Assessing methods for comparing species diversity from disparate data sources: the case of urban and peri-urban forests

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Abstract. Multi-scale forest inventory and monitoring data are increasingly being used in studies assessing forest diversity, structure, disturbance, and carbon dynamics. Also, local-level urban forest inventories are providing plot data and protocols to study tree diversity and ecosystem services in urban forests worldwide. But, differences in the sampling methods underlying these disparate protocols and data sources is a non-trivial concern in formulating comparative analyses. We assess commonly used methods for comparing tree diversity in peri-urban and urban forests when available data have different sample sizes, plot sizes, and sampling intensities. We present methods for appropriately evaluating species richness, as well as methods for comparing species distributions via community data matrices. Using permanent plot data from the southeastern United States, we present a case study comparing urban and peri-urban forests along a north–south gradient, and assessing species richness and the ecological homogenization hypothesis. Our findings indicate that comparisons of tree species richness among communities, or forest types, are often inconclusive since commonly used sample sizes do not provide precise estimates of the number of species present. While the ecological homogenization hypotheses can be tested under conditions of unequal sampling effort, we suggest robust methods such as PERMANOVA and the Raup-Crick dissimilarity index. A framework for selecting appropriate methods is also discussed. As forests are increasingly being altered by anthropogenic drivers, future studies using disparate data sources must account for differences in measurements and sampling protocols in order to produce results that are both statistically defensible and useful for science-based management.

Key words: ecological homogenization; Forest Inventory and Analysis; forest sampling; i-Tree Eco; species richness.

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INTRODUCTION

Forest composition and tree species diversity have been recognized as primary drivers of ecosystem resilience and function (Jenerette et al. 2016). For example, tree composition is a key factor in determining forest ecosystem resistance and susceptibility, and diverse forests enhance the provision of ecosystem services and goods (Chazdon et al. 1999, Kendal et al. 2014, Livesley et al. 2016). Still, questions remain about how forest dynamics in rural contexts compare to those of urban environments (Blood et al. 2016). Also, further information is needed on how the increasing use of available plot-level data in both rural and urban forests can be used to address questions regarding ecological disturbance, functionality, and homogenization (Staudhammer et al. 2015, Speak et al. 2018). Such studies of tree and plant diversity among and within forested...
ecosystems can help characterize differences and similarities in communities across different disturbance regimes and scales (Yang et al. 2017).

Comparative analyses of tree and forest data collected from different ecosystems often use different inventory and sampling protocols. This can be problematic due to varying sampling intensities, plot shapes, and sizes (Laurance et al. 1998, Hou et al. 2015). Simple comparisons, such as those concerning average tree size or number of species, are often not straightforward, even if adjustments are made for the amount of area sampled (Gotelli and Colwell 2001). However, these comparisons are of great importance, as they allow researchers and managers to not only identify research questions, but develop metrics to assess management and planning activities across different tree populations. By consolidating, formatting, and matching data sampled for different projects with different objectives, regional and international databases and clearing houses could be developed.

National-level vegetation inventories have long been a valuable research data source for ecologists, providing information on rural and managed forests that is standardized across large geographic areas. Similarly, over the last decade, local-level data are being increasingly collected in urban forests across the world using standardized protocols, allowing researchers to address regional-, national-, and continental-level applied urban ecology questions, such as those comparing species diversity and distributions (Kendal et al. 2014, Staudhammer et al. 2015, Jenerette et al. 2016, Yang et al. 2017, Speak et al. 2018). These types of data, however, are invariably based on different sampling protocols, sampling intensities, and plot sizes and shapes, as well as tree selection and measurement criteria. Nonetheless, comparisons between these datasets will become increasingly important to better understand how anthropogenic impacts affect urban and peri-urban forest structure, diversity, and even ecosystem services across multiple scales, regions, and continents.

As natural landscapes are altered by urbanization, such comparisons allow us to fill gaps in our scientific understanding of the dynamics of urban-to-rural gradients and ecosystems. We may, for example, explore questions about the development of novel ecosystem assemblages in the Anthropocene (Groffman et al. 2014). We can test hypotheses about the homogenization of species composition (Pearse et al. 2018) or the abundance and occurrence of invasive species across urban-to-rural gradients (Staudhammer et al. 2015). Similarly, data can be used to study the adequacy of human-dominated landscapes in providing adequate habitat for native tree species and fauna (Livesley et al. 2016) or to understand the resilience of different forests to climate change and anthropogenic stressors. This type of data is key in estimating and modeling the supply of ecosystem services from urban and peri-urban forests (PF; Nowak et al. 2008, Speak et al. 2018).

Comparison of specific forest characteristics, such as mortality or height, when plot sizes differ has been accomplished using statistical procedures, such as weighting (Flewelling and Monserud 2002). Assuming that the number of observations and distributional shapes are not drastically different, these quantitative samples may be compared via simple $t$-tests, or if data sources are sufficiently different, non-parametric methods such as the Kolmogorov-Smirnov or Cramer-von Mises tests may be more appropriate (Quinn and Keough 2002). Plot-based data, where plots are considered as the independent unit of observation, require mixed modeling methods to account for the potential for correlation among trees measured within the same plot (García 2006). When plots are of different sizes, these methods are still valid, but weighting schemes may be appropriate in certain situations (Schreuder et al. 1993).

Urban ecology studies regularly use area-based statistics, such as tree density (Staudhammer et al. 2015, McPherson et al. 2017). When sampling schemes use identical selection criteria, area-based variables are unaffected by plot size differences in theory; however, their variances decrease with increases in plot size (Zeide 1980), leading to different levels of uncertainty for each plot size. On the other hand, when such studies utilize datasets with disparate sampling schemes or select trees within plots with different probabilities, comparisons must be adjusted for unequal plot sizes using a bootstrap process to construct means and standard errors (McPherson et al. 2017).

Beyond measures of ecosystem structure, researchers might also be interested in comparing...
species diversity using data from disparate sources (Blood et al. 2016). However, sampling scheme is an important consideration; for example, convenience sampling was found to result in higher estimates of species diversity and more rare species, when compared to random sampling in an urban forest (Speak et al. 2018). Differences in the structural characteristics of sampling locations can also lead to differences in sampling effectiveness (Hortal et al. 2006)—even with standardized sampling techniques—which can bias estimates of species diversity. Diversity is often quantified in terms of richness and evenness, as well as community composition. Richness, however, can be difficult to measure appropriately since more species are recorded as the number and area of samples increases (May 1988). Evenness is also affected by sampling interval and intensity, but to varying degrees depending on the measure used (White 2007). Appropriate measures, such as computing expected richness at a standardized size via rarefaction, are thus necessary in order to compare communities where sample sizes are unequal (Heck et al. 1975).

