whether functional trait composition reflected urban and yard environmental filters. For example, the urban heat island should select for traits adapted to the urban heat island (e.g., many exotic species), high disturbance should select for short-lived species with high specific leaf area, and fragmentation should increase the likelihood of selfcompatible species and species dispersed by humans. We thus expected with increasing urbanization that we would see an increase in short-lived, self-pollinating plants with high specific leaf area. Furthermore, with increasing urbanization (quantified in terms of housing density), species number per unit yard area should increase, particularly in lineages dominated by exotic species, causing phylogenetic relatedness of the total flora to increase and phylogenetic diversity to decrease (cf. Cadotte et al. 2010).

We also focused on a larger scale than the urbanization gradient and sought to identify phylogenetic and functional characteristics that distinguish the yard flora from the natural-areas species pool (i.e., the natural pool from which species recruit in the study region). By investigating the phylogenetic and functional components of yard floras, we sought to further elucidate how humans affect community assembly and to test whether the results of Knapp et al. (2008*a*) and Cadotte et al. (2010) can be generalized to other areas of the world. The total yard flora should consist of species that are more closely related to each other than species in the natural-areas species pool and the functional composition of species should reflect the urban environmental filter.

### METHODS

### Study site

In summer 2008, we recorded the occurrence of spontaneously occurring vascular plant species (irrespective of abundance, excluding aquatic species) in 137 private household yards in the Minneapolis-Saint Paul metropolitan area, in Anoka and Ramsey Counties, Minnesota, USA. As part of the Twin Cities Household Ecosystem Project (TCHEP), surveys were sent to 15 000 single-family detached households. The addresses for the random sample were purchased from Survey Sampling International. We recorded the species in yards of only those homeowners who gave permission to obtain energy records (other studies conducted within TCHEP required energy records, Fissore et al. 2011) and to measure the vegetation on their property, yielding 157 households along a gradient of housing density. From these, we excluded 20 yards because data relevant for analyses was incomplete, resulting in an unbiased sample of 137 yards.

As urbanization consists of many different components, such as population density, building density, or economic activities, different parameters can be used as surrogates for urbanization intensity. Hope et al. (2003), for example, explained plant diversity in Phoenix, Arizona, USA, with family income, whereas Dobson et al. (2001) modeled species diversity with human population density and land prices. We used housing density as a surrogate for urbanization intensity, as it has been shown to have strong effects on urban plant species patterns, including composition (Godefroid and Koedam 2007).

We calculated the area of each yard (total area of the parcel less the area of house and driveway determined from high-resolution aerial photographs; Fissore et al. 2011) and overlaid our map of yard locations on a map of housing density, enabling us to assign housing density values to each yard. The area of parcels was obtained from Anoka and Ramsey Counties 2008 GIS parcel layers (Regional Parcel Dataset 2008; Metropolitan Council, St. Paul, Minnesota, USA). The housing density map (units/km<sup>2</sup>) was based on Hammer et al. (2004) and Radeloff et al. (2005), who used data from the 2000 U.S. Census.

#### Species data

We recorded species identity in household yards by surveying the entire yard area or by following transects. Transects were established wherever there were large woodlots or lawns (>20 m<sup>2</sup>). Two transects (each 2 m wide) were established in each lawn or woodlot; one covered the edge of the woodlot or lawn and the other ran through the center. Random spot checks outside transects tended not to increase species numbers, allowing us to conclude that we captured a representative sample. Species identification was supported by the floras of Lorenzi and Jeffery (1987), Steiner (2005), Kershner et al. (2008), and McCarty et al. (2008). We recorded both the cultivated flora and the spontaneous flora of yards, but only examined the spontaneous flora for the present study. Spontaneously occurring species included all species that were likely not to have been planted or sown, even if they were nonnative species. The identity, location, and prevalence of a species helped to classify it as spontaneous. Species' traits were not used to separate cultivated and spontaneous species. Most spontaneous species that we found were weeds that grew in places such as lawns, along edges of driveways, and sporadically in garden beds. Moreover, most plants growing in forested or "wild" areas appeared to have established on their own (e.g., Acer negundo L.), as did tree saplings that grew right within lawns or flower beds. We assumed that spontaneous species existed prior to house construction or volunteered after construction.

We concentrated on spontaneous species because they represent both the pool of species that escaped cultivation and might spread beyond yards, and the pool of species that occur in both the urban matrix and yards. The cultivated flora, which is determined and maintained by human choice and management activities, differs from the spontaneous flora in that it is largely kept independent of the prevailing environmental conditions: Irrigation protects cultivated species from drought; covering protects them from frost; pesticide application suppresses predators, parasites, and competitors; and weeding decreases competition pressure. All of these management activities provide

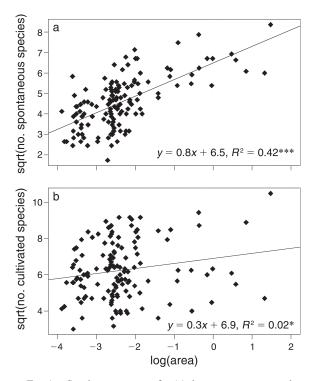


FIG. 1. Species–area curves for (a) the spontaneous vascular flora and (b) the cultivated vascular flora of 137 household yards in the Minneapolis–Saint Paul metropolitan area, Minnesota, USA. Species richness was explained with area size (originally measured in ha) in linear regression models; area size was log-transformed (Gleason 1922); species richness was square-root-transformed in order to achieve normally distributed residuals.

\* P < 0.05; \*\*\* P < 0.001.

cultivated species with a competitive advantage, which spontaneous species do not have (they are the ones that are weeded or suppressed by herbicides). As a result, cultivated species hardly follow one of the most basic ecological patterns, the species-area curve, while spontaneous yard species richness shows a strong positive relationship to area (Fig. 1). This indicates that cultivated species do not follow the same assembly rules as do spontaneous species; i.e., they are not subjected to the same environmental filters. Consequently, analyzing cultivated and spontaneous species together can blur ecological patterns. As we were interested in the way humans affect community assembly of noncultivated species, we concentrated on spontaneous species only.

