



## Taxonomic, phylogenetic, and functional composition and homogenization of residential yard vegetation with contrasting management

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### ABSTRACT

Urban biotic homogenization is expected to be especially important in residential yards, where similar human preferences and management practices across environmentally heterogeneous regions might lead to the selection of similar plant species, closely related species, and/or species with similar sets of traits. We investigated how different yard management practices determine yard plant diversity and species composition in six cities of the U.S., and tested the extent to which yard management results in more homogeneous taxonomic, phylogenetic, and functional plant communities than the natural areas they replace or than relatively unmanaged areas at the residential-wildland interface (“interstitial” areas). We categorized yards based on fertilizer input frequency and landscaping style: high-input lawns, low-input lawns, and wildlife-certified yards. We defined homogenization as decreased average  $\beta$ -diversity and decreased variance in  $\alpha$ -diversity in yards when compared to natural and interstitial areas. We found that all residential yard types regardless of their management were functionally more homogeneous for both  $\alpha$ - and  $\beta$ -diversity than the natural and interstitial areas. Nevertheless, wildlife-certified yards were functionally more similar to natural areas than lawn-dominated yard types. All yard types were also more homogeneous in phylogenetic  $\alpha$ -diversity compared to natural and interstitial areas, but more heterogeneous in taxonomic  $\alpha$ -diversity. Within yards, taxonomic, phylogenetic and functional diversity were weakly correlated, highlighting the importance of examining multiple dimensions of biodiversity beyond taxonomic metrics. Our findings underscore the ecological importance of gardening practices that both support biodiversity and create residential plant communities that are functionally heterogeneous.

### 1. Introduction

The majority of humans now live in urban areas, and the global urban population is expected to increase by 2 million people in the next 30 years, from 7.6 billion currently to 9.8 billion in 2050 (United Nations, 2018). The unprecedented expansion of urban areas will continue to transform the ecosystems of the world, with profound consequences for biodiversity (McKinney, 2008). Disentangling the effects of urbanization on biodiversity is essential to developing adaptive conservation strategies and designing more sustainable urban landscapes (Aronson et al., 2017).

Urbanization can induce both biotic differentiation (Aronson,

Handel, La Puma, & Clemants, 2015; Kühn & Klotz, 2006) and homogenization (La Sorte et al., 2014; McKinney, 2006) at different spatial scales. Biotic homogenization is characterized by the increase in taxonomic, phylogenetic, or functional similarities of biota over space and time (Olden & Rooney, 2006). Urban areas in different regions are frequently described as under-going homogenization whereby they are compositionally more similar (i.e., have lower  $\beta$ -diversity; Fig. 1) than the natural areas they replace (Grimm et al., 2008; Groffman et al., 2017; Kühn & Klotz, 2006; McKinney, 2006; Pearse et al., 2018). In this regard, taxonomic homogenization points to an increased similarity in species composition across a set of ecological communities (Olden & Rooney, 2006), while phylogenetic homogenization represents

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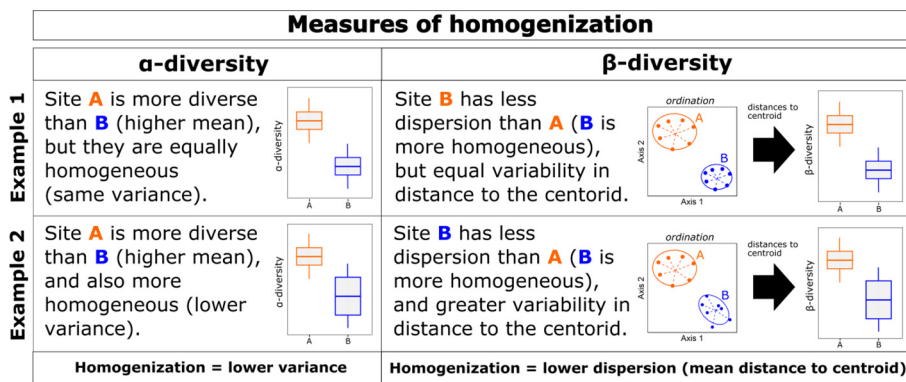


Fig. 1. Diagram exemplifying how homogenization is interpreted in the context of this study for any biodiversity dimension (taxonomic, phylogenetic, or functional). For  $\alpha$ -diversity, homogenization is represented by lower variance between groups. For  $\beta$ -diversity, homogenization is represented by reduced multivariate dispersion between groups (i.e., lower mean distance between sites and the centroid of their group). Plots in  $\beta$ -diversity represent composition similarities (ordination axes) within and across groups. In case example (1), site A has on average higher  $\alpha$ -diversity than site B, but they share similar variances. Therefore, neither site is more homogeneous than the other in terms of  $\alpha$ -diversity. However, site B is more homogeneous than A in terms of  $\beta$ -diversity because B has lower multivariate

dispersion around the centroid. In case example (2), site A has on average higher  $\alpha$ -diversity than site B, but it is also more homogeneous than B because of its lower variance. For  $\beta$ -diversity, site B is more homogeneous than A because it has lower multivariate dispersion to the centroid than A, despite having higher variance.

increased similarity in the evolutionary lineages comprising an assemblage (Winter et al., 2009). For example, if two different cities host two different oak (*Quercus*) species, testing for taxonomic homogenization will not capture their similarity, but testing for phylogenetic homogenization will. In contrast, these two cities can host two distantly related species with similar functional traits such as plant height, thus being functionally similar but phylogenetically dissimilar. Increased similarity in functional diversity indicates a simplification of the whole ecosystem and has been associated with decreased ecosystem resilience in natural environments (Olden, LeRoy Poff, Douglas, Douglas, & Fausch, 2004).

Given that both natural and anthropogenic selection operate on species functional traits (McKinney & Lockwood, 1999), taxonomic and phylogenetic homogenization are expected to be reflected in trait composition, and potentially result in functional homogenization (Olden et al., 2004). Nonetheless, correlations among taxonomic, phylogenetic, and functional  $\beta$ -diversity have been shown to vary widely, depending on the number of traits included in the analysis, and their identity and redundancy, among other factors (e.g., Brice, Pellerin, & Poulin, 2017; Sonnier, Johnson, Amatangelo, Rogers, & Waller, 2014; Winter et al., 2009). Because results can vary across urban areas and depend on the traits examined, and on the urban stressors acting on those traits (Knapp et al., 2012; Williams, Hahs, & Vesik, 2015), examining biotic homogenization and its long-term consequences is best accomplished by encompassing all dimensions of biodiversity.

Urban areas are often assumed to host higher taxonomic ( $\gamma$ ) diversity (Grimm et al., 2008; Kühn, Brandl, & Klotz, 2004), but lower phylogenetic diversity (Knapp, Winter, & Klotz, 2017; Ricotta et al., 2009) or functional diversity (La Sorte et al., 2018; Nock, Paquette, Follett, Nowak, & Messier, 2013), than adjacent natural areas. Within urban areas, the diversity among individual plant communities (i.e.,  $\alpha$ -diversity) has not yet been investigated in relation to that of native communities, even though reduced variance in  $\alpha$ -diversity across communities can also be interpreted as a form of homogenization (Fig. 1). For example, two communities hosting the same number of species might be considered more similar than two communities with disparate numbers of species, regardless of species identity. This knowledge gap makes it difficult to interpret homogenization patterns across different spatial scales and levels of diversity.

