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The evolutionary diversity of urban forests depends on their land-use history

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Abstract

Urbanization leads to strong modifications of landscape structure and ecosystem functioning, and urban areas are spreading rapidly. The aim of this study was to investigate how phylogenetic diversity and composition of tree species are affected by urbanization itself and land-use history. We found that species richness, rarefied species richness and phylogenetic diversity are all affected by the land-use history of urban forests. Indeed, forests that regenerated from cropland, and particularly those regenerated from denuded landscapes, showed strong phylogenetic clustering, which was also related to their high perimeter-area ratio. Our analyses of phylogenetic composition show that urban forests without land-use history are compositionally indistinguishable from mature, non-urban forests. These two forest types house a diversity of evolutionary lineages and no specific lineage is a strong indicator of these forest types. In contrast, the two urban forest types with anthropogenic land-use history have a few, distinct lineages that are strongly associated with each of them, respectively. Overall, our results suggest that urban forests without previous land-use can house substantial amounts of angiosperm evolutionary diversity, which highlights the importance of preserving natural forest fragments as cities expand. This study highlights the substantial value of tropical urban forests and the importance of considering information on land-use history, even when studying urban environments.

1 Introduction

Anthropogenic disturbance events such as land-use change and habitat fragmentation have influenced important ecological processes across the world. These events cause the retraction of natural landscapes and shape regional species pools by determining whether lineages adapt to new environmental conditions or become extinct (Hoffmann and Sgró 2011). Land-use change of tropical landscapes is considered one of the main threats to global biodiversity (Lewis et al. 2015), causing high species loss, replacement of forest specialists by generalists and reduction of ecological functions and phylogenetic diversity (Olden et al. 2004; Gibson et al. 2011; Van Meerbeek et al. 2014; Socolar et al. 2016).

Urbanization leads to strong modifications of landscape structure and ecosystem functioning (Seto et al. 2013), and urban areas are spreading at fast rates (Secretariat of the Convention on Biological Diversity 2012). The world's population is projected to increase by 2.3 billion people over the next 30 years, with the majority of this growth concentrated in urban centers (UN Department of Economic and Social Affairs 2013). Cities can thus represent a significant threat to biodiversity and ecosystem function.

Forests within urban areas are vulnerable to environmental stresses caused by fragmentation and edge effects, such as higher average temperatures (Beninde et al. 2015; LaPoint et al. 2015), as well as air and soil pollution (Zimmerman, et al. 2005; Nowak and Dwyer 2007). These environmental modifications can filter out species intolerant of novel environmental conditions and benefit the ones with traits that allow persistence in anthropogenic habitats, a phenomenon that can lead to biotic homogenization (McKinney 2006; Williams et al. 2009).

Most ecological studies of forests focus on old-growth forests, due to the idea that they better reflect natural processes. However, human-disturbed forests can provide important ecosystem services, and efforts should be taken to better understand secondary forests (Chazdon et al. 2003). Urban forests provide a variety of societal goods and services such as air filtering, heat moderation, water storage, filtration, drainage and habitat refuges for animal and plant populations (Bolund and Hunhammar 1999; Park et al. 2010). Further, exposing people to nature can improve quality of life and inspire future action for biodiversity conservation (McKinney 2006; Whitburn et al. 2018). Because people tend to occupy cities in regions of high biodiversity (Cincotta et al. 2000), there is a need to understand the ways in which urban centers act as biodiversity filters and how we can maximize the retention of urban biodiversity and the ecosystem services it provides.

Environmental selection pressures faced by species from urban forests may favor certain traits or functional groups, and to the extent that closely related species are functionally similar, entire lineages may disappear from urban forests, which may negatively impact ecosystem function and reduce the breadth of lineages to which people living around urban forests are exposed (McKinney 2006; Williams et al. 2009; Aronson et al. 2016; Nero et al. 2017; Palma et al. 2017; Raymundo et al. 2018; Santana et al. 2018; Silva-Junior et al. 2018). Phylogenetically poor plant communities are more susceptible to a variety of anthropogenic impacts, such as the invasion of exotic plant species, which can potentially lead to further erosion of diversity (Gerhold et al. 2011). Lineage diversity, often quantified using phylogenies, has been shown to be a better predictor of ecosystem function than species richness in some studies (Clark et al. 2012; Cadotte 2013; Hines et al. 2014). Therefore, when studying changes in biodiversity of urban forests, it is important to assess not only taxonomic diversity and composition, but also evolutionary, or lineage, diversity and composition (Cadotte et al. 2008; Faith et al. 2010; Forest et al. 2010; Dexter et al. 2019).

Most tropical urban forests do not represent fragments of intact forest, but were instead regenerated from agricultural or other man-made landscapes (Kowarik and Lippe 2018), which means that successional processes must also be considered when evaluating the taxonomic and evolutionary diversity of urban forests (Chazdon 2008; Williams et al. 2015). Previous research has shown that species richness and lineage diversity increase over the course of succession, and further, that the number of lineages in regenerating plots is even less than that expected given their low species richness, i.e. earlier successional plots show phylogenetic clustering (Letcher 2010; Ding et al. 2012; Norden et al. 2012; Ribeiro et al. 2016). Meanwhile, fragment size and shape impose additional filters, with small forest fragments being exposed to a variety of edge effects that can lead to communities being dominated by few species with a similar and small set of traits unable to sustain ecological processes (Santos et al. 2008).