To identify functional and phylogenetic characteristics that distinguish the spontaneous yard flora from the natural-areas species pool, we used the flora of Cedar Creek Ecosystem Science Reserve as the natural-areas species reference site (again excluding aquatic species; data *available online*).<sup>9</sup> Cedar Creek is a 2200-ha Long-Term Ecological Research area located 50 km north of Minneapolis–Saint Paul at 45.401° N, 93.201° W. Its natural areas comprise the three major biomes of Minnesota (southern boreal forest, mixed eastern deciduous forest, and tallgrass prairie). Thus, the flora of Cedar Creek is representative of south-central Minnesota and provides a reasonable representation of the natural-areas species pool relevant for the Minne-apolis–Saint Paul region.

### Phylogenetic data

We constructed two literature-based phylogenetic trees for both the total list of spontaneous yard species and the total list of Cedar Creek species following previously described methods (Webb and Donoghue 2005). The first tree (Supplement 1) was assembled collaboratively by the Ecophylogenetics working group (EcoPhyWG) at the National Center for Ecological Analysis and Synthesis (Beaulieu et al. 2012). This tree was pruned for our yard species and species of Cedar Creek, separately. Additional taxa were added to the EcoPhyWG tree and assembled by hand in Mesquite (Maddison and Maddison 2006) based on the Plants Database of the USDA (available online).<sup>10</sup> The second phylogenetic tree (Supplement 1) was from the APG III tree (APG 2009) using the online application Phylomatic (Webb and Donoghue 2005; available online),<sup>11</sup> resolving the families by hand in Mesquite based on the literature and pruning it to the floras of yards and Cedar Creek. For all trees, we calculated branch lengths by assigning minimum fossil ages from Wikstrom et al. (2001, with the phylocom module BLADJ). The phylogenies were further pruned to the taxa for each yard. Pruning and phylogenetic analyses were done in R (R Development Core Team 2009), with the packages "ape" (Paradis et al. 2004) and "picante" (Kembel et al. 2010). We used two different trees because each phylogeny is a hypothesis about the real relationships between species and might still differ from the true situation. We assumed that using two trees would strengthen our results or indicate uncertainties.

### Functional data

We chose functional traits related to dispersal, phenology, photosynthesis, competition, pollination, persistence, regeneration, and reproduction (Table 1; Appendix A), and assigned traits to species. All traits were categorical, except for seed dry mass and specific leaf area. Traits included species native/exotic status (which is not a biological trait but a description of origin; however, for simplicity, we call it a trait hereafter). Trait data came from a range of databases (Table 1; Appendix A). For continuous traits, we assumed that variation within a species was less than between species, which has been demonstrated in other studies (Reich et al. 1999, Kattge et al. 2011). Therefore, it is reasonable to use trait data

<sup>9</sup> http://www.cedarcreek.umn.edu/plants1

<sup>&</sup>lt;sup>10</sup> http://plants.usda.gov/

<sup>11</sup> http://www.phylodiversity.net/phylomatic

| Trait                                 | Database(s)   | Source(s)  |  |
|---------------------------------------|---|--|--|
| Dispersal                             | LEDA,† TRY‡   | Kleyer et al. (2008);<br>Poschlod et al. (2003), Díaz et al. (2004), Moles et al. (2005),<br>Royal Botanic Gardens Kew (2008), Kattge et al. (2011)  |  |
| Leaf longevity                        | BiolFlor,§ Flora of North America   | Kühn et al. 2004;<br>Flora of North America Editorial Committee 1993–2009  |  |
| Life span                             | BiolFlor,§ European Garden Flora<br>Flora of North America, PLANTS<br>(USDA)¶ | Walters et al. 1986–2000;<br>Flora of North America Editorial Committee 1993–2009  |  |
| Photosynthesis                        | TRY‡  | Cornelissen (1996), Cornelissen et al. (2003, 2004), Poschlod et al. (2003), Quested et al. (2003), Díaz et al. (2004), Wright et al. (2004, 2006), Craine et al. (2005), Kattge et al. (2009, 2011), Laughlin et al. (2010)   |  |
| Pollination                           | TRY‡  | Poschlod et al. (2003), Díaz et al. (2004), Kühn et al. (2004),<br>Kattge et al. (2011)  |  |
| Self-compatibility                    | BiolFlor§   | 6 ( )  |  |
| Native/exotic status<br>Seed dry mass | Vascular plant list of Minnesota#<br>TRY‡                                     | Minnesota Natural Resources<br>Cornelissen et al. (1996), Díaz et al. (2004), Louault et al. (2005),<br>Moles et al. (2005), Paula et al. (2009), Laughlin et al. (2010),<br>Kattge et al. (2011)  |  |
| Specific leaf area                    | TRY‡  | <ul> <li>Shipley (1995, 2002), Cornelissen (1996), Cornelissen et al. (1996, 1997, 2003, 2004), Atkin et al. (1997), McKenna and Shipley (1999), Meziane and Shipley (1999<i>a</i>, <i>b</i>), Fonseca et al. (2000), Shipley and Vu (2002), Loveys et al. (2003), Quested et al. (2003), Díaz et al. (2004, Wright et al. (2004, 2006), Louault et al. (2005), Cavender-Bares et al. (2006), Campbell et al. (2007), van Bodegom et al. (2008), Kattge et al. (2009, 2011), Laughlin et al. (2010)</li> </ul> |  |

TABLE 1. Traits analyzed for the spontaneous flora of 137 household yards in the Minneapolis-Saint Paul metropolitan area, Minnesota, USA.

Note: For details on trait attributes and references see Appendix A.

† Available online: http://www.leda-traitbase.org

‡ Available online: http://www.try-db.org

§ Available online: http://www.ufz.de/biolflor ¶ Available online: http://plants.usda.gov

# Available online: http://www.dnr.state.mn.us

collected in other geographic regions for our study system. This is less likely to be an issue for categorical traits. We classified species according to trait attributes (e.g., the trait pollination syndrome has the attributes insect, self, and wind pollination; Appendix A) in order to examine variation among attributes in species richness and phylogenetic diversity, and to compare the functional composition of the flora of yards with the flora of Cedar Creek.

### Analysis of species richness

We calculated species richness per unit yard area (ha), to account for variation in area among yards. We used analysis of covariance (ANCOVA) and linear regression to examine the extent to which housing density and species traits (both continuous and categorical) explained total species richness. We tested and compared five different models: (1) ANCOVA with the interactions of housing density and traits as explanatory variables; (2) ANCOVA with housing density and traits as explanatory variables, without interactions; (3) ANCOVA with traits as explanatory variables, without housing density; (4) linear regression with housing density as explanatory variable but without traits; and (5) null model (species richness per yard  $\sim$ 1).