Residential yards are components of dynamic urban landscapes in which plant community assembly is driven by the movement of plants from the regional flora and the horticultural pool through contrasting filters and sorting processes (Aronson et al., 2016; Pearse et al., 2018; Williams et al., 2009). On the one hand, the naturally assembled regional flora is influenced by historical biogeographic processes and filtered by climate, pollution, human management activities, and other abiotic constraints (Lopez, Urban, & White, 2018; Padullés Cubino

et al., 2019a; Ricklefs, 2004). Species from the regional flora can disperse from natural to residential areas and through interstitial unmanaged vegetation areas in the residential-wildland interface. On the other hand, the horticultural pool is influenced by householder socioeconomic status and their landscape preferences and priorities, and is further filtered by management activities (Kendal, Williams, & Williams, 2012; Kinzig, Warren, Martin, Hope, & Katti, 2005; van Heezik, Freeman, Porter, & Dickinson, 2013). Management activities include mowing, weeding, fertilizing, pesticide use, and irrigation, which can not only affect cultivated but also spontaneously occurring species. Overall, the combined effect of these filters can lead yards across biophysically different and geographically distant regions to have similar patterns of vegetation structure and composition (Groffman et al., 2017), making them an important study system in which to examine homogenization processes in urban ecosystems.

Previous studies have shown that floras in residential yards in the U.S. are compositionally and structurally more similar than the corresponding floras in surrounding natural areas (Pearse et al., 2018; Wheeler et al., 2017). Yet, the apparent structural homogeneity of residential yards in the U.S. can mask significant variation in management intensity and gardening practices (Groffman et al., 2016). Residential yards that exhibit similar ecological characteristics can be produced by different land management practices such as high versus low lawn fertilization or groundcover choices (Harris et al., 2012; Polsky et al., 2014), making it important to account for the effect of varying management practices on homogenization patterns.

Biotic homogenization in urban environments has been assessed either based on complete urban floras (Kühn & Klotz, 2006; La Sorte, McKinney, & Pyšek, 2007; McKinney, 2006); floras from publicly accessible urban habitats (Brice et al., 2017; Lososová et al., 2012); certain groups of species, such as lawns (Wheeler et al., 2017); or on aggregated yard floras at the city level without considering different yard management types (Pearse et al., 2018). In addition, biotic homogenization within yard floras has been associated with spontaneous but not cultivated introduced species (Padullés Cubino et al., 2019b). We build on this work by examining biotic homogenization in different types of residential yards grouped according to fertilizer input and management for wildlife (i.e., ‘high-input lawns’, ‘low-input lawns’, and ‘wildlife-certified’ yards, where ‘input’ refers to fertilizer use). We collected plant presence/absence data in 72 yards distributed among six major U.S. metropolitan areas, and compared their diversity and composition with those in nearby natural areas, protected natural areas surrounding metropolitan areas that contain typical habitats of each region, and interstitial areas, unmanaged areas at the residential-wildland interface (Table 1). Interstitial areas were important in our study because they represented unmanaged vegetation areas within cities or at the wildland-residential interface that can act as a conduit for plant dispersal between natural and urban areas (Bar-Massada,

**Table 1**  
Characteristics of the different land-use groups included in our study.

| Land-use groups          | Code | N  | Definition   |
|--------------------------|------|----|--|
| Reference natural areas  | REF  | 24 | Protected natural areas surrounding metropolitan areas that contain typical habitats of each region.   |
| Interstitial areas       | INT  | 24 | Unmanaged public lands located in the residential-wildland interface.  |
| High-input lawns         | HIL  | 24 | Yards with > 75% of either front or back yard pervious area covered by turfgrass, that had received fertilizer in the last year or whose turfgrass was maintained by a lawn-care company.  |
| Low-input lawns          | LIL  | 24 | Yards with > 75% of either front or back yard pervious area covered by turfgrass, that had not received fertilizer in the last year and whose turfgrass was maintained by homeowners.  |
| Wildlife-certified yards | WLC  | 24 | Yards that provide sustainable habitat for native wildlife. They had been certified by the National Wildlife Federation for at least 3 years. Certification requirements can be found at: <a href="http://www.nwf.org/certify">www.nwf.org/certify</a> |

Radeloff, & Stewart, 2014). Although our work is limited to the U.S., where yards are a major land-use type (Milesi et al., 2005) and are primarily grown for aesthetic purposes (Nassauer, 1988), our conclusions could be extrapolated to other countries sharing a common European gardening culture given that colonialism has resulted in widely dispersed urban areas with similar cultivated landscapes, which mimic those of their shared colonial homeland (Ignatieva & Stewart, 2009).

We addressed two questions: (1) are different types of yards taxonomically, phylogenetically, and functionally more homogeneous than natural and interstitial areas? and (2) what is the strength of the correlations between taxonomic, phylogenetic, and functional diversity in yards? For the first question, we predicted that all yard types would have lower  $\beta$ -diversity (i.e., would be compositionally more similar or homogeneous) than natural areas for all diversity dimensions. We expected this because, across different regions, shared human preferences (e.g., for savanna-like yards; Ulrich, 1986; Nassauer, 1988; Falk & Balling, 2010) and management (e.g., irrigation, fertilization) to relax climatic or resource constraints can select for a more similar set of traits than those found in natural areas, and in turn increase phylogenetic and taxonomic similarities. We predicted that interstitial areas would have intermediate levels of  $\beta$ -diversity compared to yards and natural areas because they have intermediate levels of human influence and might share a large proportion of spontaneously occurring species with yards. Within yard types, we expected wildlife-certified yards to have greater  $\beta$ -diversity across cities than the other yard types given the resources needed by wildlife. In contrast, we expected high-input lawns to have lower  $\beta$ -diversity than other yard types because they frequently contain monocultures of widely-used turfgrass species with few cosmopolitan weeds. Nonetheless, we also hypothesized that, because humans vary widely in their cultivation practices—creating landscapes that range from highly diverse to near-monocultures—residential yards would have greater variance in taxonomic  $\alpha$ -diversity than natural areas. For the second question, we expected taxonomic and phylogenetic  $\beta$ -diversity to be uncorrelated with functional  $\beta$ -diversity across yard types because traits have a tendency to phylogenetically converge under strong environmental filtering (Cavender-Bares, Ackerly, Baum, and Bazzaz, 2004; Cornwell & Ackerly, 2009).

## 2. Materials and methods

### 2.1. Site selection

We selected six major U.S. Metropolitan Statistical Areas (hereafter ‘cities’): Boston, MA (BOS), Baltimore, MD (BAL), Los Angeles, CA (LA), Miami, FL (MIA), Minneapolis-St. Paul, MN (MSP) and Phoenix, AZ (PHX) to represent six different ecological biomes and/or major climatic regions across the U.S. (Trammell et al., 2016). Within each city, we used the Tapestry Segmentation in ArcGis (ESRI, 2017) to select initially 22 distinct census block groups (Appendix S1). Tapestry is a geodemographic segmentation system that integrates consumer traits with residential characteristics to identify markets and classify U.S. neighborhoods. Neighborhoods with the most similar characteristics are grouped together, while neighborhoods with divergent

characteristics are separated.

The census block groups selected for this study included primarily single-family housing with a median income between \$45,000 and \$105,000, and were classified as neither rural nor semi-rural. Homes were at least 10 years old and were not bordered by non-residential managed green spaces, water features, or large open spaces (e.g., unmanaged natural areas) (see additional information for census block groups selection in Appendix S1).