Species richness and composition are often-reported metrics across ecological disciplines, but have particular importance in urban forests in understanding biodiversity (Livesley et al. 2016) and resistance to damage from disease and pest outbreaks (Raupp et al. 2006, Jonnes 2016). To promote urban forest tree diversity and its management, metrics of species richness have been proposed. For example, tree richness can be measured using a management indicator such as the 10-20-30 rule (Santamour 1990), which calls for no more than 10% of trees in any single species, 20% in any single genus, and 30% in any single family within a management unit such as a city. But a study across climate and land use revealed that these targets are rarely met at the species level (Kendal et al. 2014). Similarly, the ecological homogenization hypothesis, which posits that land-use change has produced similar urban residential ecosystems, bearing little similarity to the natural ecosystems they replaced (McKinney 2006), can be evaluated. Evidence of such urban homogenization has been reported across major cities in the United States and China, with hypothesized continental-scale consequences, including effects on carbon sequestration, microclimate, and other ecosystem properties (Groffman et al. 2014, Yang et al. 2017).

Recently, disparate data sources have been used for regional-scale and even continental-scale urban-to-rural analyses of woody plant community composition, similarity, species richness, and other questions such as ecological homogenization and ecosystem dynamics (Blood et al. 2016, Kendal et al. 2018). However, it is not known if methods and findings from studies using disparate data across larger study areas and different forested contexts, diverse data collection methods, and plot characteristics are indeed using methods that ensure that the underlying estimates of forest diversity and species composition are robust.

This study assesses methods for analyzing species richness and composition in light of disparate forest data sources, and how their use can affect findings and inference in comparing ecological diversity across different local, regional, and continental areas of interest. We do so by analyzing local-level urban and peri-urban forest diversity and composition across a regional gradient using data from two available yet disparate databases. Specifically, we first review the different and appropriate methodologies for using these increasingly available data for applied ecological research questions by detailing the conventional methods that have been used to characterize tree diversity, in terms of observed and estimated species richness, as well as composition values. Second, we evaluate how these different methods can influence study findings and management implications. We then present findings in a case study that evaluates several commonly used methods for analyzing tree species richness metrics and test the ecological homogenization hypothesis across different forested contexts (i.e., urban–rural gradients). Finally, we outline an approach for selecting the most appropriate methods for analyses and discuss practical considerations when considering data sampled under different methodologies.

### Methods for Analyzing Diversity and Composition

Tree sampling is most commonly accomplished via plot-based sampling protocols, and thus, we focus our review on methods applicable
to this type of sampling. Plot-based sampling requires different methods from those of individual-based protocols (sensu Gotelli and Colwell 2001), as plots involve samples of multiple, grouped individuals as replicates, rather than single individuals (Speak et al. 2018). This distinction is non-trivial in that it defines the appropriate methodology of diversity measure for estimating species richness, as well as describing composition and making comparisons thereof.

**Measurements of species richness**

When studies involve comparisons of species richness among different sites, there are many methodologies available that standardize richness data using extrapolation or rarefaction techniques (Chao and Chiu 2016). This includes non-parametric estimators, parametric species abundance models, species accumulation curves, and species–area curves. The standardizing of species richness data using extrapolation or rarefaction techniques is frequently performed in inter- and intra-site comparisons (Gotelli and Colwell 2001).

**Species accumulation curves.**—Species accumulation curves, rather than raw numbers of species, are necessary to make appropriate comparisons among communities and are commonly used to graphically display the total number of species encountered as the number of sample units is added to a pool of previously encountered species (Colwell and Coddington 1994). They are related to, but not identical with, species–area curves, which are derived from island datasets (i.e., where different areas are associated with independently sampled islands). Sampled species richness may differ between communities due to inherent differences in underlying species richness; however, they may also differ due to differences in the number of individuals counted or collected (Denslow 1995). These differences may be a reflection of resource availability or habitat conditions, but may also be simply due to sampling effort (Gotelli and Colwell 2001), as demonstrated in comparisons of logged vs. unlogged forests (Cannon et al. 1998, Chazdon et al. 1999, Hubbell 1999). Gotelli and Colwell (2001) recommended that raw richness only be compared if species accumulation curves clearly indicate that an asymptote has been reached in both populations of interest, highlighting the need for estimating total population pools.

When sampling effort is equal (e.g., the same number of plots and same plot size used) and sample-based curves are used, comparisons of richness can still be problematic, as datasets can differ in the mean number of individuals per sample (Cannon et al. 1998). To make comparisons in this case, the number of species, tree or otherwise, accumulated should be plotted as a function of accumulated individuals instead of samples (Gotelli and Colwell 2001). When studies utilize disparate data sources where sampling effort is unequal (Kendal et al. 2014, Blood et al. 2016), this introduces another layer of complexity, as the numbers of species increase as sampling effort increases. For most methods of species richness comparison, it is assumed that individuals have a random spatial distribution in the environment (Kobayashi 1983), sample sizes are sufficiently large, and populations are sampled in the same manner (Abele and Walters 1979).

If sample plots have different shapes and sizes, sampling bias may be introduced such that particular species are over- or under-sampled (Boulinier et al. 1998). Because richness does not in general increase linearly with abundance, simple adjustments, such as scaling the number of species per individual sampled, distort patterns in species richness (Gotelli and Colwell 2001). If species exhibit non-random spatial patterns, such as within-species clumping and segregation among species, which may occur with planted urban forests, estimates of species pools can be overestimated in small samples, and knowledge about spatial autocorrelation has not been found useful in correcting bias (Collins and Simberloff 2009). While no method is completely robust to these issues, alternative methods, such as rarefaction, can mitigate problems associated with violations in assumptions.

Accordingly, rarefaction curves have allowed researchers to compare samples of different sizes through the calculation of expected richness at a standardized size (Heck et al. 1975). Rarefaction curves are statistical expectations of their corresponding accumulation curves as the samples are re-ordered (Gotelli and Colwell 2001). Blood et al. (2016) and Nock et al. (2013), for example, used sample-based rarefaction curves to compare urban and peri-urban forest diversity by considering the number of accumulated samples. However, so-derived comparisons are in terms of
species density, instead of species richness. For these kinds of studies, which inevitably involve larger areas, species density is a more applicable measure than species richness (Gotelli and Colwell 2010). But this measure too must be used in conjunction with rarefaction in order to assess the degree to which differences in species density are attributable to patterns of individual abundance or to the shape of species accumulation curves (Gotelli and Colwell 2001).

