

Regeneration of urban forests as influenced by fragmentation, seed dispersal mode and the legacy effect of reforestation interventions

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HIGHLIGHTS

- Legacy effects of reforestation interventions shape the regeneration of urban forests.
- Species diversity of woody species is related to forest area and isolation.
- Animal-dispersed trees regenerate better than other trees in urban fragmented forests.
- Careful selection of trees based on their traits is essential in reforestation projects.

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ABSTRACT

Urban forests are highly fragmented in mega-cities, acting as islands in terms of preserving species diversity. To maintain the ecological services of urban forests, management measures such as reforestation have been implemented, which might have a long-term effect on biodiversity. To understand how fragmentation and reforestation affect the natural regeneration of urban forests, we investigated the relationship between forest area, isolation and seed dispersal mode and the diversity and composition of woody species at the tree, seedling, and sapling stages in 28 secondary forests of the mega-city of Wuhan, China. We found that the alpha diversity of woody species was positively correlated with forest area, while their beta diversity was negatively correlated with forest area. The beta diversity of nonanimal-dispersed species significantly correlated with isolation. Animal-dispersed plants had consistently a higher alpha diversity from trees to seedlings and saplings, while their beta diversity was lower than nonanimal-dispersed plants at the seedling and sapling stage. The community composition of woody plants in urban forests was largely congruent among the three life stages. However, only the communities of animal-dispersed plants were consistent across life stages in small or highly-isolated forest patches. The results show that the woody plant diversity of urban forests is largely similar to that expected by island theory. Animal-dispersed trees are more likely to regenerate successfully due to a more diverse set of species used in reforestation and their higher tolerance to urban forest fragmentation. More management measures for nonanimal-dispersed species, such as enriching and repeating reforestation, will be required to maintain their high biodiversity in urban forests.

1. Introduction

Urban sprawl has been expanding globally. It is predicted that the percentage of people living in cities will increase from 54 % in 2014 to

66 % in 2050 (United Nations, 2014). Urbanization is accompanied by changes in land use and the fragmentation of natural habitats (Haddad et al., 2015; Liu, He, & Wu, 2016). Forest remnants in the city are scattered and surrounded by high buildings, resulting in extreme cases

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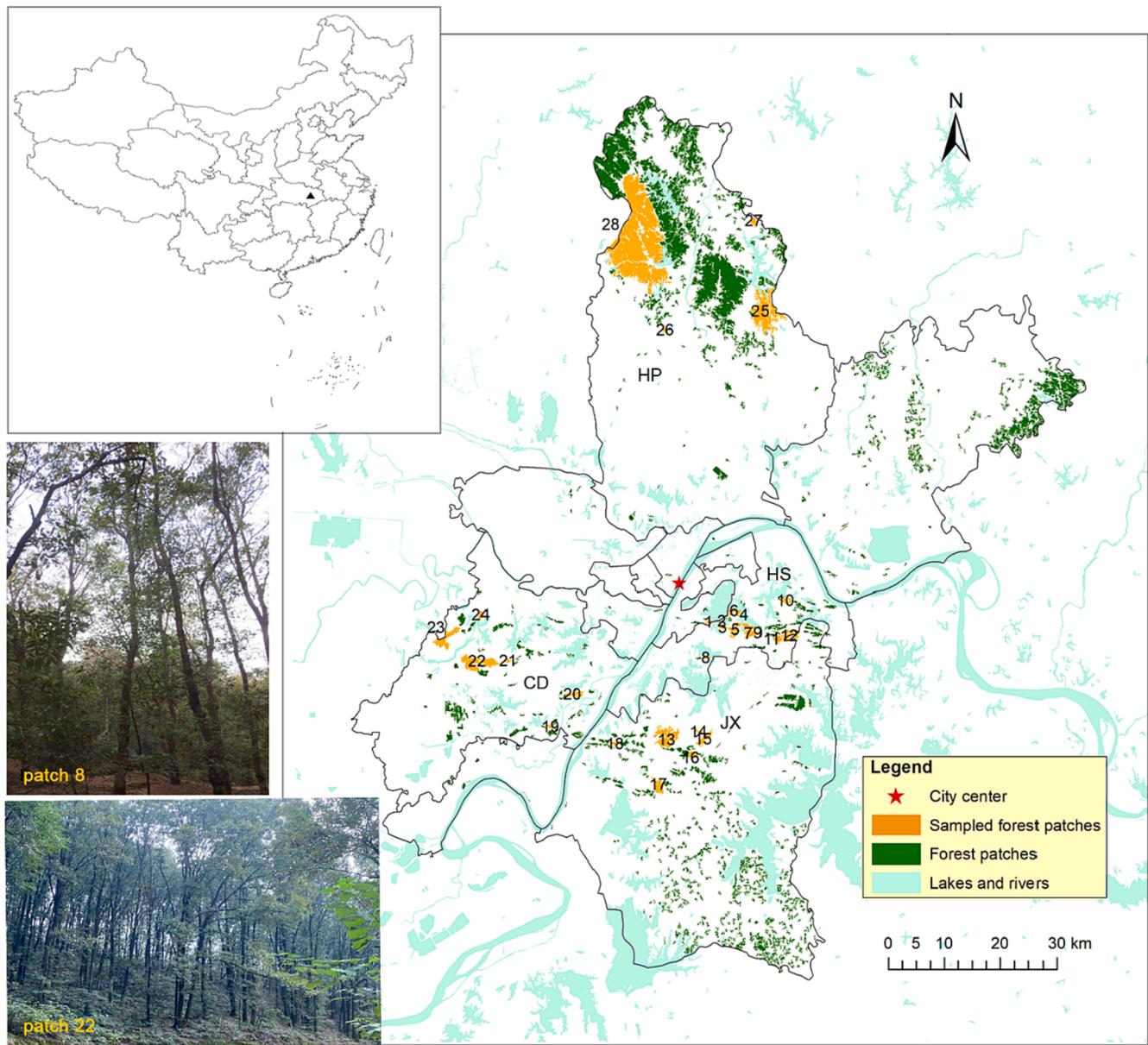