Within identified census block groups for each metropolitan area, we randomly selected 50 parcels meeting the above criteria to visually assess yard type using satellite imagery. For the high-input and low-input lawn types, homes had yards with > 75% of the front yard or back yard pervious area covered in turfgrass (Table 1). We then sent a flier to all homes fitting the criteria above (minimum 50 homes contacted) with a description of the project and a link to an online questionnaire asking about lawn management and fertilization, with an option to opt in. From all the respondents, we randomly chose four properties of each type (i.e., ‘high-input lawn’ and ‘low-input lawn’) that were at least 1 km away from each other and other sites (Table 1). High-input lawns belonged to respondents who answered ‘yes’ to the question, ‘Does your house use a lawn-care company?’ or answered ‘> 3’ to the question, ‘How many times did your lawn receive fertilizer in the past year?’ Low-input lawns belonged to respondents who answered ‘no’ to the question, ‘Has your lawn received fertilizer in the past year?’ We defined ‘wildlife-certified yards’ as yards certified by the National Wildlife Federation (NWF) as sustainably providing wildlife habitat. Residents can apply for NWF Wildlife Certified Habitat status if they provide food, water, cover, and places to raise young for wildlife plus follow some of a set of specified practices (composting, xeriscaping, native plantings, rainwater capture, etc.; see full certification requirements at <https://www.nwf.org/garden-for-wildlife/certify>). For these yards, we contacted the NWF for a list of 15 addresses for certified yards in each city that met the primary criteria and had been wildlife certified for at least three years. The NWF contacted homeowners with a description of the project and a link to an online questionnaire asking whether their yards still contained all of the features required for wildlife certification, with an option to opt in. From all the respondents that answered ‘yes’, we randomly selected four homes in each city. This resulted in 72 yards across the six cities classified as either high-input lawns (HIL) (n = 24), low-input lawns (LIL) (n = 24) or wildlife-certified (WLC) yards (n = 24) (Table 1; Appendix S1). Yard area was calculated as the total property area minus the area occupied by buildings and other artificial surfaces. It was digitalized and measured with orthoimages using ArcGis version 10 (ESRI, 2017).

We also selected between four and six natural areas in each region that represented similar ecological, topographic and edaphic features of each city (Table 1; Appendix S1: Table S1). Additionally, we selected between four and six ‘interstitial’ areas that represented minimally managed (i.e., unmown and unfertilized) public lands located in the residential-wildland interface (Table 1). To make sample sizes even between natural areas and yards, we randomly selected four natural and four interstitial areas in each of the six regions to include in our analyses (Table 1).

## 2.2. Vegetation data

Trained botanists recorded all plant species (presence/absence) within the parcel boundaries in all 72 yards across the six cities (Padullés Cubino & Narango, 2019). We sampled during the season of peak diversity (summer for BAL, BOS and MSP; spring for LA, MIA and PHX). We sampled sites in BAL, BOS, MSP and PHX in 2017 and those in LA and MIA in 2018. Although yard plants are often subspecies or cultivars, we did not attempt to classify plants below the species level. We recorded the genus for 14% of the taxa for which we could not identify the species.

Within each natural and interstitial area, we established three transects, 100 m length and 2 m wide (200 m<sup>2</sup>). The locations and directions of transects within reference natural areas were randomly assigned using GIS. All vegetation rooted within each transect area was recorded for species presence/absence. The vegetation recorded along all transects was aggregated for each natural and interstitial area, and considered as a single site. This resulted in 24 sites in the natural areas and 24 sites in the interstitial areas, which was comparable to the household sample size of each yard type (Appendix S2: Fig. S1). We then created a species list for each plot, and matched species names to The Plant List (ver. 1.1, <http://www.theplantlist.org>), using R package *Taxonstand* (Cayuela, Stein, & Oksanen, 2017). We also classified species as either native or introduced following the USDA PLANTS (<https://plants.usda.gov>) and the Encyclopedia of Life (<http://www.eol.org>) databases as explained in Appendix S3.

## 2.3. Phylogeny

We constructed a dated phylogenetic tree using an updated version of the Zanne et al. (2013) phylogeny produced by Qian and Jin (2016). We added species missing from this phylogeny at the genus level using the ‘congeneric.merge’ function in the R package *pez* (Pearse et al., 2015). Hybrids were reduced to the genus level and we excluded from the analysis species for which there were no phylogenetic data (~2%).

## 2.4. Plant traits

We collected data on three plant traits related to different ecological processes including plant dispersal, establishment, and persistence (Díaz et al., 2016; Westoby, 1998). These traits were maximum plant height (m), seed mass (mg), and specific leaf area (SLA; mm<sup>2</sup>/mg). Maximum plant height relates to competitive ability (particularly for light) and is associated with establishment and resistance to environmental disturbances (Moles et al., 2009). Seed mass influences dispersal, with small-seeded plants generally having higher dispersal capacity than large-seeded plants, although larger seeds are typically better provisioned and can confer advantages in establishment (Moles, 2005; Westoby, 1998). SLA is related to resource acquisition (Reich, 2014), photosynthetic capacity (Wright et al., 2004), and growth and competitive ability, and is positively correlated with relative growth rate across species (Garnier et al., 2001). Further details on ecological processes associated to plant traits can be found in Appendix S4. We collected all functional traits from the TRY database ([www.try-db.org](http://www.try-db.org); see Appendix S5 for specific references).

Plant trait data were not available for all species (plant height, 62% of total species; seed mass, 69%; SLA, 55%). Because deleting species with missing data from the analysis would lower the number of observations substantially, and probably bias the results because of the selective removal of species that were less well known, for these cases, we estimated the missing values using phylogenetic information from species with available trait data. Statistical gap-filling of sparse trait matrices is supported by some characteristics inherent to functional traits, such as a strong phylogenetic trait signal and structural trade-offs between traits (Swenson, 2014). To fill these gaps, we used R package *Rphylopar* (Goolsby, Bruggeman, & Ané, 2017) to first compare

available trait data across four alternative evolutionary model, and then select the best-fitting model on the basis of the lowest AIC value to impute trait data (see Appendix S6 for more details). We used the mean value in analysis when multiple values occurred for any given species. Results for analysis with original (non-imputed) trait data can be found in the Supporting Information (Appendix S2), and they are also discussed in the text.

## 2.5. Alpha-diversity

In each plot, we calculated  $\alpha$ -taxonomic diversity ( $\alpha$ -TD) as the overall number of species normalized by total vegetated area (species density). Following Faith (1992), we calculated  $\alpha$ -phylogenetic diversity ( $\alpha$ -PD) as the sum of total branch lengths in the phylogenetic tree connecting species in each plot (i.e., Faith’s PD) (Tucker et al., 2017). To produce a phylogenetic index of diversity that is independent of species richness, we calculated the standardized effect sizes of Faith’s PD (ses.PD), by comparing the observed community diversity to the null distribution of randomly assembled communities. We used the independent-swap algorithm to draw a null distribution based on 999 replicates, which retains the species richness within each plot and the relative frequency of species occurrences, but changes species co-occurrences. We constructed separate null models for reference natural areas, interstitial areas, and all yards together to account for differences in each species pool. Negative values of ses.PD indicate lower phylogenetic diversity than expected under the assumption of the null model, whereas values greater than zero indicate higher phylogenetic diversity than predicted by the null model. We calculated  $\alpha$ -PD with the ‘ses.pd’ function in R package *picante* (Kembel et al., 2010).

We computed  $\alpha$ -functional diversity ( $\alpha$ -FD) as ‘functional dispersion’ (FDis) following Laliberté and Legendre (2010). We chose FDis among the many metrics of functional diversity because it describes the distribution of species in trait space, can be used for multiple traits, is not strongly influenced by outliers and is independent of species richness. We calculated the functional distance matrix using Gower distances that tolerate missing values (Podani & Schmera, 2006) and FDis with R package *FD* (Laliberté, Legendre, & Shipley, 2014).