**Estimating species pools.**—Species pool estimators yield the total richness in a sampled population, and while they have been used across the spectrum of ecological literature, they have had less presence in forestry applications (but see, e.g., Blood et al. 2016, Cannon et al. 1998, Den slow 1995, Imai et al. 2012, Jenerette et al. 2016, Nock et al. 2013). These studies explicitly recognize that species accumulation models indicate that not all species are seen in any sampled site, and hence use species pool functions to better estimate the number of unseen species (Colwell and Coddington 1994). Numerous studies have also sought to assess the performance of richness estimators across differing sites and/or sampling schemes (for a review, see Walther and Morand 2012), with the goal of finding methods to defensibly compare across sites. For example, Chazdon et al. (1998) sought a richness estimator that was insensitive to the size and order of the sample, and the unevenness in species distribution. Since different sampling strategies are often used to assess species richness across regions, Hortal et al. (2006) reviewed the performance of 15 estimators in terms of their insensitivity to sample heterogeneity among studies. While specifically studying the effect of grain size (sensu Whittaker et al. 2001), Hortal et al. (2006) recommended the use of several widely studied (Chiarucci et al. 2003) “classical” estimators: the Abundance-based Coverage Estimator (Chao and Lee 1992), the Abundance-based Chao Estimator (Chao 1984), Bootstrap (Smith and van Belle 1984), Jackknife1 (Burnham and Overton 1979), and Jackknife2 estimators (Smith and van Belle 1984).

**Community composition comparisons**

While species richness, measured or estimated, is a univariate characteristic of the total species pool at a site, the composition of such pools has also been a topic of research interest, for example, in quantifying the effect of forest composition change after disturbances such as logging (Imai et al. 2012) or wind (Holzmueller et al. 2012). Accordingly, hypotheses may be formulated to test for differences among groups of sites (e.g., urban vs. peri-urban). Often studies have used graphical techniques to visualize similarities in the structure of multiple communities (Sitzenia et al. 2012, Imai et al. 2012, Avolio et al. 2015).

**Community structure.**—Species composition is a multivariate characteristic of a population that can be used to compare community structures. However, traditional multivariate analysis methods, such as MANOVA, make stringent assumptions which are untenable for most ecological datasets (McArdle and Anderson 2001). For example, since urban forests and PF often contain different species (Blood et al. 2016), the assumption of multivariate normality cannot be met. Thus, non-parametric methods are preferable. For example, the Mantel test (Mantel 1967) has been used to compare tree β-diversity across a tropical forest (Chust et al. 2006), and to compare species composition of forest remnants in urban areas (Godefroid and Koedam 2003). Analysis of similarities (ANOSIM; Clarke 1993) has been used to compare urban forest composition in response to hurricane (Burley et al. 2008) and recreational trail use (Ballantyne and Pickering 2015). More recently, permutational analysis of variance (PERMANOVA; Anderson 2001) has been used to compare urban forests composition across geographic and urbanization gradients (Blood et al. 2016, Yang et al. 2017, respectively), as well as to test for differences among neighborhood species compositions within an urban region (Avolio et al. 2018). All of these methods rely on measures of the distance or dissimilarity between pairs of observations or ranks and use differences among groups (e.g., locations) to test randomly selected permutations of the observations. ANOVA-like test statistics are constructed from matrices of among-sample resemblances, which may be distances, dissimilarities, or similarities, and P-values are obtained with randomly generated permutations of observations among groups (Anderson and Walsh 2013).

For comparing datasets with different sampling intensities, PERMANOVA has been documented as being the most appropriate of these methods, as it allows for the formulation of multifactorial...
hypothesis tests and formulation of several types of distance metrics (Anderson 2001). One advantage of PERMANOVA is that the method is unaffected by correlation among variables (Anderson 2001, Anderson and Walsh 2013), which may occur when species have a tendency to co-occur. However, the method is somewhat sensitive to differences in relative dispersion of points among groups. In PERMANOVA, it is assumed that the observations are exchangeable under the null hypothesis, which implies that the observations are independent and have “similar” distributions. This has often been referred to as an assumption of equal “multivariate spread” among groups, which is a multivariate analog to the assumption of homoscedasticity in univariate ANOVA. Nonetheless, Anderson and Walsh’s (2013) simulation study showed that PERMANOVA was much less sensitive to heterogeneity in dispersions than ANOSIM and the Mantel test for balanced designs.

Case Study: The Influence of Method on Hypotheses in Urban Ecology

Having outlined the available methods, we now present a case study as an example of how commonly utilized methods can be applied to disparate data sources addressing urban–rural ecology questions across different scales. Specifically, we use available and disparate plot-level data from across a region encompassing the southeastern United States. In this case study, we use data from both peri-urban USDA FIA and the South- eastern Urban Tree Inventory and Canopy (SUTIC) database. Such an approach using data from different sampling methods—but within the same general geographic study areas—allows for the evaluation of quantitative methods while isolating variability associated with geography and climate. In our discussion, we then summarize a framework for selecting the most appropriate and available methodologies for analyses using these and other similar datasets.

Data

Study sites.—Study locations from the SUTIC database were part of a collaborative project sponsored by several universities and the Southern Research Station of the USDA Forest Service.
and provided data collected from eight cities in the southeastern United States between 2008 and 2014 (Fig. 1). Four cities were sampled across the Central Appalachian Broadleaf Forest ecological province, while two cities were sampled in each of the Southeastern Mixed Forest and Outer Coastal Plain Mixed Forest ecological provinces (Bailey 1995). Trees were inventoried using randomly sampled 0.0404-ha, circular, permanent plots established within city limit boundaries with the exception of east Orlando, where plots were placed within a 200-km² pre-defined study area. (Further information about the study sites can be found in Table 1 of Blood et al. 2016.)

Urban forest data.—Urban tree data were recorded using Nowak et al.’s (2008) protocol, where each tree or palm with dbh > 2.54 cm was measured and its species name recorded within a 0.0404-ha (0.1 acre) circular plot. Other measurements included height, land use, crown width, crown light exposure, and tree location within plot. If a tree had multiple stems below dbh, it was counted as a single tree, and the largest

Fig. 1. Eight urban forest locations sampled in the southeastern United States. Red box designates the extent of the bottom left map. Bottom left map shows detail of urban (UF) and peri-urban (PF) plots in Atlanta, Georgia. Bottom right inset map shows the study region within the United States. WIN, Winchester, Virginia; CHA, Charlottesville, Virginia; ROA, Roanoke, Virginia; ABI, Abingdon, Virginia; FC, Falls Church, Virginia; ATL, Atlanta, Georgia; GNV, Gainesville, Florida; EORL, East Orlando, Florida. Ecological province was defined by USDA Forest Service ecozones (Bailey 1995).
diameters (up to six) were recorded. For specific measurement methods, refer to Nowak et al. (2008). This field plot measurement and sampling protocol is increasingly being used in cities outside the United States as model input models to estimate urban forest structure and ecosystem services (Yang et al. 2017, Speak et al. 2018). In the United States, this urban forest inventory and monitoring approach is known as the i-Tree Eco protocol within the i-Tree software suite, but is now being incorporated as part of the Urban FIA program (https://www.nrs.fs.fed.us/fia/urban/). However, we refer to these data with the name i-Tree Eco hereafter.