We tested the normal distribution of model residuals using the Kolmogorov-Smirnov test, and transformed the response variable if necessary, using the boxcox function from package "MASS" (Venables and Ripley 2002). We compared the different models with Akaike's information criterion (AIC), which has the objective "to find a compromise between model 'fit,' usually gauged by a term representing residual mean or sum of squares, and model 'complexity,' which is a function of the number of model terms" (Mac Nally 2000:662). The smaller the AIC, the better the model, i.e., we selected the model with the smallest AIC as the preferable model.

## Analysis of phylogenetic distinctness

A metric of phylogenetic diversity that is not correlated to species richness (Schweiger et al. 2008) is average phylogenetic distinctness (AvPD). This metric was originally developed by Warwick and Clarke (1998) for taxonomic data (average taxonomic distinctness), but more recently has been applied to phylogenetic data (Gerhold et al. 2008, Knapp et al. 2008a). AvPD gives the pairwise distance between any two species in the tree. It is calculated as

$$AvPD = \sum \sum_{i < j} d_{i,j} / [s(s-1)/2]$$

with  $d_{i,i}$  being the matrix of distances in the tree and s being the number of species. Phylogenetic distinctness reflects how many lineages across a phylogenetic tree appear in a species assemblage and enables us to compare different communities with respect to phylogenetic diversity: If the phylogenetic distinctness of community A is significantly larger than the phylogenetic distinctness of community B, the species in A are less closely related and encompass more diverse lineages than the species in B. In other words, if species are concentrated on few branches (closely related species), they will have lower AvPD than if they are distributed over many branches (distantly related species). Thus, a species assemblage with few but distantly related species can have a higher phylogenetic distinctness than an assemblage with more but closely related species. We calculated AvPD per yard on the basis of the APG III tree and on the basis of the EcoPhyWG tree, and modeled it with housing density and traits as described for species richness (five different models, compared with AIC).

We also compared the phylogenetic distinctness of the yard flora and the flora of Cedar Creek, based on the APG III- and the EcoPhyWG-phylogenetic trees (Supplement 1). In correspondence to each yard, we randomly chose 99 samples out of the total flora of Cedar Creek with the same number of species as the corresponding yard. We calculated phylogenetic distinctness for each of these samples and compared the 99 simulated Cedar Creek AvPD values with the corresponding yard's observed AvPD value using *z* statistic.

The species of Cedar Creek are assembled from a much larger area than the species that occur in a single yard. This difference in area might bias differences between the AvPD of yard communities and the AvPD of simulated Cedar Creek communities. Therefore, we additionally chose 99 random samples out of the regional urban species pool, which includes the flora of all the sampled yards across the Twin Cities Metropolitan area, in the same manner as described for Cedar Creek. We compared the simulated AvPD values of yards with the simulated AvPD values of Cedar Creek using the unparametric Mann-Whitney-Wilcox U test (cf. Crawley 2002).

#### Analysis of mean nearest taxon distance

Mean nearest taxon distance (MNTD) calculates, for each species in a community, the mean distance that separates it from its closest relative (nearest taxon index, NTI; Webb 2000, Kembel et al. 2010). While AvPD averages distances over all species–species pairs in a phylogenetic tree, MNTD, by averaging over pairs of nearest taxa, focuses on closely related species. It thus provides a measure of whether species assemblages are phylogenetically clustered (or even), such that closest relatives occur together more (or less) often than expected at random. We used both AvPD and MNTD to provide related but computationally different metrics for average phylogenetic diversity, on the one hand (AvPD) and phylogenetic clustering/evenness of close relatives, on the other (MNTD). We calculated MNTD per yard on the basis of the APG III tree and on the basis of the EcoPhyWG tree using the mntd function from the "picante" package (Kembel et al. 2010). Subsequently, we calculated the standardized effect size of MNTD, using picante's ses.mntd function with the "independent swap" algorithm. Standardized effect size is calculated as

$$MNTD_{ses} = \frac{(observed MNTD - mean of random MNTD)}{SD of random MNTD}$$

and shows whether observed values differ from random values. We modeled  $MNTD_{ses}$  with housing density and traits as described for species richness and phylogenetic distinctness.

Additionally, as for phylogenetic distinctness, we randomly chose, in correspondence to each yard, 99 samples out of the total flora of Cedar Creek with the same number of species as the corresponding yard. We calculated the simulated MNTD per Cedar Creek sample and compared it with the observed MNTD value of the corresponding yard using z statistic. Moreover, we randomly chose 99 samples out of the regional urban species pool, as before, and compared the simulated MNTD values of yards with the simulated MNTD values of Cedar Creek using Mann-Whitney-Wilcox U test. The comparison of AvPD and MNTD among yards and Cedar Creek indicated whether yard species are more or less closely related than expected from the natural-areas species pool.

# Analysis of phylogenetic conservatism

Further, to explore the evolutionary lability of traits associated with urbanization, we tested whether traits of species were phylogenetically conserved using two approaches. For continuous traits (seed dry mass and SLA), we used Blomberg's K (Blomberg et al. 2003), which examines observed trait evolution in relation to a Brownian motion model of evolution. A value >1 indicates higher phylogenetic signal than Brownian motion evolution (which is already high signal). These values were also compared to a null model in which the tips of the phylogeny were randomized. The Pvalue is determined from the rank of the observed relative to the null. For categorical and binary traits, we followed a similar approach to Norden et al. (2012) with Webb's (2000) nearest taxon index (NTI) and net relatedness index (NRI) to test whether the relatedness of species within each trait category was greater than expected at random, using the mean phylogenetic distance (MPD), compared to 999 randomizations in which species were randomized across the tips of a phylogeny pruned to the species list for which trait data were available.