Additionally, we also calculated the standardized effect size of mean pairwise distance (ses.MPD) (Tucker et al., 2017; Webb, Ackerly, McPeck, & Donoghue, 2002) for the phylogenetic and functional diversity components as alternative measures of  $\alpha$ -PD and  $\alpha$ -FD in each plot. MPD is one of the most robust measures for computing the phylogenetic and functional relatedness between species’ pairs belonging to a given group (Webb et al., 2002). We placed results for ses.MPD in Appendix S7 and used them to support and complement results for ses.PD and FDis (see also Appendix S7 for details on ses.MPD calculation and interpretation).

## 2.6. Beta-diversity

We created a site-by-site pairwise dissimilarity matrix with taxonomic, phylogenetic, and functional distances to compute the centroid of each land-use group: reference natural areas, interstitial areas, high-input lawns, low-input lawns, and wildlife-certified yards. For  $\beta$ -taxonomic diversity ( $\beta$ -TD), we computed the site-by-site distance matrix on the species presence-absence matrix using Sørensen’s distance in R package *vegan* (Oksanen et al., 2019). For  $\beta$ -phylogenetic diversity ( $\beta$ -PD), we computed the distance matrix on the species presence-absence matrix and the phylogenetic tree using Phylo-Sørensen’s distance in R package *betapart* (Baselga, Orme, Villegger, De Bortoli, & Leprieur, 2018). For  $\beta$ -functional diversity ( $\beta$ -FD), we computed the distance matrix on the site-by-trait matrix using Gower distances. We calculated  $\beta$ -FD as a composite measure including all three traits, and also considering traits individually. We computed the site-by-trait matrix with R package *FD* (Laliberté et al., 2014). Finally, the distance of each site to their associated group centroid (i.e.,  $\beta$ -diversity; Fig. 1) was calculated

using the function ‘betadisper’ in R package *vegan*, which reduces the original distances to principal coordinates.

## 2.7. Data analysis

We compared the overall number of species (taxonomic  $\gamma$ -diversity) among all land-use groups using smoothed species accumulation curves. Average species accumulation curves were calculated for 1000 random permutations following the analytical formula published by Colwell, Mao, and Chang (2004) in R package *vegan* (Oksanen et al., 2019). We used Pearson correlations to assess the relationship among all diversity metrics ( $\alpha$ -TD,  $\alpha$ -PD,  $\alpha$ -FD,  $\beta$ -TD,  $\beta$ -PD and  $\beta$ -FD) across all yards. The probability values were adjusted using the Holm correction for multiple testing.

To test for biotic homogenization (i.e., lower variance) in  $\alpha$ -diversity in yards compared to natural and interstitial areas (Fig. 1), we tested for equality of variances with pairwise Levene’s tests as implemented in R package *car* (Fox & Weisberg, 2011). We also used one-way analysis of variance (ANOVA) to determine whether there were any statistically significant differences between the means of  $\alpha$ -diversity metrics among land-use groups. We then used Games-Howell post-hoc tests that represent an extension of Tukey’s test for unequal variances among groups (Games & Howell, 1976). We additionally performed two-way ANOVA to test for the effect of ‘city’ and ‘management strategy’ (i.e., yard type), and their interaction, on yard  $\alpha$ -diversity.

To test for biotic homogenization (i.e., lower dispersion) in  $\beta$ -diversity in yards compared to natural and interstitial areas (Fig. 1), we tested for homogeneity of multivariate dispersions (variances) with ANOVA and Tukey’s post-hoc test (e.g., Brice et al., 2017; Müller, Buhk, Lange, Entling, & Schirmel, 2016). This method is a multivariate analogue of Levene’s test for homogeneity of variances when the distances between group members and group centroids are Euclidian distances.

To detect shifts in taxonomic, phylogenetic, and functional composition among land-use groups (i.e., the three yard types, natural areas, and interstitial areas), we tested for differences in centroid location by land-use using PERMANOVA (Anderson, 2001). We used the function ‘adonis’ in R package *vegan* (Oksanen et al., 2019) with 9,999 permutations, and R package *pairwiseAdonis* (Martinez Arbizu, 2019) for multilevel pairwise comparisons. Because this test is sensitive to differences in multivariate dispersions (i.e., significance can be caused by differences in dispersion rather than in centroid location), we used data visualization to support the interpretation of the result. Differences in taxonomic, phylogenetic, and functional  $\beta$ -diversity among land-use groups were illustrated in principal components analysis (PCoA) based on their respective distance matrix.

We repeated analyses testing for biotic homogenization separately for native and introduced species to compare the effect of each pool of species on the joint results (Appendix S3). We performed all statistical procedures in R version 3.4.1 (R Core Team, 2019) and established significance at  $\alpha < 0.05$ .

## 3. Results

### 3.1. Differences in taxonomic $\gamma$ -diversity

We identified a total of 2,554 taxa across all land-use groups. Wildlife-certified yards hosted the highest total number of species (1,408), followed by low-input lawns (1,163), high-input lawns (965), reference natural areas (772), and interstitial areas (668). Accumulation curves showed that the number of species continued to increase with sampling across all land-use groups (Fig. 2).

### 3.2. Differences in $\alpha$ -diversity

All yard types had higher taxonomic  $\alpha$ -diversity ( $\alpha$ -TD) but lower

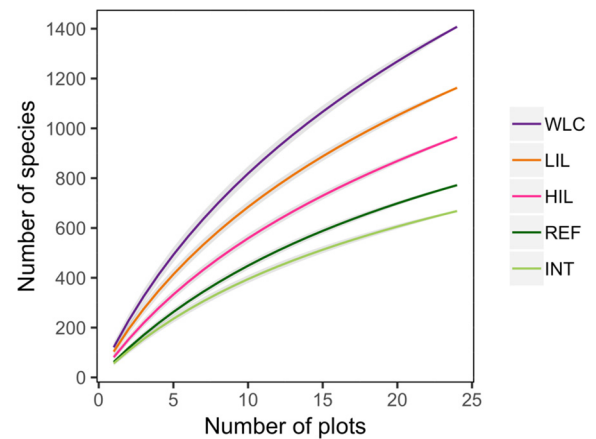


Fig. 2. Species accumulation curves from vegetation surveys conducted for each land-use group (REF = Reference natural areas; INT = Interstitial areas; HIL = High-input lawns; LIL = Low-input lawns; WLC = Wildlife-certified yards). Grey areas represent 95% confidence intervals.