Peri-urban forest data.—Using our eight urban tree study locations, we defined peri-urban areas as those falling within a 25 km radius of urban city centers where i-Tree Eco inventories were conducted. USDA FIA plots located within these areas were identified and extracted. These data ranged from suburban and rural lands to natural areas and plantations, but included only forest land. Forest land in FIA is defined as having an area of at least 0.4 ha with at least 10% canopy cover of live tree species of any size, either at the time of sampling or in the past, where the land is not subject to non-forest use which would prevent normal tree regeneration and succession (e.g., regular mowing, or intensive grazing; Woudenberg et al. 2011). Since FIA plot locations are not reported as exact spatial coordinates to comply with privacy issues, extracted locations were between 0.8 and 1.6 km of the actual plot. However, we assumed location error to have a minimal impact on analyses. Since FIA plots are measured on a cyclic basis, we obtained data measured in the years 2010–2013 for Virginia and 2009–2013 for Georgia and Florida to obtain the maximum number of tree measurements while excluding re-measured trees. In three instances, data were also extracted from surrounding states because the 25-km buffer extended past state lines (Fig. 1).

The FIA plots consist of groups of four subplots that cover an area of 0.0675 ha (0.167 ac), with a microplot ~0.00135 ha (0.003 ac) in area located within each subplot (total area = 0.0054 ha). Woody plants with dbh >12.7 cm were recorded within the entire 0.0675-ha area, but trees with dbh between 2.54 and 12.7 cm were measured only in microplots. Tree data collected included condition, species, dbh, height, and location within plot (for more information on FIA data collection, see Woudenberg et al. 2011).

Differences in tree measurement protocols and species epithets.—Several key differences exist between i-Tree Eco and FIA measurement protocols which can impact measures of diversity (Table 1). With the i-Tree Eco protocol, multiple stems that originate (or appear to originate) from the same root stock and trees that split below breast height are recorded as single individual trees with multiple diameters. In contrast, under the FIA protocol, these trees are not single individuals and are recorded as two (or more) trees. That said, each FIA tree has distance and direction from plot center recorded, and stems from trees that split between 0.3 and 1.37 m are assigned identical distance and direction. Thus, we are able to identify that these multiple stems came from the same individual. However, trees that split <0.3 m from ground level are assigned the distance and direction corresponding to the approximate location of tree pith, and thus, these locations will not be identical for these multi-stemmed individuals.

Table 1. Summary of key differences between urban (i-Tree Eco) and peri-urban (Forest Inventory and Analysis; FIA) measurement protocols.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Peri-urban FIA</th>
<th>Urban forest plot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot size</td>
<td>0.0675 ha (0.167 ac)</td>
<td>0.0404 ha (0.1 ac)</td>
</tr>
<tr>
<td>Plot shape</td>
<td>Four circular</td>
<td>One circular</td>
</tr>
<tr>
<td>Tree presence</td>
<td>All plots have trees</td>
<td>Plots can be devoid of trees</td>
</tr>
<tr>
<td>Species epithets</td>
<td>USDA PLANTS database (<a href="https://plants.usda.gov/java/">https://plants.usda.gov/java/</a>)</td>
<td>i-Tree Eco species codes (<a href="https://www.itreetools.org/eco/resources/UFORE_Species_List_Apr30_2012.xls">https://www.itreetools.org/eco/resources/UFORE_Species_List_Apr30_2012.xls</a>)</td>
</tr>
<tr>
<td>Minimum dbh</td>
<td>12.7 cm in 0.0675 ha subplots; 2.54 cm in 4 × 0.00135 ha microplots</td>
<td>2.54 cm</td>
</tr>
<tr>
<td>Multiple stems &lt;dbh</td>
<td>Recorded as two (or more) trees</td>
<td>Recorded as a single tree, up to 6 largest dbh measured</td>
</tr>
</tbody>
</table>
Peri-urban FIA tree counts could be biased upward in terms of double-counting multi-stemmed individuals. However, the measures to estimate richness outlined here utilize plot-level presence/absence data. Moreover, errors due to multiple stems only occur when splits occur below 0.3 m, and thus, we assume this error to be small. To test the veracity of this assumption, species composition analyses via PERMANOVA can be made using stem counts as well as basal area as the dependent variable.

In addition to differences between i-Tree and FIA protocols, there are differences in sampling intensity by tree size within the FIA data itself. Since trees in the 2.54–12.7 cm dbh range are only sampled in ~0.0054 of the total 0.0675-ha plot, one can avoid methodological complications by limiting studies to trees > 12.7 cm dbh. However, this limits the scope of inference of any associated hypotheses tested and reduces the sample size, especially in comparisons with urban trees where smaller trees are measured on the entirety of the 0.0404-ha plot. Following Blood et al. (2016), we assumed that tree species were uniformly distributed across the 0.0675-ha FIA plot sample area, but explicitly recognize the higher uncertainty associated with smaller trees not accounted for in this study. We used an expansion factor to adjust tree counts within microplots for their smaller sample exposure, and thus, each recorded stem in a microplot is comparable to 0.0675/0.0054 = 12.5 stems in the larger plot.

Tree taxa and species epithets can be a potential source of mismatch in identifying and coding tree and shrub species when using disparate data sources, such as the FIA and i-Tree Eco methods (Table 1). Since i-Tree Eco species codes are comprised of the first two letters of the genus and species as well as other regional user-created codes, the same species code can appear in different regions to represent multiple species. To our knowledge, there is no i-Tree Eco check to assure standardization, and there is no systematization nor standardization in species code protocols. Thus, a crosswalk must be created to recode species to a consistent coding if measures of community composition are to be compared. Moreover, USDA FIA protocols utilize a set species list, and unlisted species will not receive a species code. While this was a rare (n = 3) occurrence in our case study data, this could be a potential source of error if new exotic species invade peri-urban locations.

**Statistical analyses**

All analyses were computed in the R environment (version 3.4.1; R Core Team 2016), utilizing the vegan community ecology package (Oksanen et al. 2016). We first developed matrices of the abundances of each species by plot, although these matrices can indicate simple presence/absence (0/1) with equivalent results for most of the analyses described. While urban forest studies regularly use data from plots with no trees (Staudhammer et al. 2015), FIA plots are exclusively installed on forested land as defined by the USDA, and explicitly must include trees. Plots without trees may or may not be appropriate to include in comparative analyses of this type, depending on the research question and associated data (Table 1). To assess this difference, we first compare forested peri-urban and forested urban, thus excluding plots in urban areas where no trees were recorded. Second, we then compare forested peri-urban areas to urban areas, including plots with zero sampled trees in our species abundance matrices. (R code and sample data are available in Data S1.)