The aim of this study was to investigate how phylogenetic diversity and composition of tree species are affected by urbanization itself (urban forest fragments derived directly from intact forest) and land-use history (urban forests regenerated from cropland or otherwise denuded landscapes). To our knowledge, this is the first time urban forest fragments are compared with respect to their land-use history. At present, where urban contributions to biodiversity conservation are not entirely clear, this study represents a useful step forward for the field of urban ecology. We used field data from the Atlantic Forest domain in southeastern Brazil, one of the most threatened global biodiversity hotspots (Ribeiro et al. 2009), due largely to human population pressure and concomitant urbanization. We addressed the following main questions: 1) Does urbanization and land-use history impact phylogenetic diversity in urban forests? 2) Do differences in historical land-use intensity affect the phylogenetic composition of communities? 3) Does urbanization and/or land-use history promote loss of certain evolutionary lineages, resulting in phylogenetic clustering? We predict that urbanization and land-use history will drive loss of specific evolutionary lineages resulting in lower phylogenetic diversity. A subset of lineages should be more successful in these stressful environments, and we therefore expect consistent shifts in the phylogenetic composition of tree communities in urban forests.

2 Material and Methods

2.1 Study area

The study was conducted in twelve tropical forests located in the southeast region of Minas Gerais, Brazil (21°24’- 22°1’S and 43°18’ – 43°55’W) (Fig. 1). These forests belong to the Brazilian Atlantic Forest domain and are all classified as Semideciduous Seasonally Dry Forests (IBGE 2012), occurring from 710 to 1070 meters of altitude. Regional climate is classified as Cwb (Mesothermic climate of Köppen), defined by dry winters and mild summers. Mean annual rainfall ranges from 1497 to 1585 mm and mean annual temperature ranges from 17.6°C to 18.9ºC (Alvares et al. 2013). Soils in the region, and underneath all plots, are primarily latosols (Santos and Anjos 2013), and plots were chosen to have similar elevation and aspect, in order to reduce the influence of these factors on our results All sites were classified based on their land-use history and whether or not they are located in the urban matrix (Table 1).

All forest fragments were fully divided into plots of 20 m x 20 m. Afterward, 10 non-contiguous plots were randomly selected, considering a minimum distance to the forest edge of 20 m (except for the smallest fragments where the distance to edge was reduced to ≥ 10 m).We surveyed all trees with a diameter at breast height (DBH; 1.3 m above the ground) of ≥ 5 cm and identified trees to species level. Species identities were checked for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service (TNRS) ver. 3.2 (Boyle et al. 2013). Tree ferns and gymnosperms represent a minor proportion of diversity (0.78% of species) and individuals (7.75%) in these forests, yet their ancient divergences from angiosperms would have a large effect on phylogenetic diversity measures (Kembel and Hubbell 2006; Rezende et al. 2017). Therefore, they were excluded from analyses (sensu Hubbell 2006; Honorio Coronado et al. 2015). The final angiosperm dataset contained a total of 6663 individual trees, belonging to 378 species, 171 genera and 64 families (Table S1).

The city of Juiz de Fora, where the studied urban forests are located, is 166 years old. It experienced the history of forest degradation of the Atlantic Forest, especially related to the expansion of coffee plantations at the end of the 20th century. The city covers an area of 1435 km^2 and hosts approximately half a million inhabitants. When considering fragments with at least 3 ha, 11% of the city is in a forested state and only 4% of these forests are protected by law (SPGE 2008; SOS Mata Atlântica 2015). All urban forest fragments evaluated here are inserted in the urban matrix, including the remnant forests without anthropogenic land-use history (Fig S1).

The twelve forests were categorized into four classes with different historical land use, each one represented by three sites: a) forests outside the urban matrix where there is no documented record of human land use (i.e. forest is presumed to be mature, with the only potential anthropogenic impact being selective logging); b) forest within the urban matrix where there is no documented record of human land use; c) forests within the urban matrix that represent natural regeneration from cropland which was abandoned 70 to 80 years ago; and d) forests within the urban matrix that represent natural regeneration from completely denuded landscapes (land was subjected to earthmoving activities resulting in soil removal), with regrowth beginning 50 to 60 years ago. All mature forests are classified as legally protected reserves according to the Brazilian Forest Code. These categories were assigned according to landowner interviews, government public documents and official records, satellite images and photographs.

2.2 Phylogenetic analysis

An ultrametric calibrated phylogeny was constructed based on the new angiosperm family tree R20160415.new (Gastauer and Meira Neto 2017), which represents phylogenetic relationships among angiosperms as recently proposed by APG IV (2016). Species from the study sites were inserted in the family tree using the phylomatic function of the Phylocom 4.2 package (Webb et al. 2008). The resulting community tree was dated using the bladj (branch length adjustment) algorithm which provides mean age estimates of the nodes for which age information is available (e.g. from molecular age estimation studies).

2.3 Taxonomic and Phylogenetic Diversity metrics

We determined the species richness for sites as the sum of all species found in all plots at a given fragment or site (total area surveyed was the same at all sites). As the sites vary in the total number of trees sampled, we also determined the rarefied species count for each site, with rarefaction down to the number of individuals present at the site with the fewest number of individuals. Phylogenetic diversity (PD, in million years - myrs) was calculated as the sum of all branch lengths of a phylogeny encompassing all species in a given site (Faith 1992).