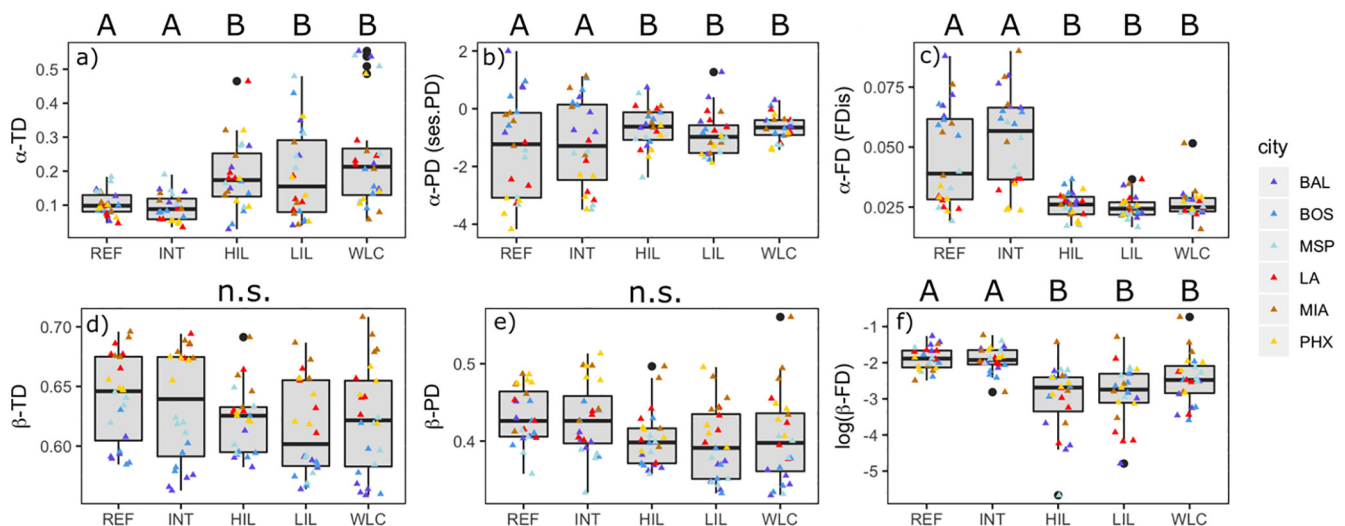
functional  $\alpha$ -diversity ( $\alpha$ -FD) than natural and interstitial areas (Fig. 3; see results of statistical tests in Appendix S8). We found no differences in mean phylogenetic  $\alpha$ -diversity ( $\alpha$ -PD) among land-use groups (Fig. 3; Appendix S8; see also results for ses.MPD in Appendix S7). However, all land-use groups showed a trend towards negative values of  $\alpha$ -PD (Fig. 3b), and phylogenetic clustering was especially important in natural and interstitial areas closer to hotter and drier and, to a lower extent, colder cities (Appendix S7). The three yard types did not differ from each other for either  $\alpha$ -TD,  $\alpha$ -PD or  $\alpha$ -FD. We found significant differences in  $\alpha$ -PD and  $\alpha$ -FD in yards among cities (Fig. S3), but the interaction between ‘city’ and ‘management strategy’ (i.e., yard type) was not significant for  $\alpha$ -TD,  $\alpha$ -PD or  $\alpha$ -FD (Appendix S8).

We found evidence of homogenization in yards compared to natural and interstitial areas for  $\alpha$ -PD and  $\alpha$ -FD (Fig. 3b-c; Appendix S9; see also results for ses.MPD in Appendix S7). In contrast, natural and interstitial areas were more homogeneous than yards for  $\alpha$ -TD (Fig. 3a; Appendix S9).

### 3.3. Differences in $\beta$ -diversity

Yards did not differ from natural and interstitial areas, or amongst management types, in taxonomic ( $\beta$ -TD) and phylogenetic ( $\beta$ -PD)  $\beta$ -diversity, as measured by differences in mean distance to the centroid (Fig. 3d-e; Fig. 4a-b), and thus were not more homogeneous taxonomically or phylogenetically in terms of  $\beta$ -diversity. Also, we found no significant differences among yard types for functional  $\beta$ -diversity ( $\beta$ -FD) (Fig. 3d-f). However, the three yard types showed consistently lower  $\beta$ -FD than natural and interstitial areas, as measured by difference from the centroid (Fig. 3f; see also ellipse size on PCoA in Fig. 4e), evidence that yards were more functionally homogeneous for this aspect of  $\beta$ -diversity. When traits were considered individually, the three yard types had lower  $\beta$ -FD than natural and interstitial areas for plant height (Fig. S2a) and specific leaf area (SLA) (Fig. S2c). In contrast, wildlife-certified yards had higher  $\beta$ -FD for seed mass than all other land-use groups (Fig. S2b). When original non-imputed trait data were considered, only high- and low-input lawns had significantly lower  $\beta$ -FD than natural and interstitial areas (Fig. S4b).

Taxonomic and phylogenetic composition was the same among yard types (same centroids locations), but different between all yard types and natural and interstitial areas (Fig. 4a-c; Appendix S10). Functional composition did not vary among land-use groups (Fig. 4e; Appendix S10). In addition, yards in the three northern cities (BAL, BOS and MSP) were taxonomically distinct from those in the three southern cities (LA, MIA and PHX) (Fig. 4b). Yards in the northern cities tended to converge with LA and PHX in terms of phylogenetic composition, but MIA



**Fig. 3.** Boxplots (median and quartiles) for  $\alpha$ - and  $\beta$ -taxonomic (TD), phylogenetic (PD) and functional (FD) diversity in each land-use group. Alpha-taxonomic diversity was normalized by total vegetated area (number of species/m<sup>2</sup>). Alpha-phylogenetic and functional diversity were calculated as the standardized effect size of Faith's PD (ses.PD) and Functional Dispersion (FDIs), respectively. Beta-diversity was measured as the distance of sites to their group centroid. Triangles are colored according to the sampled city: cool-blue colors represent northern cities (Baltimore [BAL], Boston [BOS] and Minneapolis-Saint Paul [MSP]), and warm-red colors southern cities (Los Angeles [LA], Miami [MIA] and Phoenix [PHX]; see Fig. S3 for distribution of  $\alpha$ -diversity within cities). For  $\alpha$ -diversity, different letters indicate significant differences in variances between land-use groups as per Levene's test. For  $\beta$ -diversity, different letters indicate significant differences in multivariate dispersions as per ANOVA. REF = Reference natural areas; INT = Interstitial areas; HIL = High-input lawns; LIL = Low-input lawns; WLC = Wildlife-certified yards; n.s. = non-significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

remained phylogenetically distinct from the other cities (Fig. 4d). Yards in all cities tended to converge for functional composition (Fig. 4f).

### 3.4. Contrasting effects between native and introduced species

Results considering native and introduced species together (Fig. 3) did not differ from those considering only introduced species (Fig. S6). When only native species were considered, high-input yards had significantly lower variance in  $\alpha$ -TD than reference and interstitial areas, and low-input and wildlife-certified yards did not differ from reference and interstitial areas in their variance of  $\alpha$ -TD and mean  $\beta$ -FD (Fig. S7). Introduced species contributed more to homogenization than native species for all diversity components except for  $\alpha$ -TD, where both pools of species induced differentiation (Fig. 5). The homogenizing effect of introduced species was particularly strong in wildlife-certified and low-input yards (Fig. 5).

### 3.5. Correlations between $\alpha$ - and $\beta$ -diversity

Across all yards (n = 72),  $\alpha$ -TD significantly decreased with increasing  $\alpha$ -PD,  $\alpha$ -FD,  $\beta$ -TD, and  $\beta$ -PD;  $\alpha$ -PD increased with increasing  $\alpha$ -FD; and  $\beta$ -PD increased with increasing  $\beta$ -TD and  $\beta$ -FD (Fig. 6). The strongest correlation was found between  $\beta$ -TD and  $\beta$ -PD (Pearson's  $r = 0.87$ ;  $P < 0.05$ ).