**Species richness.** To visualize the increase in the number of species encountered with increasing sampling effort, we estimated species abundances via species accumulation curves. We used the function specaccum, which uses as its default method the sample-based (i.e., plot-based) exact method to estimate an expected species accumulation curve via sample-based rarefaction (Chiarucci et al. 2003). An unconditional standard deviation is computed based on the extrapolated number of species in the data (the sample γ-diversity). Other methods are available, such as the classic random method, which uses random permutations of the data (subsampling without replacement) to estimate species accumulation curves and their associated uncertainties (Gotelli and Colwell 2001), and the Coleman estimate (Coleman et al. 1982). However, these result in slightly more conservative standard errors. The rarefaction method within this function is not appropriate for these data, as it finds expected richness assuming that individuals were samples rather than sites and neither is the so-called collector method, since it adds sites in the order they are input (Oksanen et al. 2016).
To account for the different plot sizes associated with FIA and i-Tree data, we re-scaled the axis of accumulation, multiplying by the plot size, before plotting derived species accumulation curves. We used the R function specpool to estimate the total species pool as well as the total pool of genera. This function implements several methods for a collection of sites (plots), in contrast to the function estimateR, which is appropriate for samples consisting of counts of individuals (i.e., for a single site). The bootstrap estimator (Smith and van Belle 1984) uses repeated resampling (with replacement) from the data, estimating the number of species missed. Other estimates available include two jackknife estimators and the incidence-based Chao estimator. As recommended by Hortal et al. (2006), we present results from the Bootstrap and Jackknife1 estimators. The

Fig. 2. Species accumulation curves by location for urban (light green) and FIA (dark green) data: (A) excluding plots with zero tree counts (in urban areas only) and (B) including all plots, so that plots with no trees (which occur only in urban areas) are included as zeroes in all species.
Chao estimate is also provided for comparison purposes. The Jackknife2 is not presented, as estimates of its standard error are not available.

Species composition.—We utilized PERMANOVA via the R function adonis to better understand community similarities and dissimilarities. To determine whether differences in community structure were due to urbanization, geographic area, or both, we included effects for ecological province, forest type (urban vs. peri-urban), and their interaction, utilizing 999 permutations (following Anderson and Walsh 2013). Since analyses were performed at a community level, analyses are identical with and without the inclusion of un-treed plots. To illuminate differences which might be caused by different sampling intensities by tree size, analyses were performed with species counts as well as tree basal area.

Community differences were quantified using the Raup-Crick metric and the R function raupcrick (Oksanen et al. 2016). Using a matrix of comparisons between all pairs of associations, the Raup-Crick index compares observed numbers of species with the distribution of co-occurrences (Fig. 2. Continued)
generated from 999 Monte Carlo random replicates (Chase et al. 2011). The function treats the data as binary (presence/absence) regardless of how the matrix is formulated. While there is a variant of the Raup-Crick index available in the R function vegdist, this is not appropriate for comparing FIA and i-Tree Eco data, as it assumes equal sampling probabilities for species. This results in the use of exact equations, without simulations, which would not take into account the unequal efforts in sampling in the two types of data.

To further visualize the results, we created a nonmetric multidimensional scaling (NMDS) plot utilizing the Raup-Crick dissimilarity metric to compare sites. Nonmetric multidimensional scaling is an ordination technique that finds the best rank-order agreement between actual similarities and computed distances, representing a coordinate system in the ordination space (Fas- ham 1977). We utilized the R function metaMDS, which projects the most variation along the first axis (Oksanen et al. 2016). Points in the resulting plots appear close together when the Raup-Crick dissimilarity metrics indicate their community compositions are similar (Avolio et al. 2015).

Application to evaluate species richness and the ecological homogenization hypothesis.—Finally, using these methods and the urban and peri-urban data, we analyzed how different assumptions and selected methods can influence results in answering common research questions in urban ecology. First, we compare overall tree species richness between urban (i-Tree Eco) and peri-urban (FIA) forest types, and among communities. We utilize species pool estimators and compare the accuracy and precision of such estimators with and without tree-less plots. We then examine the results in terms of our ability to make definitive statements for urban forest management in light of species accumulation curves and pools. Last, we perform a test of the ecological homogenization hypothesis, using factors to indicate ecological province and urban vs. peri-urban settings, and utilizing data based on tree counts as well as basal area.

Results

Species accumulation and richness

Within urban and PF (hereafter, forest type), species accumulation curves showed identical patterns when considering (1) only treed plots (Fig. 2A) vs. (2) both treed and un-treed plots (Fig. 2B). However, the axis of accumulation is stretched when considering the latter, and thus, comparisons of UF vs. PF are somewhat different. Although the conclusion that more sampling is necessary in order to encounter all species present in an area is reached in most urban locations, the implied sample area is more realistic when including these un-treed plots.

Regardless of forest type, estimated species richness was much higher than measured when considering the Chao and Jackknife estimators (Table 2). While the Chao estimate of the species pool (Fig. 3A) was on average ~50% higher than observed, the Jackknife estimates (Fig. 3C) were 30% higher than observed for PF and 44% higher than observed for UF. Bootstrap estimates were more conservative, with 13% and 20% higher estimated species than observed on average for PF and UF, respectively (Fig. 3B). For UF, estimated species richness was closest to observed species richness in Atlanta, which was sampled at a much higher rate than the other locations. When considering the pool of genera, similar patterns were observed, but with estimates approximately 10% closer to observed estimates (Table 2).

Estimates of species richness were slightly higher when un-treed plots were included (Table 2). While observed and estimated species richness values were very close between the two types of datasets when applying each of the estimators, there were larger, detectable differences in the standard error of these bootstrap estimates. Thus, a larger measure of uncertainty is obtained when including plots without trees in calculating the bootstrap estimator. Moreover, differences tended to be larger when the total number of plots and total number of species detected were lower (e.g., Abingdon, Virginia, USA). Nonetheless, when considered as a proportion of the total estimated species, these differences are very small (Table 2).

While the inclusion of plots with no trees would not alter the conclusions associated with comparisons of species richness among communities and/or forest types, the type of estimator used is critical. When utilizing the Chao estimator, for example, we found that confidence intervals constructed from species richness estimates and their standard errors indicate that there were
Species composition and community similarity

Table 2. Measured and estimated species and genus pools by location and forest type.