To assess the phylogenetic structure of communities, we evaluated the standardized effect size of MPD (ses.MPD) and the standardized effect size of MNTD (ses.MNTD). Mean pairwise distance (MPD) is the mean phylogenetic distance between all pairs of individuals (including conspecifics) in a community and the Mean Nearest Taxon Distance (MNTD) evaluates the average phylogenetic distance between each individual and its most closely related (non-conspecific) individual (Webb 2000; Webb et al. 2008). For the standardized effect size calculations, MPD and MNTD values were compared with 10,000 null model randomizations using the null model "phylogeny pool", which also served to test whether each community is more or less phylogenetically related than expected by chance. Negative ses.MPD and ses.MNTD values indicate phylogenetic clustering (species are distributed within clades with relatively recent common ancestors, or are more closely related than expected by chance) while positive values indicate phylogenetic overdispersion (species more evenly distributed across the whole phylogeny than expected by chance) (Webb 2000; Webb et al. 2002; Santos et al. 2010; Arroyo-Rodríguez et al. 2012). In order to investigate if PD was lower or higher than expected by chance given species richness, we also measured the standardized effect size of PD (ses.PD).

2.4 Phylogenetic Composition

To test for differences in phylogenetic composition across sites, we used phylogenetic ordinations that examine the distribution of lineages across a sample of communities. Specifically, we implemented the evolutionary principal component analysis based on Hellinger distance (evoPCAHellinger), developed by Pavoine (2016). This approach balances the influence of deep and shallow nodes in the ordination analysis and represents one of the more powerful methods to study phylogenetic patterns over environmental gradients (Pavoine 2016).

2.5 Landscape Characterization

In order to consider the possible influence of size and shape of the fragments on our results, we measured four landscape metrics for each studied fragment: i) total area (ha) (Area); ii) forest fragment perimeter (km) (Perimeter), i.e. total length of the forest fragment edge; iii) perimeter to area ratio (P:A): perimeter (in meters) divided by area (in meters); and iv) shape index (measures the complexity of the forest fragment shape compared to a standard circle; shape index is close to 1 for circular fragments and increases as fragments become more irregular). Analysis were performed using ArcGis 10.6.1 and its extension V-Late (Lang and Tiede 2003; Lang and Blaschke 2007).

2.5 Statistical analysis

The effects of land use history on species richness (SR), rarefied species richness (RSR) and phylogenetic diversity metrics (PD, ses.PD, ses.MPD and ses.MNTD.) were examined using linear mixed models with fragment as a random factor (to account for the lack of independence of plots within sites). We also tested the effects of fragment area, perimeter, P:A and shape index on the same variables (SR, RSR, PD, ses.PD, ses.MPD and ses.MNTD), together with land-use history, using linear mixed models. Model selection was based on the Akaike Information Criterion, corrected for small sample size (AICc). The set of best models (models equally supported) were considered as those with ΔAICc ≤ 2 (Burnham and Anderson 2002) for each variable. Model residuals were checked to confirm normality and homoscedasticity. Tukey post-hoc tests were used to assess the statistical differences between individual forest categories.

All analyses were performed using the R Statistical Software (R Development Core Team 2017) and the following packages: picante (Kembel 2010) multcomp (Bretz et al. 2015), lme4 (Bates et al. 2014), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton 2016), adiv (Pavoine 2018), factoextra (Kassambara and Mundt 2017) and ggplot2 (Wickham and Chang 2016).

3 Results

3.1 Phylogenetic Diversity and Structure

All raw phylogenetic diversity metrics were highly correlated with species richness, while the standardized metrics generally were not (Fig. S2). Our models indicated that species richness, rarefied species richness, phylogenetic diversity and phylogenetic structure are affected by land-use history (LUH) of urban forests (Fig 2, Table S2). We observed similar patterns for PD as we found for SR, where the highest value was found for non-urban forests (2697 myrs and 31 species) and urban forests without LUH

(2375 myrs and 26 species), while the lowest values were found for urban forests regenerated from cropland (1727 myrs and 19 species) and denudation land-use histories (800 myrs and 8 species). Urban forests regenerated from cropland and denudation LUH presented significantly lower PD than non-urban forests and urban forests without land-use history. Rarefied species richness was significantly different only between forests without LUH (non-urban and urban) and denuded forests. The same tendencies were found for the standardized metrics, where there were also negative values for urban forests regenerated from cropland (ses.PD) and especially denudation LUH (ses.PD and ses.MPD). ses.MNTD was not significantly different between forest classes, but showed strong negative values for cropland and denuded forests. These results indicate that urban forests without land-use history maintained species and phylogenetic diversity equivalent to non-urban forests, whereas cropland and denuded forests had a strong reduction in phylogenetic diversity with shifts toward phylogenetic clustering.

For the landscape metrics tested (one-way ANOVA, $p < 0.05$), only Area and P:A were significantly variable across forest types, specifically between the denuded forest (mean ± se., 1.62 ha ± 0.16 and 0.04 ± 0.01, respectively) and the other forest categories (Table S3; Table S4). Non-urban forests were on average 32.9 ha ± 14.6 in area and had a perimeter to area ratio of 0.01 ± 0.01, while urban forests and cropland forests' mean areas were 121.3 ha ± (103.3) and 15.1 ha ± 4.5, and perimeter to area ratios were 0.01 ± 0.01 and 0.02 ± 0.01, respectively. When accounting for the effects of landscape, perimeter to area ratio was negatively related to ses.PD (AICc=361.3) and ses.MNTD (AICc=368.5) (Table S5).