### Analysis of trait attribute frequency

For the analysis of species richness, AvPD, and  $MNTD_{ses}$  along the urban-to-exurban gradient, traits were used as explanatory variables, as described in

Analysis of species richness. To further work out specific functional characteristics of the spontaneous yard flora, we compared its trait attribute frequencies to the flora of Cedar Creek. For each trait, we calculated the proportion of its total possible attributes per yard (e.g., proportion of insect-, self-, and wind-pollinated species for the trait "pollination syndrome"). Subsequently, we calculated all possible log-ratios of proportions (e.g., log(insect/wind), log(selfing/wind), log(insect/selfing) using the natural logarithm). Log-ratios break the unit sum constraint of percentages that sum up to 100%, enabling largely independent statistical analyses (e.g., Aitchison 1982, Billheimer et al. 2001). Because zeros cannot be used in log-ratios, we replaced them with a very small value (cf. Fry et al. 2000). For the flora of Cedar Creek, we randomly chose 99 samples of 50 species each. For each sample, we calculated trait attribute frequency as done per yard. We compared the resulting frequency distribution of Cedar Creek with the frequency distribution of all vards using the unparametric Mann-Whitney-Wilcox U test. For phylogenetic indices, we tested two sampling procedures, i.e., the one described for phylogenetic indices, with the size of Cedar Creek samples corresponding to the number of species in a yard, and the "short-cut one" with 99 samples of 50 species each (not shown for AvPD and MNTD). The two procedures yielded the same results. Thus, we only applied the "short-cut" procedure for the trait frequency calculations to gain a clearly arranged figure.

For all analyses, we used the open-source software R (R Development Core Team 2009).

### RESULTS

### Species richness and housing density

Housing density ranged from 15 to 2314 housing units per km<sup>2</sup> (HU/km<sup>2</sup>; first distribution quartile, 255 HU/ km<sup>2</sup>; median, 540 HU/km<sup>2</sup>; third quartile, 960 HU/ km<sup>2</sup>). The total spontaneous flora contained 233 species, with a minimum of three and a maximum of 70 species/ yard (first quartile, 14 species/yard; median, 20 species/ yard; third quartile, 29 species/yard; a list of all yard species and all species of Cedar Creek is given in Supplement 2).

The linear regression model with housing density as explanatory variable, but without traits was the best out of all tested models (AIC = 781.45). It explained 24% of variance ( $R^2$  adjusted for number of predictors = 0.24, P < 0.001; Appendix B) with species richness per hectare increasing with increasing housing density (if not calculated per hectare, species richness decreased with increasing housing density; not shown). The models that included traits had much higher AIC values (interaction model, AIC = 10 150 314; no-interaction model, AIC = 10 373 554), because they were based on more data points (species with their trait attributes per yard).

Nevertheless, the models that contained traits also illustrated that housing density is the dominant explanatory variable, while traits are irrelevant for the trend of species richness along the urbanization gradient (interaction model,  $R^2 = 0.26$ , P < 0.001; no-interaction model,  $R^2 = 0.255$ , P < 0.001; traits-only model,  $R^2 = 0.016$ , P < 0.001). The null model had an AIC = 817.94.

### Phylogenetic distinctness and housing density

Trends of average phylogenetic distinctness along the gradient of housing density differed for the APG III tree and the EcoPhyWG tree. For the former, AvPD showed no trend at all: The null model had the lowest AIC (454.12), followed by the model with housing density only  $(R^2 = -0.001, \text{ not significant [n.s.]}, \text{AIC} = 455.24)$ . The models that contained traits had much higher AIC values and illustrated the irrelevance of traits, as they did for species richness (interaction model,  $R^2 = 0.026$ , P < 0.0260.001; no-interaction model,  $R^2 = 0.024$ , P < 0.001; traitsonly model,  $R^2 = 0.003$ , P < 0.001). For the EcoPhyWG tree, the model with housing density as the only explanatory variable was best with the lowest AIC (1211.48); it showed a slight decrease of AvPD with increasing housing density ( $R^2 = 0.05$ , P < 0.01). The null model had a slightly higher AIC (1217.48), and the models containing traits again had much higher AIC values and showed no real trait effect (interaction model,  $R^2 = 0.035, P < 0.001$ ; no-interaction model,  $R^2 = 0.033$ , P < 0.001; traits-only model,  $R^2 = 0.004$ , P < 0.001).

### Mean nearest taxon distance and housing density

For MNTD, different models were selected as the best model on the basis of the APG III tree and the basis of the EcoPhyWG tree, but in both cases, MNTD showed no trend across the urbanization gradient: For APG III, the model with housing density only was preferable (AIC = 356.29), but explained nothing ( $R^2$  = 0.01, n.s.); for EcoPhyWG, the null model was preferable (AIC = 340.91). Again, the models that contained traits had much higher AIC values (for APG III, interaction model,  $R^2 = 0.08$ , P < 0.001, AIC = 1 869 395; no-interaction model,  $R^2 = 0.08$ , P < 0.001, AIC = 1 872 236; traits-only model,  $R^2 = 0.006$ , P <0.001, AIC = 1932755; for EcoPhyWG, interaction model,  $R^2 = 0.02$ , P < 0.001, AIC = 1 756 849; nointeraction model,  $R^2 = 0.016$ , P < 0.001, AIC = 1 761 137; traits-only model,  $R^2 = 0.01$ , P < 0.001, AIC  $= 1\ 763\ 214$ ).

### Phylogenetic conservatism of yard species

According to the nearest taxon index and net relatedness index, exotic species within the spontaneous yard species were significantly phylogenetically conserved, such that species exotic to Minnesota were more closely related to each other than to native species. Likewise, insect-pollinated species, annual and biennial species, species with evergreen leaves, and species with overwintering green leaves were all phylogenetically TABLE 2. Phylogenetic conservatism (A) for trait attributes calculated by net relatedness index (NRI; Webb 2000) and (B) for continuous traits calculated using Blomberg's K (Blomberg et al. 2003) for the spontaneous flora of 137 household yards in the Minneapolis–Saint Paul metropolitan area, Minnesota, USA.