Fig. 1. Map of Wuhan and the 28 sampled forest patches: 12 forest patches in Hongshan district (HS, 1–12), six in Jiangxia district (JX, 13–18), six in Caidian district (CD, 19–24), and four in Huangpi district (HP, 25–28).

of forest fragmentation (Dobbs, Nitschke, & Kendal, 2017). These forests become “green islands” in a matrix of urban land uses, helping to maintain biodiversity and ecosystem services (Canedoli, Manenti, & Padoa-Schioppa, 2018; Long & Frank, 2020). Reforestation is one of the direct approaches to support the maintenance of ecological functions and services of urban forests (Williams et al., 2009; Aronson et al., 2016). However, whether these reforested areas can maintain their species diversity over time and how they are affected by fragmentation are not well known.

Woody plants communities in urban forests are influenced by several factors. First, the tree species used in reforestation directly determine the species composition of forest remnants in urban areas (Williams et al., 2009; Bremer & Farley, 2010; Aronson et al., 2016). Unlike residential gardens or planned public parks which experience consistent management, the remaining forest patches endure less human disturbance and tend to recover through natural regeneration after reforestation interventions (Turner, Lefler, & Freedman, 2005; Gong, Chen, & Yu, 2013; Nitoslawski, Duinker, & Bush, 2016). The dominant tree

species in urban forests also influence species diversity of the regenerating communities (Overdyck & Clarkson, 2012; Trentanovi, et al., 2013), suggesting that there is a legacy effect of reforestation interventions, in that the trees used in reforestation will affect the regeneration of urban forests.

Second, the species diversity of woody plants in urban forests is affected by fragmentation. According to island biogeography theory, small areas and high isolation can limit species diversity by influencing habitat quality in forests or the immigration of species from surrounding forests (MacArthur & Wilson, 1963; Wilson et al., 2016; Liu et al., 2018). In urban forests, the negative effect of fragmentation will primarily affect the regeneration of plants. First, small forest patches provide limited heterogeneous microhabitats (e.g., light conditions and soil nutrients) to maintain the emergence and survival of a diverse set of recruiting plants, limiting their alpha diversity (González-Varo, Nora, & Aparicio, 2012; Trentanovi et al., 2013; Rehling et al., 2022). Second, seed disperser loss and isolation effects induced by fragmentation might prevent long-distance seed dispersal across barriers, which further

decreases alpha diversity but increases the beta diversity of seedlings (Wandrag et al., 2017; Rogers et al., 2021; but see Tucker et al., 2019).

Furthermore, species with different modes of seed dispersal will respond differently to fragmentation in urban areas. For animal-dispersed plants, seed dispersal might be limited due to the local loss of animals that disperse seeds of respective plants (Cordeiro & Howe, 2001; Kurten, Wright, & Carson, 2015; Niu et al., 2021) or maintained due to the functional complementarity of generalist species, such as generalist birds (Cruz et al., 2013; Farwig et al., 2017; Dehling et al., 2020). In urban areas, bird communities are dominated by highly adaptable species that are not afraid of human beings and even exploit new human-made resources for food and nesting (Isaksson, 2018). These city-dwelling birds, such as thrushes (*Turdus* spp.) and blackcaps (*Sylvia atricapilla*), disperse nearly all small fleshy fruits and promote the colonization of animal-dispersed plants in urban areas (Gasperin & Aurélio Pizo, 2009; Cruz et al., 2013). Wind-dispersed plants have a greater dispersal ability to colonize new sites outside of urban forest patches, while their dispersal direction and distance might be affected by the wind turbulence created by fragmentation and the city (Laurance et al., 1998; Damschen et al., 2014). In contrast, gravity or explosion-dispersed plants have the most limited dispersal distances and are rarely dispersed to other urban forest patches (López-Martínez et al., 2013). Therefore, the seed dispersal mode of woody species also affects natural regeneration in urban forest patches.

To assess the effect of reforestation intervention, fragmentation and seed dispersal mode on the natural regeneration of urban forests, we studied the diversity and composition of woody species across adult-seedlings-saplings stages in 28 forest patches in the mega-city of Wuhan, China. These patches are located on hills and are fragmented by paved roads, buildings, and aquatic areas. All of the forest patches experienced logging during the 1950s and 1960s and reforestation during the 1970s and 1980s. After 30 years or more of natural recovery, the planted trees have formed the canopy layer and dominated at the tree stage, and were able to regenerate naturally. We predicted that the trees used in reforestation interventions, forest fragmentation (i.e., area and isolation), and seed dispersal mode of plants (animal- versus nonanimal-dispersal) would influence the natural regeneration of woody species in urban forests. We tested the following hypotheses: 1) The diversity and composition of the seedling and sapling assemblages are similar to that of the adult trees. 2) Alpha diversity of forest patches decreases as patch size decreases and degree of isolation increases, while beta diversity increases with isolation. 3) Animal-dispersed species are less affected by patch size or isolation in urban forests than nonanimal-dispersed species.