3.2 Phylogenetic Composition

Two major gradients of phylogenetic compositional variation were revealed by the first two axes of the phylogenetic ordination, which together explained 27.6% of the total variation (Fig. 3 and 4). The subsequent ten axes each individually explained less than 7% of the variation. The first axis (PC1, 15.2%) separated plots in urban forest with denudation LUH and most of the former cropland plots from the plots of the non-urban and urban forests without land use history (positive versus negative values on axis 1) (Fig. 3). This axis is positively correlated with lineages related to the Asterales clade, especially the family Asteraceae and the species *Eremanthus erythropappus*, which are abundant in urban forests with denudation LUH (Fig. 4). The second axis (PC2, 12.4%) separated most of the plots of the urban forests with cropland LUH, part of the denuded forests plots and a minor portion of urban forests without LUH from the remaining plots. In general, plots from the non-urban and urban forests without LUH have similar phylogenetic composition, which in turn differs markedly from urban forests with cropland and denudation LUH. The second axis is strongly and positively correlated with the family Melastomataceae and the genus *Miconia*, along with the Myrtales order followed by the Myrtaceae family with a less important contribution. The plots with negative values for both of these axes are composed of a mix of lineages, each with a relatively minor contribution to the variation in the ordination space, including Magnoliids, Fabids, Malvids and Lauraceae.

4 Discussion

This study has provided insights into the effects of urbanization and land-use history on the evolutionary structure of tropical tree communities. The different urban forests examined had markedly different patterns of phylogenetic diversity and composition, depending on their land-use history. In fact, there was limited impact of urbanization *per se* on these patterns, as evidenced by the similarity in terms of phylogenetic composition of non-urban forests and urban forests without anthropogenic land-use history (LUH). Urban forests without LUH are indistinguishable from intact, non-urban forests in terms of phylogenetic composition. These two forest types house a diversity of evolutionary lineages and no specific lineage is a strong indicator of these forest types. Urbanization *per se* did reduce phylogenetic diversity slightly, but this reduction was no greater than expected given the slight reduction in species richness in urban forests without LUH. The reduction in species richness in turn may be due simply to the reduced numbers of stems in urban forests without LUH, as rarefied species richness was not reduced in these forests compared to non-urban forests.

In contrast, urban forests with anthropogenic land-use history showed much lower phylogenetic diversity, and less phylogenetic diversity than expected given their observed reductions in species richness. Indeed, forests that regenerated from cropland, and particularly from denuded landscapes, showed clear evidence for phylogenetic clustering. Our analyses of phylogenetic composition help explain these results. While we did find evidence that phylogenetic clustering (ses.PD and ses.MNTD) increases with the perimeter to area ratio of the fragments, and that the denuded forests are significantly smaller when compared to the other forest fragments, these landscape metrics do not explain the other measures of phylogenetic diversity (which were all affected by land-use history), nor why forests regenerated from croplands show clustering. Thus, overall our results do point to an effect of land-use history itself on the phylogenetic diversity and structure of tree communities. The two urban forest types with LUH have few, distinct lineages that are strongly associated with each of them, respectively.

4.1 Phylogenetic Diversity and Structure

The process of urbanization has been reported to cause strong negative effects on biodiversity, with cities worldwide showing reduced species richness compared to rural sites (Mckinney 2006; Aronson et al. 2014; Lopez et al. 2018; Silva-junior et al. 2018). Although one study considering different disturbance regimes in urban forests did not find shifts in phylogenetic diversity (Ceplová et al. 2015), our findings indicate that land-use history for secondary forests, along with time since abandonment, are important drivers of phylogenetic diversity loss, while intact urban forests can be important reservoirs of evolutionary richness. The similar phylogenetic diversity and composition between non-urban and urban forests without land-use history suggests that the urban matrix itself does not represent a sufficiently strong environmental filter to cause significant phylogenetic and taxonomic losses, as long as there is no history of drastic land use changes, and on the timescales considered here. Juiz de Fora is a relatively young city (less than 170 years). While non-urban forests have the greatest tree SR, RSR and PD, urban forests without LUH still show markedly greater values than the urban forests with anthropogenic LUH. This result confirms the value of forests without land-use history, even within the urban matrix. Higher ses.PD values found in urban forests without LUH reflect accumulated lineage diversity, with many deep phylogenetic branches for communities relative to their SR (Swenson 2009).

The decrease in phylogenetic diversity shown by urban forests with cropland and denudation land-use history indicates that the effects of past disturbance events are still persisting after 50 to 80 years (depending on the land use history). A recent study (Rozendaal et al. 2019) has shown that biodiversity in abandoned pastures and cultivated fields is expected to reach the same level of species richness as undisturbed forest within 54 years, but that attaining the species composition of undisturbed forest can take centuries. In our case, the environmental filters in these forests have been strong enough that only a subset of lineages have been successful, hence the shifts in the phylogenetic composition of tree communities that we found. Strong environmental filters, such as conditions present in abandoned agricultural sites and in early successional phases, seem to have lead to colonization by close relatives, likely due to the conservatism of traits that are optimal in disturbed forest fragments (Baeten et al. 2015). As a result, pioneer species with fast-growing and disturbance-tolerant strategies are selected (Van Der Sande et al. 2016). These compositional shifts can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased light intensity and habitat desiccation), imposing additional environmental filters (Mehta et al. 2008). In addition, biotic homogenization, at least in early to mid stages of succession, can occur as the pre-disturbance biota is replaced by a set of generalist and disturbance-tolerant species with high dispersal abilities (Olden et al. 2004; Bengtsson 2010).