## 4. Discussion

Our study supported the hypothesis that residential yards in different regions of the U.S. were functionally more homogeneous than the reference natural areas they replaced, regardless of fertilizer input and management style. Plant species in yards were more similar in height and specific leaf area (SLA), but not seed mass, than their counterparts in natural areas. Furthermore, functional homogenization was driven by introduced species in low-input and wildlife-certified yards. However, functional composition (i.e., the location of groups' centroids) did not vary significantly between yards and natural areas. Despite contrasting taxonomic and phylogenetic composition between yards and natural areas, we found no support for taxonomic

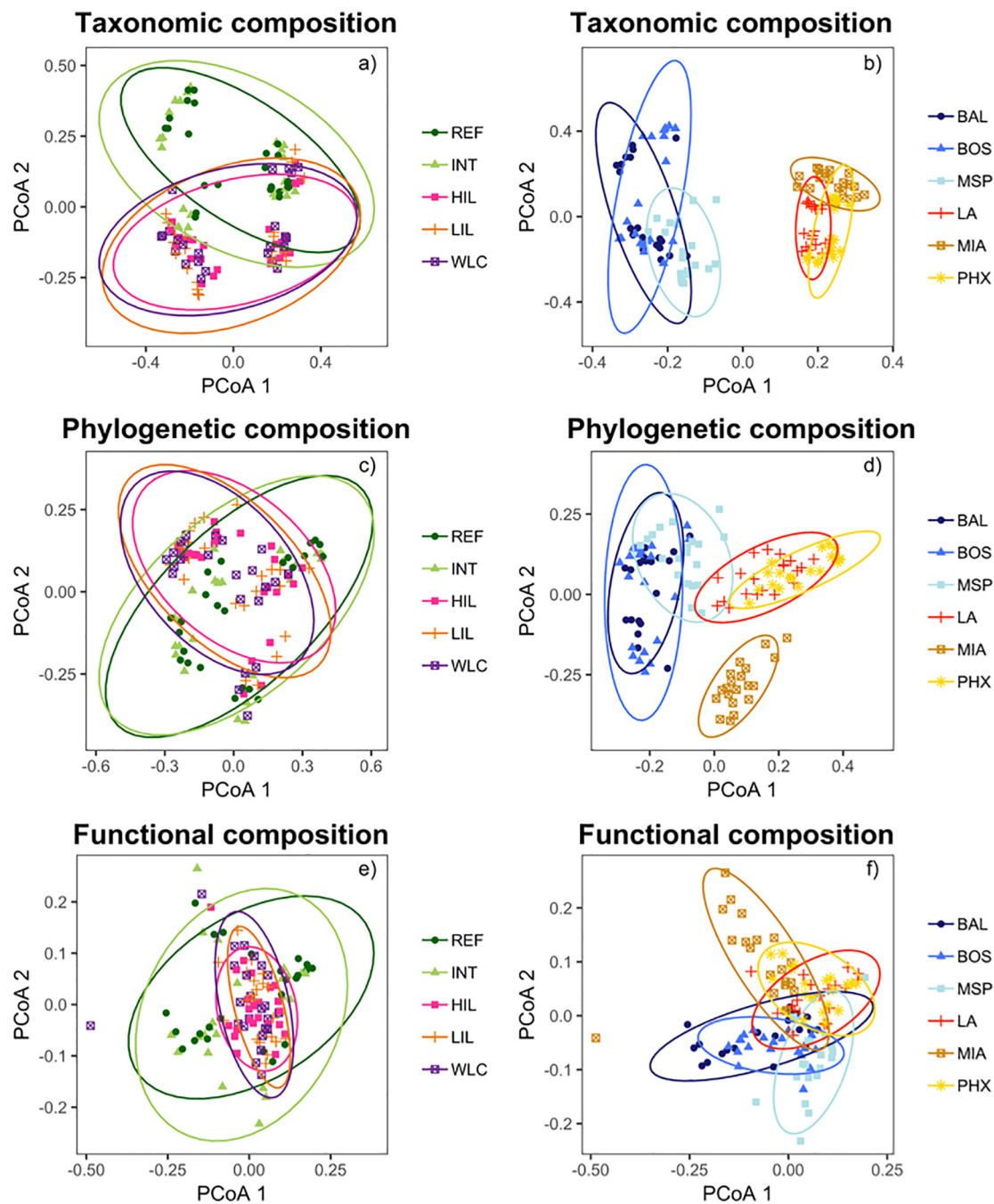
homogenization of residential yards, and limited support for phylogenetic homogenization (only for  $\alpha$ -diversity). In fact, as predicted, yards had greater variability in species richness per unit area than natural areas. Interstitial areas, which we hypothesized would show intermediate characteristics between natural and urban areas, did not differ from natural areas in any of our diversity metrics.

Even though different degrees of fertilization and landscaping style had a limited effect on the biotic homogenization of residential yards, our findings corroborated that wildlife-certified yards were slightly more functionally heterogeneous than high- and low-input lawns, mainly because of a higher variation in seed mass. However, fertilizer input and managing yards for wildlife did not induce shifts in species and phylogenetic composition among yard types across the U.S. Several factors, which are linked to the environmental and anthropogenic filters acting on urban yard floras, can help explain these results.

### 4.1. Biotic homogenization of different yard types

Urbanization has previously been linked to biotic homogenization (Grimm et al., 2008; Groffman et al., 2017; McKinney, 2006). Unlike other studies that examined this process in public urban areas (Brice et al., 2017; Lososová et al., 2012), or by aggregating data at the city level (La Sorte et al., 2007; Pearse et al., 2018), we found that individual residential yards were more functionally similar to each other than to adjacent natural and interstitial areas of equivalent size. Functional homogenization of yards was consistent across the three yard types for both  $\alpha$ - and  $\beta$ -diversity. Pearse et al. (2018), who also examined homogenization patterns in yards across the U.S., found evidence of phylogenetic homogenization of both cultivated and spontaneous floras. However, they reported no evidence of functional homogenization for tree height and leaf traits, which they partially attributed to limited statistical power. Here, we increased statistical power by assessing biotic homogenization not at the city but at the yard level. As proposed by others (Groffman et al., 2017; Larson et al., 2016), we argue that functional homogenization in our yards likely arose from the combination of similar filtering processes imposed by human preferences and behaviors.

Although determining the exact causes of biotic homogenization in

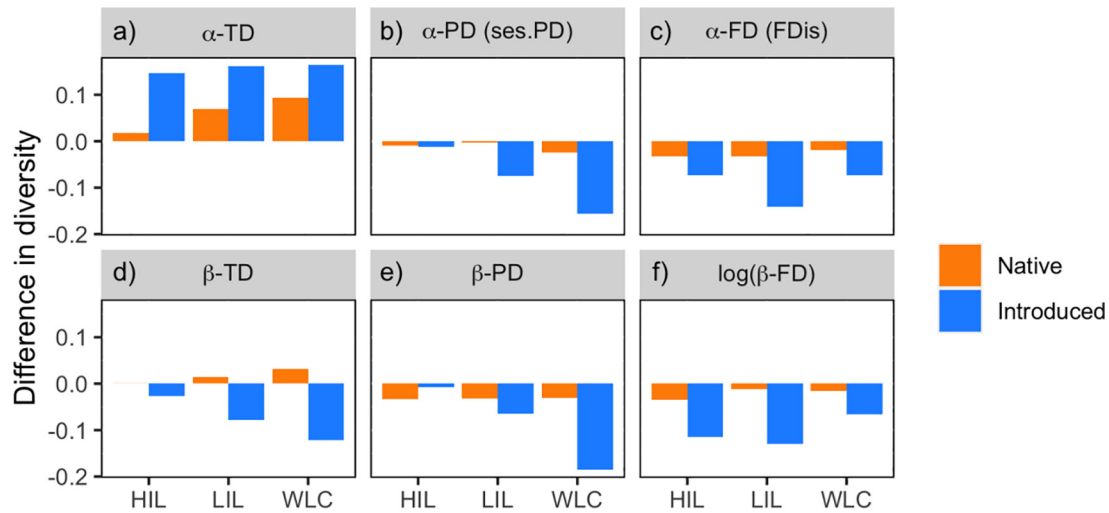


**Fig. 4.** Multivariate dispersion of taxonomic (a-b), phylogenetic (c-d), and functional (e-f) plant composition. In plots ‘a’, ‘c’, and ‘e’, sites are clustered by land-use groups, and in plots ‘b’, ‘d’, and ‘f’, sites are clustered by city. Beta-diversity was measured as the distance of sites to their group centroid, here represented on the first two axes of PCoA. Ellipses represent 95% confidence intervals. Symbols and colors represent land-use groups: REF = Reference natural areas; INT = Interstitial areas; HIL = High-input lawns; LIL = Low-input lawns; WLC = Wildlife-certified yards. Plots for taxonomic, phylogenetic, and functional composition of yards alone within cities are presented in Fig. S5.