2. Methods

2.1. Study area

We conducted our study in Wuhan, one of the most rapidly developing cities in China. In the last three decades, the land area for urban construction has increased approximately seven times in this city (Dai et al., 2017). In 2020, the city reached an area of 8 569.15 km² and a population of 12.4 million (Wuhan Municipal Bureau of Statistics, 2021). The terrain in this area is mostly flat with small hills. Construction is expanding in flat areas, while hilly terrain is protected as forest remnants without land use change. The forest remnants in Wuhan comprise approximately 40 000 ha, ranging from 0.1 to 10 000 ha in area, and are located from the center of the city to its outskirts (Dai et al., 2017). The larger forest patches are located in the outskirts, indicating that urbanization leads to intense forest fragmentation (Fig. 1). The area has a middle subtropical monsoon climate with a mean annual temperature of 16.7 °C and annual precipitation of 1200–1400 mm. The typical vegetation is subtropical evergreen–deciduous mixed broad-leaved forest.

We selected 28 forest patches of at least 10 ha in area and distributed

across four districts, namely, Hongshan, Caidian, Jiangxia, and Huangpi, as study sites (Fig. 1, Appendix A). Each forest patch is isolated by impervious surfaces or aquatic areas, and all have experienced reforestation interventions and then naturally recovered at least 30 years. The common trees used in reforestation in those patches are native species: *Pinus massoniana*, *Cinnamomum camphora*, *Cunninghamia lanceolata*, and *Quercus* spp. (e.g., *Q. variabilis*, *Q. chenii*, *Q. serrata*). Planting one tree species in one plot (i.e. monoculture) was the main reforestation practice in Wuhan forests, while several plots were divided within a forest patch and different tree species were planted.

The area, perimeter, and land use type of the surrounding areas within a 1 km zone around each forest patch were calculated in ArcGIS. We used the percentage of non-forest area in the 1 km zone around each forest patch as an isolation index; i.e., the higher the isolation index, the smaller the forested area around the focal patch.

2.2. Plant sampling

We used line transects and sampling circles to survey the plants in forest patches and to monitor woody plant species diversity and composition from July to August in 2018 and 2019. The number of transects differed among forest patches, increasing with the forest area. It was determined by extrapolating sample coverage (Chao & Lee, 1992), to guarantee the completeness of data coverage of at least 90 % for each forest patch. Sample coverage is an index of the completeness of field samples based on the number of detected rare species (Chao & Lee, 1992; Chao & Jost, 2012). We conducted one transect in forests with an area of <100 ha, two transects in those with an area between 100 ha and 800 ha, four in those of more than 800 ha, and six in the largest forest which had an area of 10 000 ha. All transects were randomly selected and were at least 50 m away from the forest edge and pathways to reduce human disturbance and edge effects and at least 500 m away from each other to reduce interference.

Transect length was approximately 1000 m. Along each line transect, a sampling circle with a diameter of 5 m was established every 20 m to record woody plant species. All individuals larger than 1 cm in diameter at breast height (DBH) in the sampling circle were identified, measured, and recorded as established trees (DBH ≥ 5 cm) or saplings (DBH < 5 cm) according to their DBH size. To monitor seedling recruitment, a 1 m² quadrat was randomly selected in each sampling circle. In each seedling quadrat, individuals of woody species <1 m in height were identified and recorded. All detected species were categorized by seed dispersal mode: 1) animal-dispersed species, 2) wind-dispersed species, or 3) gravity/explosion-dispersed species (Diogo, Fortunato & Costa, 2015). We grouped wind-dispersed species and gravity/explosion-dispersed species as nonanimal-dispersed species for analysis due to their small sample sizes.

2.3. Data analysis

To identify the dominant species in each forest patch during the three life stages (tree, seedling, sapling), we calculated the proportion of each species and considered the three most abundant species as dominant species. Because of differences in the sampled area per patch, we extrapolated sample coverage and calculated the Hill–Simpson diversity value based on equal coverage (the lowest coverage among all patches) as the alpha diversity. Hill–Simpson diversity considers both species number and abundance in a community (Chao et al., 2014). Measuring Hill–Simpson diversity with equal coverage has been shown to reduce bias in biodiversity comparisons when sample sizes are not consistent (Roswell, Dushoff, & Winfree, 2021). We also calculated beta diversity between pairwise patches using Chao’s dissimilarity index, which considers the number of unrecorded species pairs and is similarly suitable for studies with different sample sizes (Chao et al. 2005). We then calculated the mean beta diversity for each patch, which describes the mean community dissimilarity to other patches. Finally, we used

Table 1

Effects of plant life stage (tree, seedling, sapling), forest area, isolation, species' seed dispersal mode, and their two-way interactions on alpha diversity (Hill–Simpson index) and beta diversity (mean of Chao's dissimilarity) of the woody plant communities in urban forests of Wuhan, China.