The failure of certain evolutionary lineages to colonize sites with anthropogenic land-use history was accompanied by shifts in phylogenetic structure across forests with and without land-use history. Land-use change and the existence of large edge areas is known to cause phylogenetic clustering, as a response to the strong environmental filters and intense habitat change (Santos et al. 2008; Santos et al. 2010; Arroyo-Rodríguez et al. 2012; Arroyo-Rodríguez et al. 2013; Munguía-Rosas et al. 2014; Andrade et al. 2015; Prescott et al. 2016). Small forest fragments with higher exposure to edge effects can lead to communities being dominated by a few species with a similar set of functional traits (Santos et al. 2008; Tabarelli et al. 2008). Biotic filters become increasingly important in the later stages of succession, while environmental filtering dominates in the early stages and during secondary regeneration (Connell and Slatyer 1977; Letcher 2010; Ding et al. 2012; Letcher et al. 2012; Norden et al. 2012; Purschke et al. 2013; Stadler et al. 2017). Meanwhile, intensity of disturbance has been shown to alter successional trajectories (Chazdon et al. 2003; Lugo 2004; Letcher 2010; Whitfeld et al. 2012).

Following abandonment of intensive agriculture, the first shrub and tree recruits either emerge from the seed bank or tend to be wind- or bird-dispersed species with small seeds, which in turn require direct light or high temperatures to germinate (Uhl and Jordan 1984; Vázquez-Yanes, C. and Orozco-Segovia 1984; Stadler et al. 2017). These compositional shifts can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased habitat desiccation), imposing additional environmental barriers for forest succession (Mehta et al. 2008).

The denudation (earthmoving) activities affect soil physical properties, causing loss of soil structure and fertility by compaction and surface sealing (Craul 1999). This sort of disturbance is extremely severe, due to the machinery used for substrate compaction, which eliminates nutrient stocks and plant propagules by removing all topsoil (Uhl et al. 1982; Pinard et al. 1996). Therefore, regeneration depends strictly on seed dispersal into the site, and is further limited to species adapted to deeply impoverished soils (Uhl et al. 1982). Soil degradation and loss is a frequent scenario in urban areas, due to rapid development and poor practices like grading and topsoil removal (Craul 1999). In addition, in our study, due to the high perimeter to area ratios of the denuded forest fragments, species may have faced extra environmental barriers from edge effects, such as increased light intensity, wind disturbance and altered microclimate (Turner and Corlett 1996; Laurance et al. 2006; Tabarelli et al. 2008).

4.2 Phylogenetic Composition

Forests with different histories of land-use change are expected to diverge in taxonomic and phylogenetic composition due to differences in the effects of disturbance, and to the interaction of land-use change with particular environmental conditions (Arroyo-Rodríguez et al. 2013). As predicted, land-use history showed strong effects on phylogenetic composition, with specific clades being favored. In addition, the perimeter to area ratios, which are higher in forests with a denudation history and which show a correlation with ses.PD and ses.MNTD, may have influenced phylogenetic composition, considering the role of edge effects on species composition (Santos et al. 2008). Forests with denudation LUH were strongly associated with members of the Asteraceae family and relatives, especially *Eremanthus erythropappus*, well known for their role as pioneer species (Gavilanes and Filho 1991; Scolforo et al. 2014) and for their general preference for habitats with poor soils that are not densely forested (Luna-vega 2010; Ribeiro et al. 2016b; Borges et al. 2019). Forests with cropland LUH also showed taxa usually identified as pioneers and invasive species in tropical forests, including those belonging to genera such as *Miconia* and some Myrtaceae such as *Syzigium* (Dalling et al. 1998; Fonseca and Carvalho 2012). These taxa belong to the Rosid clade, which was related to early succession in tropical forests in Costa Rica (Norden et al. 2012).

Phylogenetically poor plant communities are especially susceptible to invasion by exotic plant species, which can have long-lasting effects on tropical forests during succession (Martin et al. 2004; Chazdon 2008; Clark et al. 2012). These species colonize habitats after disturbance events that affect resource availability, including denudation, agricultural activities, fires or soil eutrophication (Funk and Vitousek 2007; Denslow 2008). Indeed, urban forests with denudation land-use history showed dominance of not only exotic species, but native disturbance-adapted species that can proliferate in degraded conditions (Marvier et al. 2004; Ribeiro et al. 2016a). *Pinus elliottii* is an exotic species which is very abundant in two of the three sites with denudation LUH. This species shows an aggressive competitive behavior, forming dense monospecific stands, similar to pioneers species in post disturbance forests (Chazdon 2008; Menon and Carvalho 2012). The novel habitat characteristics promoted by past disturbances, edge effects and human activity creates conditions for the formation of novel assemblages, with alien species being in a competitive advantage, which in the absence of human intervention, will reproduce and trigger new trajectories of succession and ecosystem function (Lugo 2004; Stadler et al. 2017).