yards is beyond the scope of this study, we tested for the effect of varying management styles on these patterns. Our results suggest that the degree of functional homogenization of yard floras did not depend on yard management strategy or the adoption of gardening practices to support wildlife. However, by visually inspecting the dispersion of functional  $\beta$ -diversity of land-use groups (Fig. 3f and 4e), we detected that wildlife-certified yards were more functionally heterogeneous than high- and low-input yards, potentially resembling natural areas (see also Fig. S4b). This higher heterogeneity was mainly driven by higher variation in species’ seed mass in wildlife-certified yards in relation to other yard types. This in turn could result from an increase in the

variability of fruit and seed sizes as a consequence of homeowners’ interest in providing food for a wide range of wildlife. Therefore, encouraging the transition from lawns with high levels of fertilizer inputs to more wildlife-promoting yards could play an important role in replicating ecological functions provided by native ecosystems, insofar as the traits we measured capture ecologically meaningful aspects of ecological function. Whether this increase in functional heterogeneity in yards consistently translates into greater provision of ecosystem services remains a question for further research.

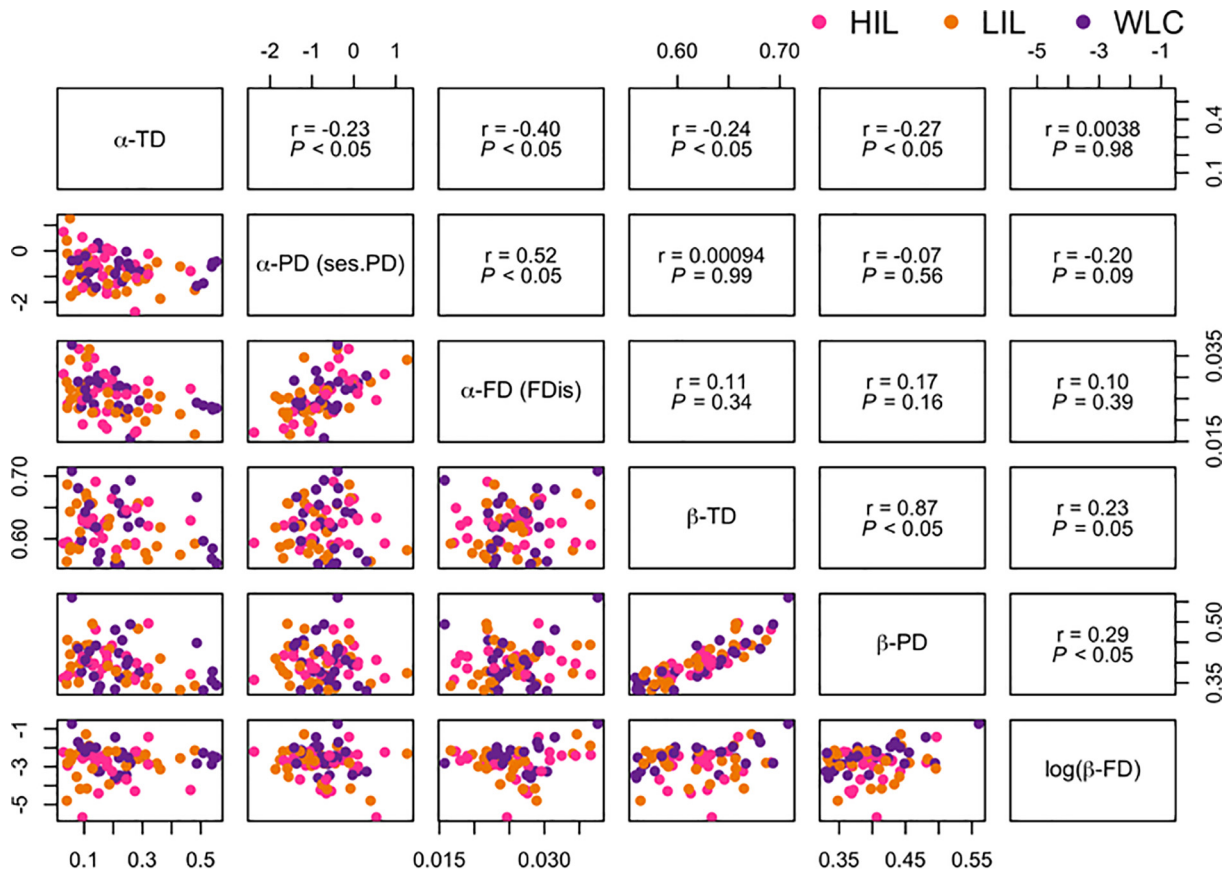
Functional diversity was calculated by means of three critical functional traits (plant height, seed mass and SLA) that capture a large



**Fig. 5.** Differences in the variance of  $\alpha$ -diversity (measured as standard deviation) and in mean  $\beta$ -diversity of each biodiversity component (i.e., taxonomic [TD], phylogenetic [PD], and functional [FD]) associated with native and introduced species across yard types. Differences associated with each pool of species were calculated as the diversity value including both natives and introduced species, minus the diversity value without that pool of species. Diversity values were previously standardized to allow comparisons. Negative values indicate the pool of species contributed to homogenization, while positive values indicate the pool of species contributed to differentiation. HIL = high-input lawns; LIL = low-input lawns; WLC = wildlife certified yards.

part of the ecologically significant differences among species, including resource acquisition and dispersal (Díaz et al., 2016; Westoby, 1998). Comparisons of  $\beta$ -functional diversity for individual traits revealed that functional homogenization in yards was mainly driven by similarities in plant height and SLA, but not so much in seed mass. However, mean

community trait values did not vary among land-use groups (Fig. S2), likely because our study only accounted for species presence/absence and not their abundance. Therefore, given that high- and low-input yards were covered > 75% by turfgrass, functional differences between these two yard types and wildlife-certified yards could be greater than



**Fig. 6.** Pearson correlations between all diversity metrics:  $\alpha$ - and  $\beta$ -taxonomic (TD), phylogenetic (PD), and functional (FD) in yards (HIL = high-input lawns; LIL = low-input lawns; WLC = wildlife-certified yards). Alpha-taxonomic diversity was calculated as species richness normalized by plot area. Alpha-phylogenetic and functional diversity were calculated as the standardized effect size of Faith's PD (ses.PD) and Functional Dispersion (FDIs), respectively. Beta-diversity for each site was calculated as the site distance to its group centroid.



we report here because of the high abundance of functionally similar (i.e., low-statured, small-seeded, and high SLA) herbaceous species and the associated reduction in vegetation structural complexity arising from having species with varying heights. Considering other plant traits related to the provision of ecosystem services and the support of wildlife that were not included in this study, such as plant pollination strategy, nectar production, flowering duration, fruit or seed edibility or lifespan, would offer complementary measures of function that could enrich comparisons of functional diversity between residential yards that vary in management practices and natural environments. Also, the collection and publication of additional trait data, particularly from species in urban habitats, would allow further corroboration of our conclusions.