| A) Calculated using NRI                          |                                |   |   |                                |   |                                      |
|--|--------------------------------|---|---|--------------------------------|---|--------------------------------------|
| Trait  | N.taxa                         | mpd.obs                                   | mpd.null.mean                             | mpd.obs.rank                   | mpd.ses                                   | NRI                                  |
| Native/exotic status                             |                                |   |   |                                |   |                                      |
| Exotic<br>Native                                 | <b>362</b><br>262              | <b>62.98</b><br>66.00                     | <b>64.27</b><br>64.25                     | <b>1</b><br>1000               | - <b>2.96</b><br>2.93                     | <b>2.96</b><br>-2.93                 |
| Self-compatibility                               |                                |   |   |                                |   |                                      |
| Self-compatible<br>Self-incompatible             | <b>78</b><br>30                | <b>62.37</b><br>67.77                     | <b>63.75</b> 63.76                        | <b>28</b><br>984               | - <b>1.97</b><br>2.05                     | <b>1.97</b><br>-2.05                 |
| Pollination syndrome                             |                                |   |   |                                |   |                                      |
| Insect<br>Self<br>Wind                           | 96<br>75<br>31                 | <b>58.47</b><br><b>61.02</b><br>67.11     | <b>62.70</b><br><b>62.70</b><br>62.66     | 1<br>14<br>999                 | - <b>8.69</b><br>- <b>2.32</b><br>2.68    | <b>8.69</b><br><b>2.32</b><br>-2.68  |
| Photosynthetic pathway                           |                                |   |   |                                |   |                                      |
| $C_3$<br>$C_4$                                   | <b>148</b><br>17               | <b>63.62</b><br>63.24                     | <b>64.54</b><br>64.86                     | <b>3</b><br>309                | - <b>3.29</b><br>-0.53                    | <b>3.29</b><br>0.53                  |
| Life span  |                                |   |   |                                |   |                                      |
| Annual<br>Biennial<br>Perennial                  | <b>161</b><br><b>65</b><br>641 | <b>61.73</b><br><b>56.13</b><br>64.75     | <b>64.16</b><br><b>64.22</b><br>64.21     | 5<br>1<br>993                  | -2.69<br>-5.50<br>2.48                    | <b>2.69</b><br><b>5.50</b><br>-2.48  |
| Leaf longevity                                   |                                |   |   |                                |   |                                      |
| Evergreen<br>Summer green<br>Overwintering green | <b>24</b><br>69<br><b>18</b>   | <b>56.36</b><br>66.31<br><b>58.00</b>     | <b>64.27</b><br>64.28<br><b>64.45</b>     | 3<br>925<br>19                 | -3.20<br>1.40<br>-2.16                    | <b>3.20</b><br>-1.40<br><b>2.16</b>  |
| Dispersal syndrome                               |                                |   |   |                                |   |                                      |
| Wind<br>Self<br>Human<br>Water<br>Animal         | 56<br>50<br>65<br>29<br>92     | 62.27<br>62.09<br>61.91<br>61.46<br>62.68 | 64.25<br>64.11<br>64.23<br>64.14<br>64.26 | 118<br>127<br>66<br>124<br>109 | -1.20<br>-1.17<br>-1.53<br>-1.17<br>-1.29 | 1.20<br>1.17<br>1.53<br>1.17<br>1.29 |
| B) Calculated using Blomb                        | berg's K                       |   |   |                                |   |                                      |
| Trait  | N.taxa                         | K.obs                                     | K.null.mean                               | K.obs.rank                     | K.ses                                     |                                      |
| Specific leaf area<br>Seed dry mass              | 100<br><b>135</b>              | 0.49<br><b>1.03</b>                       | 0.51<br><b>0.59</b>                       | 592<br><b>31</b>               | -0.24<br><b>1.44</b>                      |                                      |

*Notes:* Significant values (P < 0.05) are given in boldface and indicate that observed MPD values were significantly lower than expected under a null model in which species were randomized across the tips of the phylogeny (tip swap) or that observed K values were significantly higher than expected under the same null (tip swap). Abbreviations for calculations using NRI are: N.taxa, number of taxa; mpd.obs, observed MPD; mpd.rand.mean, mean of 999 random MPD samples; mpd.rand.sd, standard deviation of 999 random MPD samples; mpd.obs.rank, rank of the observed relative to the null MPD; mpd.ses, standardized effect sizes for MPD (observed MPD – mean null MPD)/SD null MPD; and NRI, net relatedness index. Abbreviations for calculations using Blomberg's K are: K.obs, observed K value; K.null.mean, mean null model K value; K.rank, rank of the observed K relative to the null; and K.ses, standardized effect size of K (observed K – mean null K)/SD null.

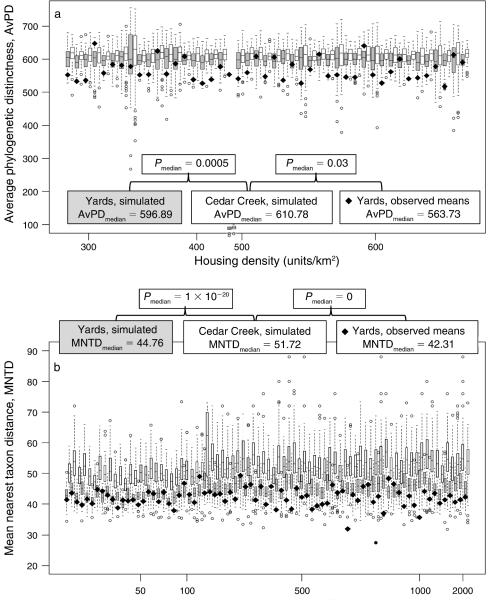
conserved (Table 2). For self-compatible, self-pollinated, and  $C_3$  species, NRI was significant, but NTI was not. Dispersal syndromes showed significant results with NTI, but not NRI (only NRI shown in Table 2). Blomberg's *K* showed that seed dry mass was phylogenetically conserved for the species in the regional urban pool, while SLA was not (Table 2).

## Phylogeny of the yard flora vs. the Cedar Creek flora

Compared with the natural-areas species pool of Cedar Creek Ecosystem Science Reserve, the flora of household yards had lower phylogenetic diversity, as indicated by significantly lower AvPD values for both the APG III and the EcoPhyWG trees. This was true for both the observed and the simulated AvPD values of yards (see Fig. 2a for the APG III tree, and Appendix C). Likewise, closely related species within the flora of household yards were significantly more clustered, as indicated by significantly lower MNTD values, both for the observed yard and the simulated yard assemblages, than for the simulated assemblages of the Cedar Creek flora (Fig. 2b; Appendix C).