<table>
<thead>
<tr>
<th>Location and forest type</th>
<th>No. species</th>
<th>Chao With un-treed</th>
<th>Only treed</th>
<th>Jackknife With un-treed</th>
<th>Only treed</th>
<th>Bootstrap With un-treed</th>
<th>Only treed</th>
</tr>
</thead>
<tbody>
<tr>
<td>WIN UF</td>
<td>71</td>
<td>127.4 ± 25.8</td>
<td>127 ± 25.6</td>
<td>107.6 ± 7.7</td>
<td>107.3 ± 7.7</td>
<td>86.7 ± 4.1</td>
<td>86.6 ± 3.8</td>
</tr>
<tr>
<td>WIN PF</td>
<td>34</td>
<td>45.8 ± 12.7</td>
<td></td>
<td>40.8 ± 2.9</td>
<td></td>
<td>37 ± 1.7</td>
<td></td>
</tr>
<tr>
<td>CHA UF</td>
<td>84</td>
<td>132.3 ± 20</td>
<td>132.2 ± 20</td>
<td>125.4 ± 9.2</td>
<td>125.3 ± 9.2</td>
<td>102.2 ± 5.1</td>
<td>102.2 ± 4.9</td>
</tr>
<tr>
<td>CHA PF</td>
<td>41</td>
<td>47 ± 6</td>
<td></td>
<td>47.9 ± 2.9</td>
<td></td>
<td>44.4 ± 1.8</td>
<td></td>
</tr>
<tr>
<td>ROA UF</td>
<td>106</td>
<td>157.6 ± 21.5</td>
<td>157.4 ± 21.4</td>
<td>147.8 ± 7.8</td>
<td>147.6 ± 7.8</td>
<td>124.2 ± 4.4</td>
<td>124.2 ± 4.2</td>
</tr>
<tr>
<td>ROA PF</td>
<td>44</td>
<td>58 ± 10.9</td>
<td></td>
<td>55.7 ± 3.9</td>
<td></td>
<td>49.3 ± 2.2</td>
<td></td>
</tr>
<tr>
<td>ABI UF</td>
<td>52</td>
<td>72.5 ± 10.8</td>
<td>72.3 ± 10.7</td>
<td>76.7 ± 6.2</td>
<td>76.4 ± 6.1</td>
<td>63.3 ± 3.8</td>
<td>63.2 ± 3.5</td>
</tr>
<tr>
<td>ABI PF</td>
<td>57</td>
<td>75.4 ± 12.9</td>
<td></td>
<td>71.7 ± 4.1</td>
<td></td>
<td>63.6 ± 2.5</td>
<td></td>
</tr>
<tr>
<td>FC UF</td>
<td>56</td>
<td>85.2 ± 14.4</td>
<td>85.1 ± 14.4</td>
<td>84.2 ± 7</td>
<td>84.1 ± 7</td>
<td>68.6 ± 3.8</td>
<td>68.6 ± 3.6</td>
</tr>
<tr>
<td>FC PF</td>
<td>38</td>
<td>46.5 ± 6.5</td>
<td></td>
<td>49.4 ± 4.9</td>
<td></td>
<td>43.5 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>ATL UF</td>
<td>98</td>
<td>124.4 ± 12.7</td>
<td>124.4 ± 12.7</td>
<td>127.9 ± 5.6</td>
<td>127.9 ± 5.6</td>
<td>111.7 ± 3.3</td>
<td>111.7 ± 3.2</td>
</tr>
<tr>
<td>ATL PF</td>
<td>46</td>
<td>72.1 ± 17.1</td>
<td></td>
<td>63.4 ± 6.3</td>
<td></td>
<td>53.4 ± 3.3</td>
<td></td>
</tr>
<tr>
<td>GNV UF</td>
<td>62</td>
<td>81.2 ± 10.1</td>
<td>81.1 ± 10</td>
<td>86.6 ± 7.1</td>
<td>86.5 ± 7</td>
<td>73.4 ± 4</td>
<td>73.3 ± 3.9</td>
</tr>
<tr>
<td>GNV PF</td>
<td>32</td>
<td>43.9 ± 9.5</td>
<td></td>
<td>42.8 ± 4.9</td>
<td></td>
<td>36.9 ± 2.8</td>
<td></td>
</tr>
<tr>
<td>EORL UF</td>
<td>69</td>
<td>119.7 ± 25.1</td>
<td>119.5 ± 25</td>
<td>100.7 ± 7</td>
<td>100.6 ± 7</td>
<td>82.5 ± 3.7</td>
<td>82.5 ± 3.6</td>
</tr>
<tr>
<td>EORL PF</td>
<td>30</td>
<td>77.1 ± 42.3</td>
<td></td>
<td>43.5 ± 4.9</td>
<td></td>
<td>35.5 ± 2.4</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Since un-treed plots are not measured with FIA, PF estimates by definition only include treed plots. UF, urban forests; PF, peri-urban forests; WIN, Winchester Virginia; CHA, Charlottesville, Virginia; ROA, Roanoke, Virginia; ABI, Abingdon, Virginia; FC, Falls Church, Virginia; ATL, Atlanta, Georgia; GNV, Gainesville, Florida; EORL, East Orlando, Florida.

significant differences between urban and PF only in Winchester, Charlotte, and Roanoke, Virginia, USA. We also found, utilizing the Chao estimator, that there were very few confidence intervals that did not overlap, indicating differences among locations only for extreme cases, such as urban forests in Abingdon with those in Atlanta and Roanoke. Conversely, when using the bootstrap and jackknife estimators, we found that there were significant differences in all locations except Abingdon. Results were also similar when examining differences among locations within forest type. Likewise, when using the Jackknife or Bootstrap estimator, many more pairs of locations were found to have non-overlapping confidence intervals in terms of species and genus richness.

Species composition and community similarity

Our PERMANOVA results utilizing basal area and tree counts were very similar, with both analyses indicating that species distributions were different depending on ecological province ($P = 0.001$) and forest type (UF vs. PF; $P = 0.001$; Table 3). Neither analysis indicated that the forest type significantly interacted with ecological province, indicating that the effect of forest type was similar across province. On the other hand, the partitioning of the variance among effects was somewhat different when considering basal area vs. tree counts, as indicated by a smaller forest type vs. province interaction effect ($P = 0.098$ vs. $P = 0.059$).

For PF, whether in a more natural state or under industrial production, we would expect that species composition across province would differ, to optimize climatic and geographic conditions. If the hypothesis of ecological homogenization was supported, we would expect a different outcome for urban forests; species composition across urban communities would not be significantly different by province. These two conditions would manifest in a significant interaction between forest type and province. However, we
see only very weak evidence in support of the hypothesis (Table 3), at least in terms of tree diversity using both tree counts and tree basal area.