	Alpha diversity (log)			Beta diversity	
	df	F	P	F	P
Plant life stage	2	15.396	<0.001	27.268	<0.001
Forest area (log)	1	24.884	<0.001	23.537	<0.001
Isolation	1	1.777	0.246	8.409	0.004
Dispersal mode	1	63.734	<0.001	32.675	<0.001
Life stage × Area	2	1.452	0.237	0.884	0.415
Life stage × Isolation	2	0.690	0.503	0.848	0.430
Life stage × Dispersal	2	1.076	0.343	43.312	<0.001
Dispersal × Area	1	0.296	0.587	1.834	0.178
Dispersal × Isolation	1	0.008	0.930	3.801	0.054

multiple linear regression models to estimate the effect of reforestation (life stage), fragmentation (patch area and isolation), seed dispersal mode, and their interactions on alpha diversity and on beta diversity of forest communities, respectively. The data were unbalanced when considering both patch area and isolation, e.g., there were only two forests with a large area and low isolation (Appendix B). Thus, we did not model the interaction between area and isolation. Alpha diversity and patch area was log-transformed to guarantee normalized residuals and homoscedasticity.

To detect the legacy effect of reforestation interventions on the community composition of natural regeneration, i.e., seedlings and saplings, we conducted nonmetric multidimensional scaling (NMDS) analyses based on Bray–Curtis distance for plant communities at the three life stages (tree, seedling, sapling) and then conducted Procrustes tests to evaluate the congruence of NMDS among different stages. To estimate the influence of seed dispersal mode, forest area, and isolation on the legacy effect of reforestation interventions, we also conducted NMDS and Procrustes analyses for animal-dispersed and nonanimal-dispersed species in all sampled forest patches and then in small and

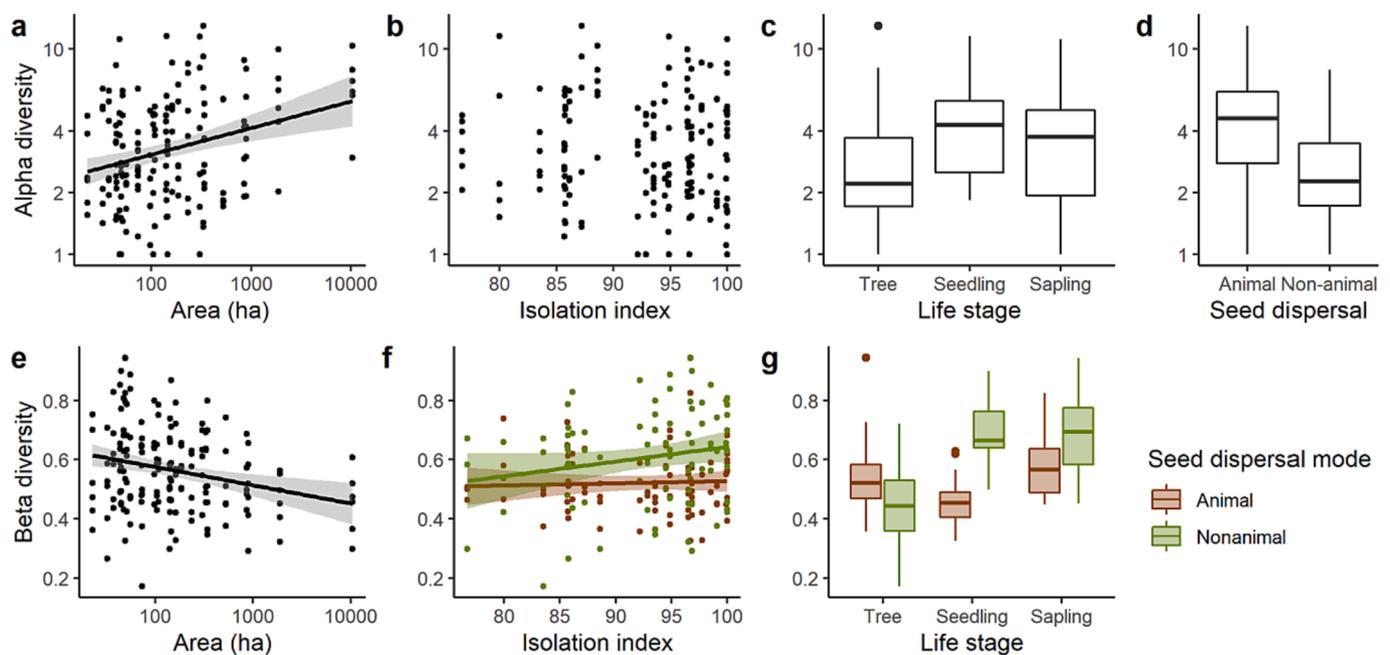


Fig. 2. Relationships between urban forest characteristics (area, isolation, life stage and seed dispersal mode) and species alpha (Hill–Simpson index, (a)–(d)) and beta diversity (mean Chao's dissimilarity, (e)–(g)) of the woody plant communities in Wuhan, China. Note the log10 scales for alpha diversity and area.