# Trait attributes of the yard flora vs. the Cedar Creek flora

The comparison of the flora of yards to the flora of the natural-areas species pool at Cedar Creek revealed clear characteristics of yards. Yards contained higher proportions of self-dispersers, species dispersed by humans or water, summer-green and overwinteringgreen species, a much greater proportion of exotic



Housing density (units/km<sup>2</sup>)

FIG. 2. Variation of (a) average phylogenetic distinctness (AvPD) and (b) mean nearest taxon distance (MNTD) for the spontaneous flora of household yards along a gradient of housing density in the Minneapolis–Saint Paul metropolitan area, Minnesota (black dots) compared to AvPD and MNTD of simulated random samples for (1) the total spontaneous flora of all yards (gray boxplots), and (2) the flora of Cedar Creek Ecosystem Science Reserve north of Minneapolis–Saint Paul (white boxplots). Both AvPD and MNTD were calculated on the basis of the APG III tree. Boxplots show the median (line), 25–75% quartiles (boxes), ranges (whiskers), and extreme values (circles). The insets summarize test statistics over all yards and their corresponding random samples; full test statistics are given in Appendix C. For AvPD, the figure had to be divided into three parts; shown here are data from yards in areas of intermediate housing density, with data for yards in areas of low and high housing density shown in Appendix C. Housing density is not ordered linearly along the *x*-axis, but according to yards. AvPD and MNTD are pairwise distances (given in millions of years; measured along the branches of the phylogenetic tree including the tree's basal node). See *Methods* for details.

species, more annuals, biennials,  $C_4$  species, selfpollinating, and self-compatible species than the natural-areas species pool (Fig. 3). Moreover, species of the yard flora had, on average, higher specific leaf area than Cedar Creek species (Fig. 3i). Accordingly, the flora of Cedar Creek had a reversed pattern, i.e., it included a greater proportion of wind-dispersed, evergreen, and native species,  $C_3$  species, wind-pollinated, and self-incompatible species than the spontaneous yard flora (Fig. 3). Also, plant species of Cedar Creek had, on

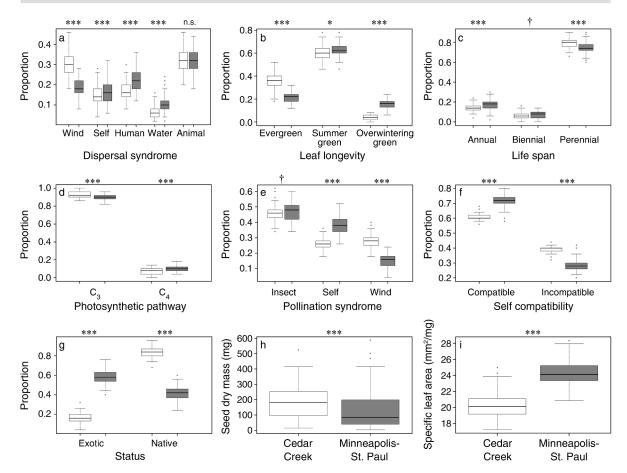


FIG. 3. Proportion of trait attributes in the spontaneous flora of 137 household yards (gray boxplots) in the Minneapolis–Saint Paul metropolitan area, Minnesota, and the flora of Cedar Creek Ecosystem Science Reserve, Minnesota, USA (used as the natural-areas species pool; white boxplots): (a) dispersal syndrome, (b) leaf longevity, (c) life span, (d) photosynthetic pathway, (e) pollination syndrome, (f) self-compatibility, (g) native/exotic status, (h) seed dry mass, and (i) specific leaf area. Boxplots represent median (line), 25–75% quartiles (boxes), ranges (whiskers), and extreme values (circles) of value distributions. Proportions were calculated as log-ratios of proportions. The *y*-axes for categorical traits (a–g) show proportion on a scale from 0 to 1. To calculate distributions, 99 samples of 50 species were drawn randomly from the yard flora and the Cedar Creek flora each; comparison was done with Mann-Whitney-Wilcox U tests. For continuous traits, mean values were compared. See *Methods* for details.  $\dagger P < 0.1$ ; \*P < 0.05; \*\*\* P < 0.001; n.s., P > 0.1.

average, heavier seeds than yard species (Fig. 3h). The remaining trait attributes showed less than  $\pm 5\%$  difference between the two floras.

The largest differences between the flora of yards and the flora of Cedar Creek were those found for overwintering-green species (fourfold decrease from yards to Cedar Creek), and exotic species (3.7-fold decrease from yards to Cedar Creek). Note that overwintering-green species have a high amount of exotic species in both the yards and Cedar Creek (yards, 81% exotics vs. 19% natives; Cedar Creek, 75% exotics vs. 25% natives). Thus, the strong decrease of overwintering-green species from yards to Cedar Creek can be explained with their exotic status. The smallest changes were found for self- and animal-dispersed species, summer-green species, biennials, perennials, C<sub>3</sub> species, and insect-pollinated species (all <1.1-fold difference; Appendix D).

### DISCUSSION

A habitat's environmental conditions act like filters, which select species from the regional species pool that can persist and thrive under such conditions, while excluding species that cannot (e.g., Williams et al. 2009). Natural environmental filters such as climate, disturbance, isolation, and competition act in both urban and nonurban environments. In intensively managed landscapes like cities, humans manipulate these filters and create novel conditions, which would not exist otherwise, such as the suppression of a selected set of species by pesticides or the introduction of exotic species. The creation of novel conditions by humans results in novel species communities with a species composition that has not existed before (Hobbs et al. 2006). Novel communities can differ from known communities in their phylogenetic and functional composition, and in turn, differ in their potential to react to environmental

changes (e.g., Morlon et al. 2011), and in ecosystem functions and services. Urban areas, which represent habitats drastically altered by humans, are "laboratories" for the study of novel species communities. Within urban areas, household yards are a common type of novel habitat. Yard management by individual homeowners involves cultivation, weeding, herbicide application, augmentation of nutrient and soil moisture conditions, and other activities that alter both local and regional species pools (Niinemets and Peñuelas 2008). Global trading overcomes natural dispersal barriers and distributes species in human-managed yards all over the world, making horticulture a critical driver of species invasions (Reichard and White 2001). By focusing on the phylogenetic and functional aspects of spontaneous vascular plant communities in yards, we sought to understand the assembly of novel, humaninfluenced plant communities and to understand the consequences of human management activities for phylogenetic diversity and ecosystem services.