The matrix of the Raup-Crick dissimilarity indices showed mostly high values for Winchester’s urban forest, indicating that it was very dissimilar to its, and all other regional, PF (Table 4). Only the UF of other Virginia cities was similar to Winchester’s UF. In contrast, the other Virginia UF s had somewhat different patterns of similarity. The Charlottesville UF was only dissimilar to the Abingdon PF. While the Roanoke and Abingdon UFs were similar to all UFs and PFs in Virginia, the Falls Church UF was only dissimilar to the Virginia PFs. Atlanta’s UF was very similar to its PF, and also that of Falls Church, while it had fairly high dissimilarity with all other forests. Regionally, Gainesville’s UF was only similar to Atlanta’s PF and the other Florida locations in both UF and PF, while East Orlando’s UF was only similar to its PF and Gainesville’s forests. These results are further corroborated with the corresponding NDMS plot (Fig. 4). Under the hypothesis of ecological homogenization, we would expect that urban forest locations would be closer to each other than to those of PF in Fig. 4. But, for most of the sites sampled, urban forests and their peri-urban counterparts are fairly close, indicating low values of dissimilarity, and therefore indicating a lack of urban homogenization. However, Winchester and Falls Church, Virginia, indicate different species composition patterns from those of their regional peri-urban counterparts. This gives partial, weak support to the hypothesis of ecological homogenization in terms of trees based on presence/absence data in these locations.

**DISCUSSION**

Studies across the globe are beginning to use available, but disparate datasets to better...
understand urban ecosystem dynamics and to make analyses and inferences regarding regional- to continental-scale woody vegetation diversity, composition, and ecosystem functionality (Kendal et al. 2014, 2018, Blood et al. 2016). Yet as shown above, the assumptions and statistical methods used with these data can influence results and can have implications for the certainty with which results are communicated regarding urban-rural ecosystem diversity and homogeneity.

Species diversity measures, for example, can be used to better understand complex community structure and to develop practices to make forests resilient to disease, pests, and climate change. For instance, such tenants as the 10-20-30 rule (Santamour 1990) are subject to misinterpretation when based on data collected using different sampling intensities (Kendal et al. 2014). To evaluate this commonly applied guideline, urban forests need to be assessed to test if they contain no more than 10% of any tree species, 20% of any genus, and 30% of any family. Thus, evaluating the effectiveness of this rule requires certainty when estimating the proportion of individuals in each species, each genus, and each family. However, as the number of samples in the forest sampling protocol increases, the number of genera will always reach an asymptote sooner than that of the....

Table 3. Permutational ANOVA (PERMANOVA) partitioning of the sums of squares using species by community.

<table>
<thead>
<tr>
<th>Response</th>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree counts</td>
<td>Forest Type</td>
<td>1</td>
<td>0.907</td>
<td>0.907</td>
<td>4.168</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Province</td>
<td>2</td>
<td>1.594</td>
<td>0.797</td>
<td>3.661</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Forest type × Province</td>
<td>2</td>
<td>0.693</td>
<td>0.347</td>
<td>1.593</td>
<td>0.059</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>10</td>
<td>2.177</td>
<td>0.218</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Forest Type</td>
<td>1</td>
<td>0.679</td>
<td>0.679</td>
<td>6.979</td>
<td>0.001</td>
</tr>
<tr>
<td>Basal area</td>
<td>Province</td>
<td>2</td>
<td>1.386</td>
<td>0.693</td>
<td>7.125</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Forest type × Province</td>
<td>2</td>
<td>0.319</td>
<td>0.160</td>
<td>1.642</td>
<td>0.098</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>10</td>
<td>0.972</td>
<td>0.097</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: DF, degrees of freedom; SS, sums of squares; MS, mean squares. P-value is computed with pseudo (approximate)-F-value.

Table 4. Raup-Crick dissimilarity values between all pairs of locations and forest types.

<table>
<thead>
<tr>
<th>Loc Type</th>
<th>WIN UF</th>
<th>CHA UF</th>
<th>ROA UF</th>
<th>ABI UF</th>
<th>FC UF</th>
<th>ATL UF</th>
<th>GNV UF</th>
<th>EORL UF</th>
</tr>
</thead>
<tbody>
<tr>
<td>WIN UF</td>
<td></td>
<td>0.590</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CHA UF</td>
<td>0.089</td>
<td>0.009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ROA UF</td>
<td>0.052</td>
<td>0.001</td>
<td>0.011</td>
<td>0.002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ABI UF</td>
<td>0.042</td>
<td>0.005</td>
<td>0.001</td>
<td>0.001</td>
<td>0.003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FC UF</td>
<td>0.002</td>
<td>0.014</td>
<td>0.080</td>
<td>0.512</td>
<td>0.090</td>
<td>0.685</td>
<td>0.055</td>
<td>0.751</td>
</tr>
<tr>
<td>ATL UF</td>
<td>0.988</td>
<td>0.201</td>
<td>0.891</td>
<td>0.024</td>
<td>0.838</td>
<td>0.197</td>
<td>0.931</td>
<td>0.413</td>
</tr>
<tr>
<td>GNV UF</td>
<td>0.996</td>
<td>0.328</td>
<td>1.000</td>
<td>0.804</td>
<td>1.000</td>
<td>0.968</td>
<td>0.993</td>
<td>0.851</td>
</tr>
<tr>
<td>EORL UF</td>
<td>0.999</td>
<td>0.461</td>
<td>0.999</td>
<td>0.500</td>
<td>0.995</td>
<td>0.882</td>
<td>0.987</td>
<td>0.769</td>
</tr>
</tbody>
</table>

Notes: Italicized values indicate the dissimilarity between urban and peri-urban forests in the same location. UF, urban forests; PF, peri-urban forests; WIN, Winchester Virginia; CHA, Charlottesville, Virginia; ROA, Roanoke, Virginia; ABI, Abingdon, Virginia; FC, Falls Church, Virginia; ATL, Atlanta, Georgia; GNV, Gainesville, Florida; EORL, East Orlando, Florida.
number of species, except when samples contain 100% monobasic taxa (Gotelli and Colwell 2001). Moreover, our results indicate that sampling intensities in studies of urban and PF were rather inadequate in estimating the number of species and genera present. Unless one can assume that unobserved species occur in very low numbers—which may be reasonable in some locales—the evaluation of this rule is problematic, as numbers of species as well as individuals will have additional uncertainty. Estimates of the numbers of species are often reported without considering unseen species and are therefore underestimates. For example, Pearse et al. (2018) collected data from 21 to 30 urban household yards and 3 to 6 natural area sites in their study of ecological homogenization across seven metropolitan areas. While using identical sampling protocols can help mitigate issues associated with inadequate sampling intensity, rarefaction should be used to estimate uncertainty associated with measured richness.

The specific research questions being posed in urban ecology studies should drive the selection of methods and data collected. For example, our results indicate that the inclusion of plots with no trees, while having little impact on species pool estimates, can greatly affect the shape of the species accumulation curve, leading researchers to make different conclusions about the adequacy of sampling methods. The choice of pool estimator is also important, and using the recommended bootstrap method with these kinds of sample types results in more conservative estimates of species richness, except where sampling intensity was high (e.g., Atlanta; Blood et al. 2016). We found, as expected, that estimates of species pools were most variable where the total number of samples and species detected were low.