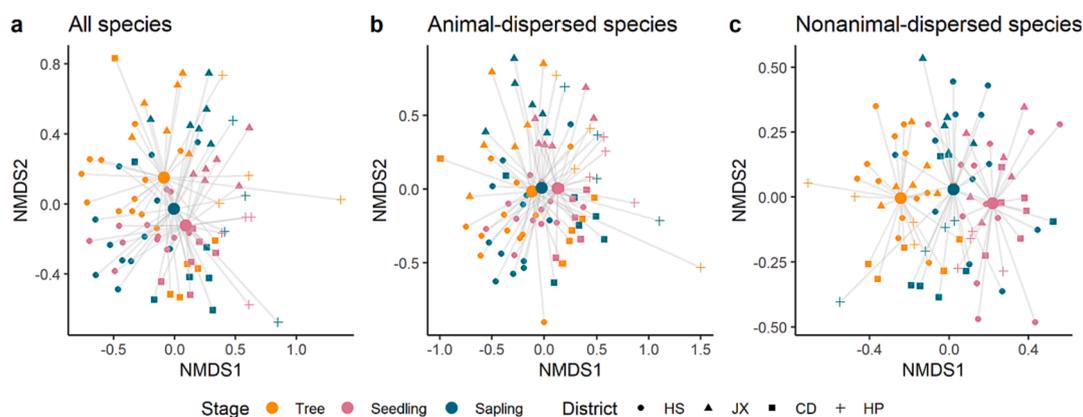


Fig. 3. Nonmetric multidimensional scaling ordinations of communities of (a) all woody species, (b) animal-dispersed species, and (c) nonanimal-dispersed species. Colored points represent communities at different life stages: tree, seedling, and sapling, and symbols refer to different districts: HS, Hongshan; JX, Jiangxia; CD, Caidian, and HP, Huangpi. The largest points depict the centroid of each life stage.

Table 2

Procrustes tests for the community similarity among different life stages in animal- and nonanimal-dispersed assemblages in forest patches with different areas or isolations.

	Animal-dispersed species			Nonanimal-dispersed species		
	<i>m</i> ²	<i>r</i>	<i>P</i>	<i>m</i> ²	<i>r</i>	<i>P</i>
Small patches						
Tree vs Seedling	0.659	0.583	0.003	0.758	0.491	0.030
Tree vs Sapling	0.480	0.721	<0.001	0.855	0.381	0.187
Seedling vs Sapling	0.223	0.881	<0.001	0.854	0.381	0.185
Large patches						
Tree vs Seedling	0.516	0.696	0.008	0.483	0.718	0.003
Tree vs Sapling	0.246	0.868	<0.001	0.630	0.607	0.030
Seedling vs Sapling	0.745	0.504	0.142	0.230	0.877	<0.001
Less-isolated patches						
Tree vs Seedling	0.702	0.545	0.121	0.807	0.439	0.334
Tree vs Sapling	0.649	0.592	0.075	0.746	0.503	0.180
Seedling vs Sapling	0.394	0.778	0.001	0.719	0.530	0.144
Highly-isolated patches						
Tree vs Seedling	0.326	0.820	<0.001	0.596	0.635	<0.001
Tree vs Sapling	0.308	0.832	<0.001	0.849	0.388	0.143
Seedling vs Sapling	0.187	0.901	<0.001	0.855	0.381	0.162

large forests and in less- and highly-isolated forests separately. To do so, we classified the sampled forests as small if the area was less than the mean for all 28 patches (*n* = 17) or large (*n* = 11) patches and as less-isolated if the isolation index was lower than the mean (*n* = 10) or highly-isolated (*n* = 18) patches. Procrustes analysis is an effective concordance analysis for shape matrices by finding the best fit (the minimum sum-of-squares distance) between two matrices via isomorphic scaling, translation, reflection, and rotation (Peres-Neto & Jackson, 2001). Because the 28 forest communities were clustered into four groups according to districts (see NMDS results), we conducted 9 999 block permutations in Procrustes analysis, considering districts as blocks. However, Procrustes analysis for parts of patches, such as a group of small, large, or less- or highly-isolated patches, was implemented with 9 999 standard permutations because they were not equally distributed across different districts. We transformed species data using the Hellinger transformation to reduce the weight of rare species before applying NMDS and Procrustes analysis.

All data analyses were conducted in R 4.0.4 (R Core Team, 2021). Coverage-based Hill-Simpson diversity was calculated with the iNEXT 2.0.20 package (Hsieh, Ma, & Chao, 2016), and beta diversity, linear regression, NMDS, and Procrustes tests were performed with the vegan 2.5–7 package (Oksanen et al., 2020).

3. Results

Across the 4.2 ha sampling area, we recorded 7 213 trees and 7 273 saplings belonging to 95 and 112 species, respectively. Across the 0.21 ha of seedling sampling plots, we detected 8 905 seedlings belonging to 107 species. In the tree assemblages, animal-dispersed species had the highest abundance (3 558 individuals of animal dispersal, 2 880 of wind dispersal, and 775 of gravity/explosion dispersal) and richness (60 species of animal dispersal, 18 of wind dispersal, and 17 of gravity/explosion dispersal) among the three dispersal modes (Appendix C). The proportion of animal-dispersed individuals increased from 49.1 % at the tree stage to 80.7 % at the seedling stage and decreased to 65.1 % at the sapling stage. The proportion of gravity/explosion-dispersed individuals was the lowest for the tree stage (10.7 %), followed by the seedling stage (11.3 %), and then the sapling stage (21.6 %), while that of wind-dispersed species rapidly declined from the tree stage (39.9 %) to the sapling (13.1 %) and seedling stages (8.0 %). The species richness in each dispersal mode showed little variation across the three life stages: 63.2 % – 68.7 % for animal-dispersed species, 16.8 % – 17.9 % for gravity/explosion-dispersed species, and 12.5 % – 18.9 % for wind-dispersed species.