### Phylogenetic diversity of spontaneous yard floras

The central finding of our study is a decrease of phylogenetic diversity from the natural-areas species pool to the yard flora: Both indices that we used, AvPD and MNTD, are significantly lower for the yard flora than expected from random samples of the natural-areas species pool, with yard species being on average more closely related to each other and encompassing fewer lineages than species of the natural-areas species pool from which species recruit within the study area. This result supports the outcome of the small number of studies currently available on the effects of urban land use on phylogenetic plant diversity. It concurs with a German study where floras of urban areas were phylogenetically less distinct than floras from nonurban areas (Knapp et al. 2008a) and with a study of California grasslands with different levels of invasion by nonnatives (Cadotte et al. 2010). In the study in Germany, the drop in phylogenetic distinctness from nonurban to urban areas was especially pronounced in species groups characterized by trait attributes maladapted to urban areas (e.g., perennials and species maladapted to drought), while species well adapted to typical urban conditions (e.g., short-lived species and self-pollinators) were phylogenetically more distinct in urban areas. In the California study, a general pattern of homogenization and lower phylogenetic diversity was found in more invaded communities (Cadotte et al. 2010). Accordingly, the phylogenetic distinctness of the total spontaneous flora in our study yards was reduced by the high number of cosmopolitan and exotic species. Cosmopolitan species tend to have a higher affinity to urban areas (Knapp et al. 2009) and a lower taxonomic diversity than rare species (Ricotta et al. 2008). Communities with high proportions of exotics tend to have a lower phylogenetic diversity than those dominated by native species (Ricotta et al. 2009, Cadotte et al. 2010).

Yards have exceptionally high numbers of exotic plant species: In our study, 59% of all spontaneous yard species were exotic, while only 16% of Cedar Creek species were exotic to Minnesota (Fig. 3g). Consequently, lineages specific to yards were also mostly exotic, while lineages specific to Cedar Creek were mostly native to Minnesota (Appendix E). Similarly, Loram et al. (2008) found 70% exotic species in the household yard floras of the UK, including both cultivated and spontaneous species. The percenatges of exotics in yards even exceeds the percentage of exotics in complete urban floras (including land areas beyond yards): Pyšek (1998a) showed an average of 40% of exotic plant species for 54 Central European cities; U.S. cities have percentages between 18% and 34% (calculated from species numbers given in Ricotta et al. 2009). Accordingly, yards are centers of exotic species diversity within cities.

The high amount of exotic species in our study yards and their effects on phylogenetic diversity (Cadotte et al. 2010), together with the fact that cultivation is a major pathway for species introductions (Reichard and White 2001, Dehnen-Schmutz et al. 2007), suggests that species cultivation causes a chain of human-induced filters that govern the assembly of yard communities. First, only a restricted number of lineages are commonly used for cultivation as shown by Pyšek (1998b): Although cultivated species originate from many different parts of the world, they often belong to a small range of plant families such as Leguminosae, Rosaceae, and Solanaceae, which are overrepresented among species introduced as crops or ornamentals. Similarly, of 3138 ornamental and crop species cultivated in Germany, 479 species are Asteraceae, while all other families are represented with <200 species (Schmiedel 2010). Correspondingly, spontaneous exotic species in our study yards were phylogenetically conserved. In other words, being exotic was restricted to a smaller range of lineages than would be expected at random, as also found by Cadotte et al. (2010). Second, cultivated species are biased toward fast and abundant germination (Chrobock et al. 2011), which increases their chances of propagating spontaneously and thus to "escape" cultivation. Some species are predisposed to escape more often than others (e.g., annuals more often than perennials; Dehnen-Schmutz et al. 2007), which favors lineages that possess "proescaping" traits. Lastly, not every escaped species can persist: Those that cannot thrive with the given environmental conditions (yard management and urban conditions, in our case) will vanish again, which restricts the number of lineages that become permanent parts of the spontaneous species pool. As a consequence, the phylogenetic diversity of spontaneous yard floras decreases. This pathway via cultivation is part of the "human preferences" filter described by Williams et al. (2009). However, they predicted phylogenetic diversity

to increase with the introduction of exotic species in novel habitats. Our study shows that the opposite is the case.

Along the gradient of housing density, we found no difference in phylogenetic diversity or phylogenetic clustering; all yards were similar with respect to AvPD and MNTD, which may reflect the environmental homogeneity of yards. These results also emphasize that phylogenetic patterns are scale dependent (Cavender-Bares et al. 2006, Willis et al. 2010). At our large scale (yards vs. Cedar Creek), the drop in phylogenetic diversity with urbanization was clear; on the small scale (yards along the urban to exurban gradient), there was no clear trend.

In contrast, yards along the urban to exurban gradient differed with respect to species richness per hectare, which clearly increased with increasing housing density. This is a pattern shown by numerous studies (e.g., Walters 1970 for Great Britain, Dobson et al. 2001 for parts of the United States) that is not specific to household yards, but driven by urbanization more broadly. While exotic species generally tend to enrich urban floras, our comparison of the urban yard communities to those of Cedar Creek indicates that the higher urban species richness is accompanied by a decrease in phylogenetic diversity. This decrease of phylogenetic diversity indicates a loss of evolutionary information and a homogenization of plant communities, which could result in a loss of potential to react to environmental changes (e.g., Morlon et al. 2011). With closely related exotic species becoming distributed all over the world, and a range of native species becoming locally extinct, the tendency toward homogenization and loss of evolutionary information has global consequences (Winter et al. 2009). Climate change appears to drive a phylogenetically biased loss of plant species (Willis et al. 2008), and urban land use appears to be another driver of phylogenetic loss.

### Functional composition of spontaneous yard floras

The second aspect of our study, the change of functional composition with urbanization, points out consequences of land use change for ecosystem functions and services. The high disturbance regime characteristic of urban areas (e.g., human presence, traffic, building activities) and of household yards (e.g., mowing, recreation) supports species with short regeneration cycles such as annuals, including species with high specific leaf area (and thus, reduced investment in longlasting leaves; Fig. 3c, i). Moreover, horticulture supports short-lived (annual) species that have a higher probability of propagating spontaneously from the pool of cultivated species (Dehnen-Schmutz et al. 2007). Of course, the relatively low proportion of spontaneous perennials in urban yards (which in turn increases the relative amount of annuals) also results from the low number of spontaneous tree species (not shown). Tree saplings are often removed by yard owners by mowing

and weeding because these species are perceived as untidy and potentially dangerous (Kirkpatrick et al. 2007). Disturbance also promotes species with small seeds (again reduced investment in plant organs allowing fast recreation cycles). In our study, seed dry mass was phylogenetically conserved, indicating that the environmental filters selecting for small seeds at the same time select for closely related plant species.