Surprisingly, there were no detectable differences between non-urban and urban forests without LUH in their phylogenetic composition. In general, they house a variety of major clades such as Magnoliids, Malvids and Fabids, which may be expected due to the higher phylogenetic diversity of these sites compared to forests with land use history. The nodes that represent these clades are deep in the phylogeny, which increases phylogenetic diversity in sites where they co-occur.

5 Conclusion

Overall, our results provide the remarkable finding that undisturbed urban forests are irreplaceable in their broader contribution to the biodiversity of urban landscapes, holding substantial amounts of angiosperm evolutionary diversity, but that this depends on the urban forests being intact fragments of natural forest. While secondary forests can be important in supporting tropical biodiversity (Dent and Wright 2009; Letcher and Chazdon 2009), our findings suggest that 'intact' urban forests are irreplaceable in their broader contribution to the biodiversity of urban landscapes. While our study cannot determine whether the low evolutionary diversity of secondary urban forests is due to the land-use history *per se* or the interaction of land-use history with the urban environment, it is clear that these secondary forests house greatly reduced evolutionary diversity. Our study highlights the importance of preserving natural forest fragments as cities expand. We strongly recommend the protection of urban forest areas without land-use history. This study indicates the importance of considering information on land-use history, even when studying urban environments, to fully understand process that drive patterns of diversity and community assembly.

Conflict of Interest: The authors declare that they have no conflicts of interest.

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Illustrative materials

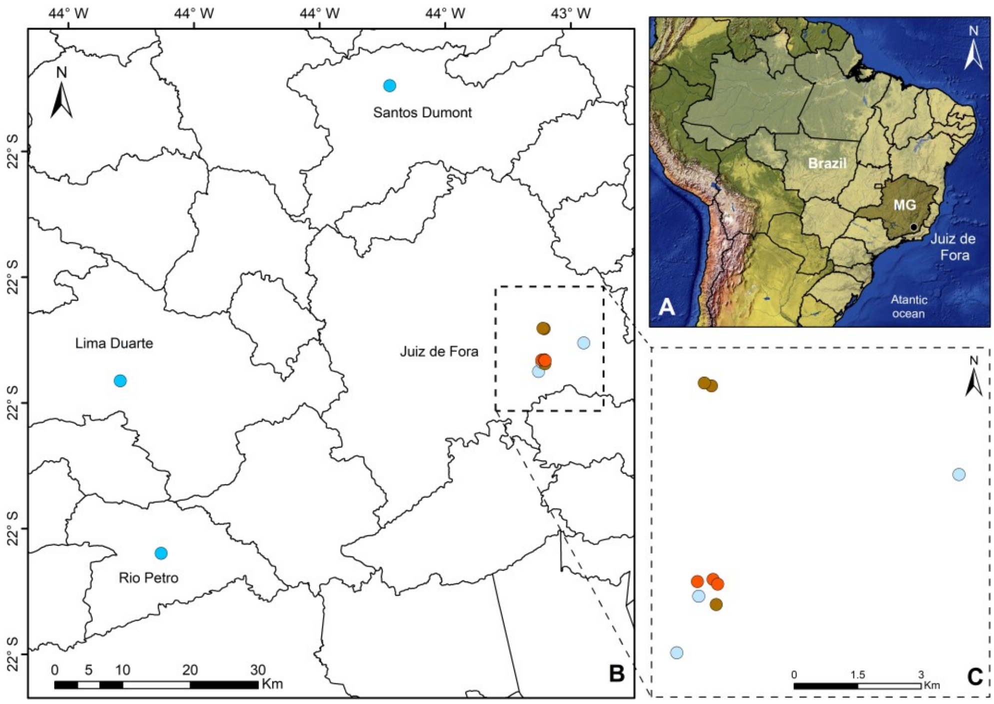

Fig. 1 Geographic location of the study area in the southeast region of Minas Gerais, Brazil. Names and information about forests are given in Table 1. A) Location of Minas Gerais in Brazil; B) Distribution of all sampled forests; C) Distribution of sampled urban forests within the city of Juiz de Fora. The circles correspond to sampled forests, blue: mature, non-urban forests, light blue: urban forests without anthropogenic land-use history, brown: urban forests regenerated from cropland, orange: urban forests regenerated from denuded landscapes.

Table 1 Characterization of twelve tropical forest fragments sampled in this study. *LUH* land use history. *NUF* non-urban forests, *UF* urban forests, *CRUF* cropland regenerated urban forests, *DRUF* denudation regenerated urban forests, *Area* (ha), *Perimeter* (Km), *P:A* (perimeter to area ratio), *Shape Index*, *BA* (Basal Area, m^2), *Density* (Individuals/ha), Mean *DBH* (Diameter at Breast Height, cm), *Native/Non-native* (Number of native and non-native species).