Table A

Patch characteristics and the dominant woody plants and their percentage at three life stages in 28 forest patches in Wuhan, China.

	Patch characteristic			Dominant species		
	Area (ha)	Isolation	District	Tree	Sapling	Seedling
P01	44.9	96.85	HS	<u>Cc (48.4)</u> , <u>Qc (23.0)</u> , <u>Pm (6.6)</u>	<u>Cc(40.0)</u> , <u>Cg(17.1)</u> , <u>Lg(12.9)</u>	<u>Cc(62.0)</u> , <u>Qc(13.0)</u> , <u>Cg(10.0)</u>
P02	22.9	93.52	HS	<u>Cc (39.4)</u> , <u>Lf (28.9)</u> , <u>Qc (8.3)</u>	<u>Cc(70.6)</u> , <u>Ll(7.1)</u> , <u>Of (6.3)</u>	<u>Cc(33.2)</u> , <u>Cg(22.1)</u> , <u>Qc(5.5)</u>
P03	56.1	94.86	HS	<u>Cc (68.8)</u> , <u>Pm (14.6)</u> , <u>Qc (6.4)</u>	<u>Cc(55.8)</u> , <u>Tf(8.8)</u> , <u>Of (6.8)</u>	<u>Cc(60.7)</u> , <u>Cs(5.2)</u> , <u>Tf (5.8)</u>
P04	73.2	83.52	HS	<u>Cc (19.3)</u> , <u>Pm(16.7)</u> , <u>Qc(16.1)</u>	<u>Cc(46.0)</u> , <u>Mj(8.0)</u> , <u>Ic (7.0)</u>	<u>Cc(59.8)</u> , <u>Qc(6.3)</u> , <u>Of (6.0)</u>
P05	144.8	92.17	HS	<u>Cc (77.3)</u> , <u>Lc(9.8)</u> , <u>Pm (7.6)</u>	<u>Ll(35.8)</u> , <u>Ab(13.2)</u> , <u>Lg(9.4)</u>	<u>Cc(29.0)</u> , <u>Cs(15.0)</u> , <u>Ll(13.0)</u>
P06	161.4	97.77	HS	<u>Cf(25.7)</u> , <u>Cc (21.2)</u> , <u>Pm(11.4)</u>	<u>Cc(19.9)</u> , <u>Bp(8.5)</u> , <u>Pt (8.2)</u>	<u>Cc(37.3)</u> , <u>Qc(8.4)</u> , <u>Of (8.4)</u>
P07	340.0	93.54	HS	<u>Pm(23.3)</u> , <u>Cc (31.2)</u> , <u>Ed(6.5)</u>	<u>Lg(32.3)</u> , <u>Cc(17.7)</u> , <u>Ll(8.3)</u>	<u>Cc(54.0)</u> , <u>Of(8.0)</u> , <u>Co (4.8)</u>
P08	37.4	86.14	HS	<u>Cc(34.0)</u> , <u>Qc(14.4)</u> , <u>Pm(10.3)</u>	<u>Cc(28.2)</u> , <u>Pt(12.0)</u> , <u>Ic(12.0)</u>	<u>Qc(64.6)</u> , <u>Cc(14.7)</u> , <u>Sx(3.9)</u>
P09	32.6	85.79	HS	<u>Pm(26.0)</u> , <u>Ic(19.2)</u> , <u>Cc (13.0)</u>	<u>Ll(14.6)</u> , <u>Lg(12.4)</u> , <u>Dl(12.4)</u>	<u>Cc(35.1)</u> , <u>Mj(10.0)</u> , <u>Za(5.7)</u>
P10	104.6	92.88	HS	<u>Cc (43.2)</u> , <u>Lf (27.4)</u> , <u>Cl (18.9)</u>	<u>Cc(43.2)</u> , <u>Lf(25.8)</u> , <u>Cc(11.9)</u>	<u>Co(9.6)</u> , <u>Rc (10.0)</u>
P11	140.1	76.71	HS	<u>Pm(22.2)</u> , <u>Ic(22.2)</u> , <u>Qv(13.9)</u>	<u>Ic(22.0)</u> , <u>Cg(18.4)</u> , <u>Cl(16.3)</u>	<u>Cg(26.0)</u> , <u>Cc(13.0)</u> , <u>Cl(15.0)</u>
P12	330.3	87.22	HS	<u>Pm(53.8)</u> , <u>Lc(13.1)</u> , <u>Qs(4.8)</u>	<u>Lc(51.6)</u> , <u>Qc(8.6)</u> , <u>Rc(5.4)</u>	<u>Cc(21.0)</u> , <u>Qc(15.0)</u> , <u>Lc(12.0)</u>
P13	891.4	96.85	JX	<u>Lg(19.5)</u> , <u>Pm(13.5)</u> , <u>Lc (12.0)</u>	<u>Lg(35.6)</u> , <u>Lc(16.8)</u> , <u>Cs(8.8)</u>	<u>Cs(21.1)</u> , <u>Lt(12.7)</u> , <u>Ic (8.7)</u>
P14	47.9	100	JX	<u>Pm(49.7)</u> , <u>Lc(32.7)</u> , <u>Cs(7.0)</u>	<u>Lc(59.2)</u> , <u>Qs(5.7)</u> , <u>Hj (4.3)</u>	<u>Gj(37.6)</u> , <u>Qs(9.4)</u> , <u>Cs (8.2)</u>
P15	234.2	100	JX	<u>Pm(35.2)</u> , <u>Qs(11.1)</u> , <u>Ll(9.3)</u>	<u>Lc(27.0)</u> , <u>Qs(18.0)</u> , <u>Vn(19.7)</u>	<u>Qs(14.0)</u> , <u>Gj(14.0)</u> , <u>Vn(10.0)</u>
P16	142.6	79.96	JX	<u>Cl(54.0)</u> , <u>Cc(12.7)</u> , <u>Pm(17.3)</u>	<u>Lc(49.1)</u> , <u>Cc(11.9)</u> , <u>Cl(6.8)</u>	<u>Gj(15.2)</u> , <u>Cc(9.5)</u> , <u>Ic (11.4)</u>
P17	303.9	94.89	JX	<u>Cl(85.7)</u> , <u>Lc(3.9)</u> , <u>Ic (2.5)</u>	<u>Ic(23.6)</u> , <u>Lc(19.5)</u> , <u>Cl(16.9)</u>	<u>Cl(18.8)</u> , <u>Kp(11.1)</u> , <u>Qs(9.7)</u>
P18	73.0	85.70	JX	<u>Lc(35.6)</u> , <u>Pm(14.1)</u> , <u>Qs(19.6)</u>	<u>Lc(65.7)</u> , <u>Lg(9.5)</u> , <u>Qs(8.7)</u>	<u>Qs(52.1)</u> , <u>Cc(9.1)</u> , <u>Lc (5.0)</u>
P19	51.5	85.74	CD	<u>Cc(37.6)</u> , <u>Cs(9.9)</u> , <u>Bp(6.4)</u>	<u>Lg(21.9)</u> , <u>Cc(16.7)</u> , <u>Dh(13.5)</u>	<u>Cc(25.0)</u> , <u>Bp(10.0)</u> , <u>Sj(11.0)</u>
P20	186.1	94.51	CD	<u>Cc(31.0)</u> , <u>Cl(24.1)</u> , <u>Ic(11.0)</u>	<u>Dh(39.6)</u> , <u>Lc(10.4)</u> , <u>Cc(9.8)</u>	<u>Cc(24.0)</u> , <u>Cj(15.0)</u> , <u>Of(10.0)</u>
P21	44.0	98.53	CD	<u>Qv(28.9)</u> , <u>Pm(20.4)</u> , <u>Cl(8.6)</u>	<u>Qv(37.2)</u> , <u>Cl(11.8)</u> , <u>Ll(11.8)</u>	<u>Cc(16.0)</u> , <u>Vn(14.0)</u> , <u>Qv(11.0)</u>
P22	856.3	96.53	CD	<u>Qv(53.7)</u> , <u>Cl(14.1)</u> , <u>Cc(11.2)</u>	<u>Vn(30.6)</u> , <u>Qv(18.9)</u> , <u>Cc(11.2)</u>	<u>Qv(18.6)</u> , <u>Cc(12.1)</u> , <u>Sj(8.5)</u>
P23	528.1	99.09	CD	<u>Qv(45.6)</u> , <u>Pm(22.7)</u> , <u>Cc(8.9)</u>	<u>Qv(23.2)</u> , <u>Vn(20.5)</u> , <u>Dh(11.6)</u>	<u>Qv(27.0)</u> , <u>Cc(17.0)</u> , <u>Dh(12.0)</u>
P24	97.9	99.89	CD			