The fragmentation of urban areas and the resulting isolation of yards from seminatural habitats or parks are reflected in the increased proportion of self-dispersers and self-pollinated species in the yard flora (Fig. 3a, e, f). Isolation can keep pollinators and biotic dispersers from visiting a yard, thus the "do it yourself" strategy is advantageous (Niinemets and Peñuelas 2008). Similarly, human-dispersed species were more frequent in yards than at Cedar Creek (Fig. 3a); humans are a mobile dispersal vector, able to move among isolated habitat patches. In contrast, wind exposure, and thus, the likelihood of wind dispersal, is limited if species grow in the lee of buildings, which is common for plants in household yards. In urban environments in Germany, wind-dispersed species were also less frequent than in rural areas (Knapp et al. 2008b); and in urban Australian grasslands, wind-dispersed species had an increased risk of extinction (Williams et al. 2005).

The urban heat island effect in Minneapolis-Saint Paul (e.g., Winkler et al. 1981) is reflected in a higher proportion of  $C_4$  species in the vard flora in contrast to the natural-areas species pool. Given their higher water use efficiency and heat tolerance, C<sub>4</sub> species are likely to be better adapted than C3 species to elevated temperatures and reduced atmospheric moisture found in urban habitats (Fig. 3d). Evergreen species did not appear to benefit from the urban heat island (Fig. 3b), as might be expected from the temperature-driven spread of evergreen broad-leaved species from Mediterranean areas into temperate regions (Walther et al. 2002). However, studies on this kind of climate-driven spread mainly refer to shrubs and trees, while evergreen species in our study yards were all herbaceous (evergreen species are defined as species having green leaves all year long; Appendix A). The low proportion of evergreen species in the yard flora partly reflects the restricted habitat spectrum of urban areas: Evergreen yard species were mainly associated with industrial habitats, meadows, weedy communities, and cultivated communities, and represented escaped ornamental species, lawn species, and weeds. Overwintering-green species (which develop their leaves in the vegetation period, but keep them in winter and lose them in the next year's spring or early summer; see Appendix A; e.g., Vicia villosa Roth) were more frequent in yards than at Cedar Creek, a pattern that is closely correlated to the high amount of exotic species among overwintering-green species (also reflected in the phylogenetic conservatism within overwintering-green species). Moreover, many of these species are originally associated with agricultural habitats such as

*Capsella bursa-pastoris* (L.) Med. or *Thlaspi arvense* L. However, intensification of agriculture and modern techniques of seed bank cleaning have reduced the diversity of this group of species in rural areas (cf. van Elsen 2000), leaving them relegated to urban areas.

In brief, the typical spontaneous yard species is shortlived, fast growing, does not invest much energy in longlived organs, produces small seeds (and thus, many; Westoby 1998), pollinates and disperses itself or uses humans as dispersal vectors, and is adapted to high temperatures. This profile is also typical for urban plant species beyond yards (Chocholoušková and Pyšek 2003, Sudnik-Wójcikowska and Galera 2005, Knapp et al. 2008*b*), showing that environmental filters of yards and broader urban areas cannot be easily separated. The high impact of exotic species on the yard flora in this study indicates that the cultivation of plant species plays a key role in the composition of the spontaneous yard flora and for all species that migrate out of yards into the urban matrix.

By changing the functional composition of floras, urbanization and yard management impact ecosystem processes and services: Decomposition will likely proceed faster if biomass is provided in short time intervals (short-lived species) and is easily degradable (high specific leaf area; i.e., increased nitrogen rates in leaf litter). If self-pollinating species are promoted by the urban environment, and thus increase in the regional species pool, cascading effects on pollinators are possible: More self-pollinated plants will support fewer pollinators.

### Concluding remarks

Both phylogenetic and functional aspects distinguished the flora of household yards in the Minneapolis-Saint Paul metropolitan area from the natural-areas species pool, while the yards themselves shared a high degree of similarity along a housing density gradient (except for species richness). Accordingly, yard management and homeowner preferences, which are similar among yards, equalize differences between species assemblages (Marco et al. 2008, Faggi and Ignatieva 2009), but different management preferences will have different impacts on plant diversity in yards (as shown by a parallel study in the Minneapolis-Saint Paul study area; J. Cavender-Bares et al., unpublished manuscript). Cultivating a higher proportion of native species is likely to have positive effects on the phylogenetic diversity of plant species. Thus, supporting native species in household yards has the potential to foster a range of evolutionary strategies.

Human actions have added more filters to the existing environmental filters that drive the assembly of species communities. Recent research on urban plant communities is proceeding in understanding these anthropogenic filters. This knowledge will support the adaptation of nature conservation and the management of ecosystem services to global change.

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### SUPPLEMENTAL MATERIAL

#### Appendix A

Trait attributes used for the analysis of trait attribute frequency, phylogenetic distinctness, and phylogenetic diversity of trait attribute groups for the spontaneous yard flora (*Ecological Archives* E093-179-A1).

# Appendix B

Variation of spontaneous vascular plant species richness in yards along the gradient of housing density, calculated with a linear regression model (*Ecological Archives* E093-179-A2).

### Appendix C

Average phylogenetic distinctness and mean nearest taxon distance calculated on the basis of the APG III tree and the EcoPhyWG tree for the spontaneous yard flora and the flora of Cedar Creek Ecosystem Science Reserve (*Ecological Archives* E093-179-A3).

# Appendix D

Hierarchy of differences in trait attribute frequency between the spontaneous flora of yards and the flora of Cedar Creek Ecosystem Science Reserve (*Ecological Archives* E093-179-A4).

#### Appendix E

Representation of species in the yard flora and in the flora of Cedar Creek Ecosystem Science Reserve and their position within the phylogenetic tree (*Ecological Archives* E093-179-A5).

#### Supplement 1

Phylogenetic trees for the spontaneous yard flora and for the flora of Cedar Creek Ecosystem Science Reserve, based on the EcoPhyWG tree and the APG III tree (*Ecological Archives* E093-179-S1).

#### Supplement 2

List of vascular plant species occurring either in the spontaneous yard flora or in Cedar Creek Ecosystem Science Reserve (*Ecological Archives* E093-179-S2).