Forest	**Category**	**Coordinates**		**Area (ha)**	**Perimeter (km)**	**P:A**	**Shape Index**	**AB (m^2)**	**Density (Ind/ha)**	**Mean DBH (cm)**	**Native/Non-native**
BN	NUF	21°24'45"S	43°34'25"W	32.73	2.95	0.01	1.46	13.31	33.28	13.53	284/0
FS	NUF	21°48'14"S	43°55'52"W	47.19	4.26	0.01	1.75	17.44	43.59	13.98	336/0
ML	NUF	22°1'58"S	43°52'37"W	18.81	1.81	0.01	1.18	15.04	37.61	12.39	314/0
LAJ	UF	21°47'29"S	43°22'33"W	84.38	5.36	0.01	1.65	10.40	26.00	12.82	246/0
PDA	UF	21°45'13"S	43°18'58"W	273.86	8.39	0.00	1.43	10.39	25.99	11.46	305/0
EDF	UF	21°46'46"S	43°22'17"W	5.06	1.47	0.03	1.85	9.87	24.68	13.17	236/0
EM	CRUF	21°46'52"S	43°22'3"W	4.34	1.30	0.03	1.76	6.75	16.87	11.25	209/1
URB	CRUF	21°44'5"S	43°22'7"W	14.85	1.94	0.01	1.42	6.66	16.65	10.57	135/0
SEC	CRUF	21°44'3"S	43°22'12"W	26.04	2.91	0.01	1.61	8.47	21.19	9.78	218/0
ICB	DRUF	21°46'35"S	43°22'18"W	1.44	0.70	0.05	1.64	9.95	24.88	12.52	127/7
PIN	DRUF	21°46'33"S	43°22'6"W	1.97	0.63	0.03	1.26	8.21	20.52	11.93	59/1
CAN	DRUF	21°46'37"S	43°22'2"W	1.45	0.75	0.05	1.75	4.14	10.36	10.23	52/1

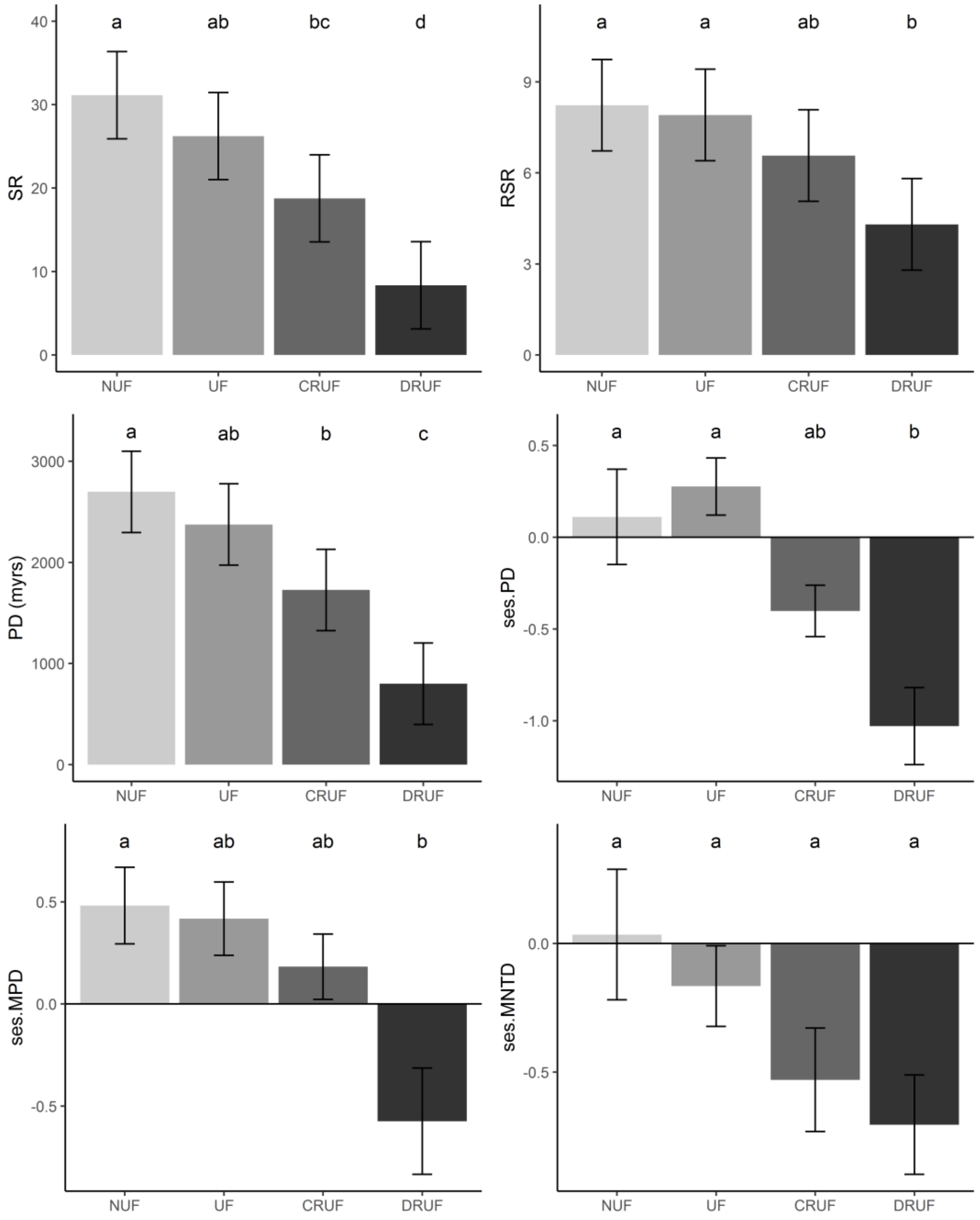

Fig. 2 The effects of land-use history on species and phylogenetic diversity metrics represented by mean values for twelve forests from the Brazilian Atlantic Forest, located in the southeast state of Minas Gerais, Brazil. *NUF* non-urban forests, *UF* urban forests, *CRUF* cropland regenerated urban forests, *DRUF* denudation regenerated urban forests. Different letters indicate significant differences among mean values ($p < 0.05$) based on pairwise comparisons in mixed linear models (Tukey's HSD). Error bars represent 95% confidence intervals. *SR* Species Richness, *RSR* Rarefied Species Richness, *PD* Phylogenetic

diversity, *ses.PD* standardized effect size of Phylogenetic Diversity, *ses.MPD* standardized effect size of Mean Pairwise Distance, *ses.MNTD* standardized effect size of Mean Nearest Taxon Distance