(continued on next page)

Table A (continued)

Patch characteristic				Dominant species		
Area (ha)	Isolation	District	Tree	Sapling	Seedling	
P25	1885.3	96.50	HP	<i>Qv</i> (57.7),	<i>Qv</i> (23.0),	<i>Qv</i> (41.8),
				<i>Cf</i> (23.7),	<i>Cc</i> (19.5),	<i>Cc</i> (20.7),
				<i>Pm</i> (9.6)	<i>Ss</i> (13.8)	<i>Dh</i> (6.8)
				<i>Pm</i> (50.3),	<i>Vn</i> (30.3),	<i>Vn</i> (13.7),
P26	49.6	96.68	HP	<i>Cl</i> (14.0),	<i>Lg</i> (9.2),	<i>Lg</i> (8.0), <i>Gp</i>
				<i>Lf</i> (7.0)	<i>Rc</i> (8.3)	(6.6)
				<i>Pm</i> (94.7)	<i>Vn</i> (46.4),	<i>Vn</i> (51), <i>Sj</i>
					<i>Ts</i> (17.9),	(13), <i>Za</i>
P27	107.8	100	HP	<i>Pm</i> (68.9),	<i>Lg</i> (24.1),	<i>Sj</i> (23), <i>Vn</i>
				<i>Lf</i> (10.4),	<i>Vn</i> (23.6),	(13), <i>Qa</i>
				<i>Qa</i> (5.7)	<i>Ps</i> (10.8)	(12)
				<i>Vn</i> (17.2),	<i>Vn</i> (11.0),	
P28	10359.6	88.62	HP	<i>Cl</i> (15.3),	<i>Cj</i> (11.9),	<i>Sj</i> (8.3), <i>Lb</i>
				<i>Qa</i> (8.3)	<i>Lg</i> (10.6)	(8.3)