While a variety of species composition estimators have been used in the urban ecology literature (e.g., ANOSIM and the Mantel test; Oksanen et al. 2016), simulation studies recommend the use of PERMANOVA to account for heterogeneity that may be exacerbated by differences among sampling intensities (Anderson and Walsh 2013). We demonstrate that this method can indeed be used with species counts or basal area depending on the research hypothesis. Assuming a strict cutoff of significance ($P = 0.05$), our results support the assumption that this type of analysis is robust to the sampling method for these two data sources, with smaller trees sampled at different rates in PF vs. UF. Taking a more nuanced view, this interpretation could, however, demonstrate the influence of smaller trees or shrubs; when considering comparisons using basal area as a proxy for tree size, differences in the interactive effect of forest type and province were weaker. That is, with larger trees having more weight in the analyses, the PF vs. UF tree diversity differences were more consistent by ecological province, as evidenced by the larger $P$-value of the interaction. We note that the i-Tree Eco protocol does not differentiate between small-dbh trees and shrub growth forms; thus, mature urban hedges and forest shrub patches are counted as trees (Nowak et al. 2008). Sampling details such as these may influence results, depending on the prevalence of such observations (Staudhammer et al. 2015).

Previous urban ecology studies that test the hypothesis of ecological homogenization have used Jaccard’s index (McKinney 2006), Sørensen’s index (Pearse et al. 2018), Bray-Curtis similarity
(Yang et al. 2017, Avolio et al. 2018), and a variety of qualitative methods, as well as specifically designed protocols which have included data on herbaceous vegetation and soils (Groffman et al. 2014). Our study, which further incorporated disparate data sources, demonstrates that the Raup-Crick dissimilarity indices, based on presence/absence data, are robust to sampling differences. Thus, the use of such indices is key in future studies in that they give insight into compositional similarities among communities that are sampled at different intensities.

Our results suggest that UFs and PFs were very similar within a particular region in the United States. This gives evidence against the hypothesis of ecological homogenization in urban ecosystems, at least in terms of tree diversity (Blood et al. 2016). This disagrees, in part, with findings from Pearse et al. (2018) and Groffman et al. (2014). While these studies found evidence of homogenization across urban areas in the United States, their studies included a wider array of plant and taxonomic groups, rather than just being focused on trees. In terms of the numbers of tree species present, our research agrees with that of Kendal et al. (2018), who found that native and urban tree population realized climatic niches that had substantial overlap; in most cities we analyzed, we found similar species lists, though urban areas almost always contained more species. The few exceptions occurred in Falls Church and Winchester, Virginia, the northernmost cities in our database. While further research is needed, we hypothesize that a more nuanced study including land use and the frequency of land-use change (following Yang et al. 2017) in local-scale urban-to-rural gradients and areas might shed light on this result.

Given current knowledge of the available methods for situations when there are differing sampling intensities and non-homogeneous species distributions, and the results of our case study, we recommend specific analytical methods for quantifying diversity using disparate data sources in urban–rural forested contexts and across different scales (Table 5). While not exhaustive of all possible situations, the process outlined can be more generally applied to other cases where data with differing sampling intensities and non-homogeneous tree/shrub species distributions are utilized, as a defensible method for making comparisons of species diversity.

### CONCLUSION

This study provides one of the first assessments of statistical methods that are being used in an increasing number of studies of woody plant diversity, homogenization, and functionality. We, however, do note some limitations. First, our analyses were limited to data collected with two standardized methods. We also explicitly recognize that some aspects of the protocol differences are worthy of further study. For example, unequal

<table>
<thead>
<tr>
<th>Measurement and method</th>
<th>Recommendations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species richness</strong></td>
<td></td>
</tr>
<tr>
<td>Species accumulation curves</td>
<td>If curves clearly show an asymptote has been reached, then raw richness can be compared utilizing species density should be used to make comparisons</td>
</tr>
<tr>
<td>Species pool estimators</td>
<td>If curves show an asymptote has not been reached, then rarefaction curves (Heck et al. 1975)</td>
</tr>
<tr>
<td></td>
<td>If species are homogenous among sites, many estimators are unbiased (see Hortal et al. 2006)</td>
</tr>
<tr>
<td></td>
<td>If samples are heterogenous among sites, three estimators are recommended: incidence-based Chao (Chao and Lee 1992), Bootstrap (Smith and van Belle 1984), and Jackknife (Burnham and Overton 1979)</td>
</tr>
<tr>
<td><strong>Community composition</strong></td>
<td></td>
</tr>
<tr>
<td>Community structure</td>
<td>If species have equal multivariate spread among groups, use Analysis of Similarities (Clarke 1993) or Mantel test (Mantel 1967). If species have heterogeneous dispersion, use PERMANOVA (Anderson 2001)</td>
</tr>
<tr>
<td>Dissimilarity metrics</td>
<td>If α-diversity is similar, use Jaccard’s or Sørensen’s index (Koleff et al. 2003). If α-diversity is dissimilar, use the Raup-Crick measure (1979)</td>
</tr>
</tbody>
</table>
sampling intensity of smaller trees in the FIA protocol requires development of a differential measure of uncertainty in richness and composition estimates. Second, an area of interest to researchers that we did not review is the vast number of indices used to characterize species evenness and beta diversity. Also we do not attempt to address the controversies that exist regarding the appropriate and inappropriate use of diversity indices. (See Smith and Wilson 1996 and Anderson et al. 2011 for thorough reviews of these topics.)

However, our analyses do examine methods that are appropriate to make valid comparisons of peri-urban forest data available from national-level databases (e.g., FIA), and local-level urban forest data (e.g., i-Tree Eco) collected in the southeastern United States. In our case study, we demonstrated differences in community structure and species richness between PFs and UFs, noting that sampling intensities in urban areas were usually inadequate. As local-level, plot-based data become increasingly available in North America, Europe, Australia, China, and Latin America, there will be increased opportunity for studies that compare urban and peri-urban ecosystems across biomes as well as across the globe. Thus, appropriate and robust methods for making comparisons are necessary and important in making meaningful conclusions about the differences and similarities of these two different forest types. This becomes increasingly important as urban areas are used as a proxy for future conditions under climate change, and often are the epicenters of invasive species establishment and other socio-ecological disturbances.

These methods will help in establishing a framework to enable researchers and managers to evaluate the possible impacts of these anthropogenic changes on forests. In the United States, future public access to urban FIA data will begin to address some of these issues. However, the development of, and participation in, international research networks that make available such data can also begin to address some of these issues of limited access. Given the ecological challenges presented in the Anthropocene, robust methods and available datasets are key in understanding the functionality, nativity, and diversity of urban and peri-urban woody vegetation across all biomes of the world.

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LITERATURE CITED


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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2450/full