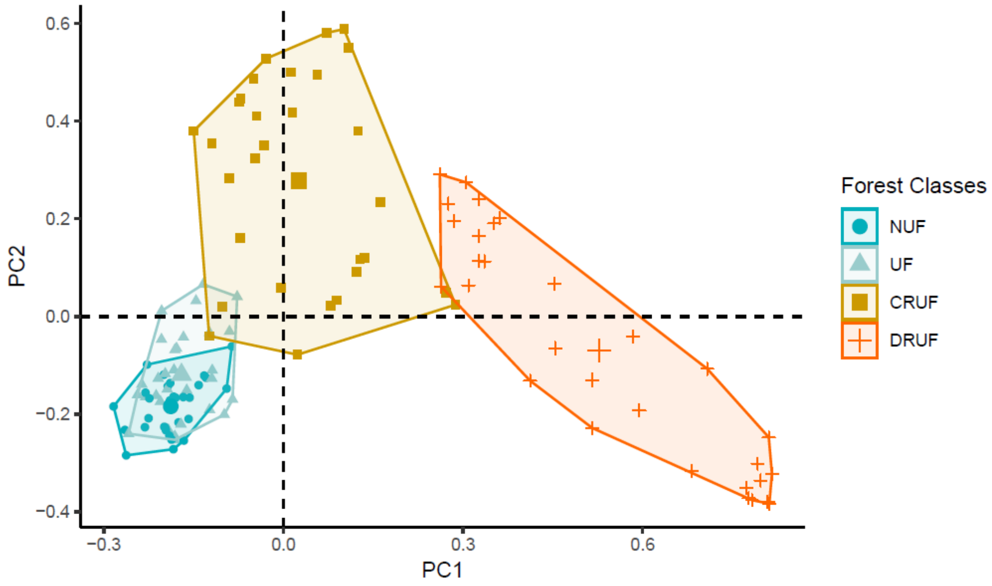

Fig. 3 First two axes (PC1 and PC2) from a principal component analysis with Hellinger distance as the coefficient of dissimilarity (evoPCAHellinger), showing the distribution of plots according to their phylogenetic composition. Point represents individual plots sampled across twelve tropical forests from the Brazilian Atlantic Forest, located in the southeast region of Minas Gerais, Brazil. *NUF* non-urban forests, *UF* urban forests, *CRUF* cropland regenerated urban forests, *DRUF* denudation regenerated urban forests

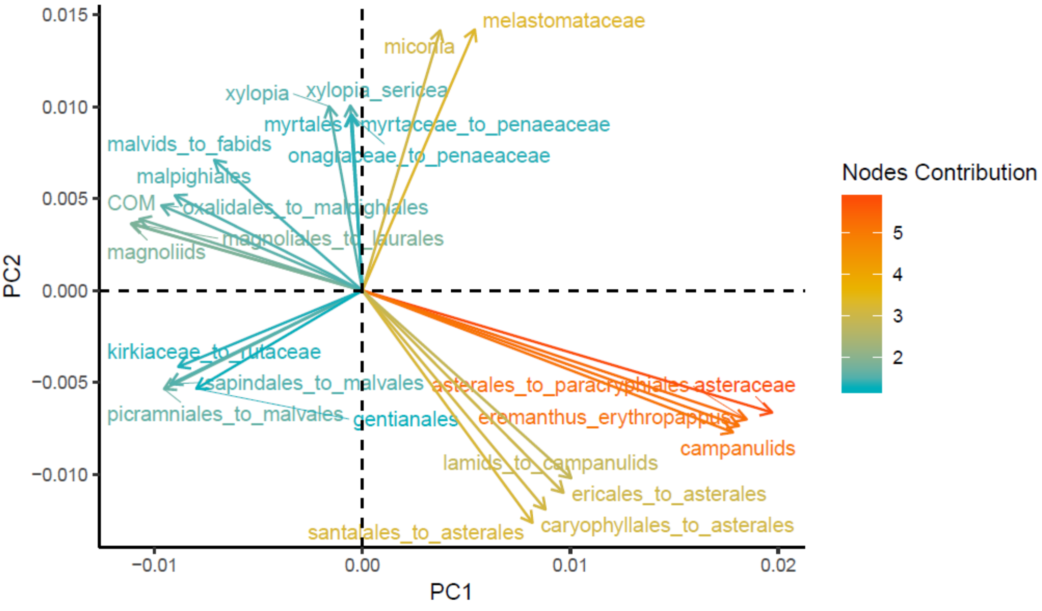

Fig. 4 First two axes (PC1 and PC2) from a principal component analysis with Hellinger distance as the coefficient of dissimilarity (evoPCAHellinger), showing the influence of each lineage in determining the position of the plots in the ordination. Lineages are indicated by an arrow (whose direction and size relate to the correlation with the first two axes and the strength of that correlation).