Although yards were taxonomically and phylogenetically distinct from natural and interstitial areas, we found no statistical support for taxonomic and phylogenetic homogenization of yard floras. In other words, yards and natural areas were similarly heterogeneous in terms of species and lineages. This contrasts with previous results from [Pearse et al. \(2018\)](#) who examined biotic homogenization considering species pools at the city level, and reflects the influence of environmental filtering (e.g., extreme climate variation) and biogeographic processes in driving taxonomic and phylogenetic  $\beta$ -diversity of plant assemblages in highly managed urban landscapes at the continental scale. According to our results, although human management and preferences strongly influence taxonomic and phylogenetic  $\beta$ -diversity in yards at the local scale, the effect of these factors is largely overwhelmed by climatic filtering and biogeographic processes at larger spatial scales (see also [Padullés Cubino et al., 2019a](#)). This climatic filtering and biogeographical processes similarly affect  $\beta$ -diversity of species and lineages in natural and interstitial areas and residential yards. Only phylogenetic  $\alpha$ -diversity was consistently more homogeneous in yards than in natural and interstitial areas, implying less heterogeneity in the representation of the branches of the tree of life found in individual yards.

Previous studies have shown that plants in urban environments can have opposite effects on homogenization processes depending on their residence time, with more recently introduced species that have not achieved their potential range increasing differentiation, and those that have had sufficient time to disperse into the most suitable habitats increasing homogenization ([Lososová et al., 2012](#); [Olden & Poff, 2003](#)). In this regard, non-native cultivated species in yards in the U.S. have been shown to contribute to differentiation, because they are generally yard-specific, whereas cosmopolitan non-native spontaneous species contribute to homogenization ([Padullés Cubino et al., 2019b](#)). In our study we did not distinguish between cultivated versus spontaneous species pools, but we did classify them as either native or introduced. Former research has indicated that a large fraction of the introduced pool of species in yards corresponds to cultivated species, while native species are often classified as spontaneous ([Padullés Cubino et al., 2019b](#); [van Heezik et al., 2013](#)). We showed that both pools of species generally contributed to biotic homogenization in residential yards, although introduced species had a stronger homogenizing effect, particularly for  $\beta$ -functional diversity ([Fig. 5](#) and [Fig. S6](#)). This finding highlights the importance of promoting native species in urban areas to support native ecosystem functions and functionally heterogeneous urban habitats.

#### 4.2. Compositional variation within yard types

Fertilization use and gardening for wildlife had no significant effect on taxonomic, phylogenetic, or functional composition of yards across the U.S. However, in our study we classified yards based on whether or not they used fertilizer, and did not quantify the amount of applied fertilizer, or the frequency of applications per year. Thus, collecting more specific data on fertilizer application rates could help refine our conclusions. In addition, the effect of other management practices not included in our study, such as mowing, weeding, or irrigation, on biotic homogenization cannot be determined here. Nonetheless, our results

showed that plant taxonomic and phylogenetic composition in yards were largely influenced by location, with yards in the three northern cities being taxonomically and phylogenetically distinct from those in the south (especially from those in Miami; [Fig. S5a-b](#)), a pattern also evident in natural and interstitial areas. Moreover, yards in the three southern cities shared more species with natural and interstitial areas than those in the north (see ellipse size in [Fig. 3b](#)), potentially acting as reservoirs of native biodiversity, even though this did not automatically translate into higher functional similarity ([Fig. 3c](#)). We emphasize that many ecological and biogeographic processes could lead to these empirical patterns. For example, native plants in southern and hotter areas in the U.S. could be more adapted to extreme high temperatures, or possess more desired attributes by homeowners than their northern counterparts. More fundamentally, these results reflect that the influence of the horticultural and regional pools of species on yard composition is context dependent. A deeper understanding of plant distribution and composition in residential yards, especially within any one city, would require additional data across diverse ecologic and socioeconomic contexts to achieve a better representation of the flora found in these urban ecosystems.

#### 4.3. Relationship between $\alpha$ - and $\beta$ -diversity in yards

Our finding that urban vegetation has greater species richness (taxonomic  $\gamma$ -diversity) than natural areas was similar to previous studies (e.g., [Kühn et al., 2004](#); [Pearse et al., 2018](#)). The gain in species richness per unit area in yards was associated with phylogenetic homogenization (i.e., lower  $\beta$ -diversity). However, this gain in species did not have a significant effect on functional homogenization, which we interpret as a form of functional redundancy. This phenomenon is usually identified when different species within an ecosystem contribute in equivalent ways to an ecosystem function, such that one species can substitute for another ([Lawton & Brown, 1993](#)). In yards, human management generally provides additional resources, such as water and nutrients, and reduces the number of competitors, such as weeds, which could help support a great variety of cultivated species with similar ecological functions.

Empirical studies have reported significant correlations between taxonomic and functional  $\beta$ -diversity ([Brice et al., 2017](#); [Sonnier et al., 2014](#); [Villéger, Grenouillet, & Brosse, 2014](#)), although this relationship usually depends on the traits examined ([Baiser & Lockwood, 2011](#)). In our study, phylogenetic, but not taxonomic  $\beta$ -diversity, was significantly yet weakly correlated with functional  $\beta$ -diversity. This finding implies that changes in functional distinctiveness occurred simultaneously with a change in phylogenetic distinctiveness, and may suggest that environmental filtering operates on species traits that then influence phylogenetic composition.

## 5. Conclusions

Private yards were functionally more homogeneous than either natural or unmanaged interstitial areas, regardless of whether they were managed with higher fertilizer inputs or to promote wildlife. However, wildlife-certified yards were functionally closer to natural areas than lawn-dominated yard types, particularly when only native species were considered. These results highlight that encouraging the transition from lawns with high levels of fertilizer inputs to more wildlife-promoting yards that support native species can produce landscapes that are more functionally similar to native ecosystems, and thus able to sustain native biodiversity. Additionally, increasing the number of species in yards does not necessarily contribute to reducing functional homogenization at large spatial scales. Taxonomic and phylogenetic homogenization were also weakly correlated with functional homogenization, and thus are not appropriate surrogates for functional diversity in yards. Scaling-up our conclusions to broader geographical areas and using complementary sampling designs with

more case studies that consider species' abundance and alternative plant functional traits can provide complementary insights into biotic homogenization patterns in urban areas. Our findings can be used for policymakers and built-environment professionals throughout the world aiming to design and manage private urban landscapes, as sub-urban areas and their vegetation expand globally.

#### CRedit authorship contribution statement

**Josep Padullés Cubino:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Jeannine Cavender-Bares:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition. **Peter M. Groffman:** Conceptualization, Writing - review & editing, Project administration, Funding acquisition. **Meghan L. Avolio:** Conceptualization, Writing - review & editing, Funding acquisition. **Anika R. Bratt:** Investigation, Writing - review & editing. **Sharon J. Hall:** Conceptualization, Writing - review & editing, Funding acquisition. **Kelli L. Larson:** Conceptualization, Writing - review & editing, Funding acquisition. **Susannah B. Lerman:** Conceptualization, Writing - review & editing, Funding acquisition. **Desiree L. Narango:** Data curation, Writing - review & editing. **Christopher Neill:** Conceptualization, Writing - review & editing, Funding acquisition. **Tara L.E. Trammell:** Conceptualization, Writing - review & editing, Funding acquisition. **Megan M. Wheeler:** Investigation, Writing - review & editing. **Sarah E. Hobbie:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2020.103877>.

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