Forest patches were sampled in four districts: Hongshan (HS), Jiangxia (JX), Caidian (CD) and Huangpi (HP). Dominant species are the top three species with the largest abundance at each stage in each forest patch. *Ab*, *Acer buergerianum*; *Bp*, *Broussonetia papyrifera*; *Cc*, *Cinnamomum camphora*; *Cf*, *Cupressus funebris*; *Cg*, *Cyclobalanopsis glauca*; *Cj*, *Camellia japonica*; *Cl*, *Cunninghamia lanceolata*; *Co*, *Camellia oleifera*; *Cs*, *Castanopsis sclerophylla*; *Dh*, *Dalbergia hupeana*; *Dl*, *Diospyros lotus*; *Ed*, *Elaeocarpus decipiens*; *Ej*, *Eriobotrya japonica*; *Gj*, *Gardenia jasminoides*; *Gp*, *Glochidion puberum*; *Ic*, *Ilex chinensis*; *Kp*, *Koelreuteria paniculata*; *Lb*, *Lespedeza bicolor*; *Lc*, *Loropetalum chinense*; *Lf*, *Liquidambar formosana*; *Ll*, *Ligustrum lucidum*; *Lg*, *Lindera glauca*; *Mj*, *Mallotus japonicus*; *Oj*, *Osmanthus fragrans*; *Ps*, *Platycarya strobilacea*; *Pm*, *Pinus massoniana*; *Pt*, *Pittosporum tobira*; *Qa*, *Quercus aliena*; *Qc*, *Quercus chenii*; *Qs*, *Quercus serrata*; *Qv*, *Quercus variabilis*; *Rc*, *Rhus chinensis*; *Sj*, *Serissa japonica*; *Ss*, *Symplocos sumuntia*; *Tf*, *Trachycarpus fortunei*; *Ts*, *Triadica sebifera*; *Vn*, *Vitex negundo*; *Za*, *Zanthoxylum armatum*. Species underlined are animal-dispersed species.

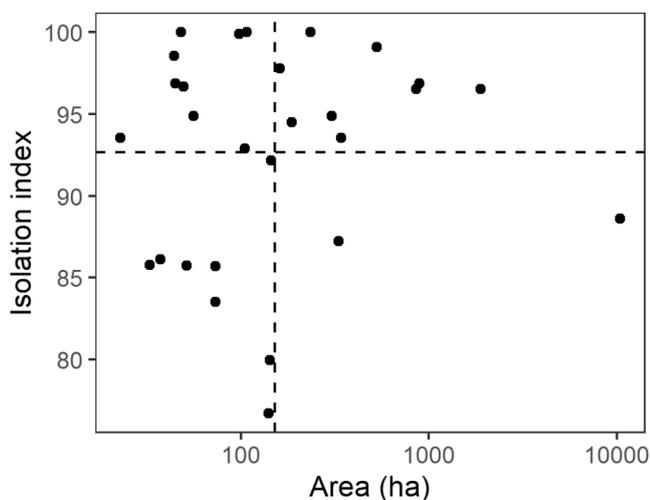


Fig. B. Relationship between forest area and isolation index of the 28 sampled forest patches. Dashed lines indicate the mean of the isolation index and the mean of the log-transformed area.

Among the dominant tree species in forests, *P. massoniana* and *C. lanceolata* were the most common wind-dispersed species (Appendix A, D). Both were dominantly distributed across all four districts at the tree stages but no longer dominated any forests at the seedling stage, except for *C. lanceolata* in two forest patches (Appendix A). In contrast, the dominant animal-dispersed species differed across the four districts, with *Q. chenii* dominating in Hongshan district, *Q. variabilis* in Caidian district, *Q. serrata* mainly in Jiangxia district, and *C. camphora* in all but Huangpi district (Appendix A). Most of them were consistently dominant at the tree, seedling and sapling stages in their respective forests.

3.1. Relationships between species diversity and urban forest characteristics

The sample coverage in forests was consistently high across plant life stages, with a minimum of 0.90 and a median of 0.98 for trees, 0.97 for saplings, and 0.98 for seedlings (Appendix C). Alpha diversity (Hill–Simpson diversity based on equal coverage) was significantly affected by patch area, life stage, and seed dispersal mode but was not related to isolation or their interactions (Table 1, Fig. 2). Overall, alpha diversity was positively related to forest area (Fig. 2a). Among the plant life stages, seedling and sapling assemblages had a higher alpha diversity than tree assemblages (Fig. 2c). Animal-dispersed species had a higher alpha diversity than nonanimal-dispersed species (Fig. 2d).

The beta diversity (Chao’s dissimilarity index) of forests was related to plant life stage, patch area, isolation, dispersal mode, and the interaction of life stage and dispersal mode (Table 1, Fig. 2). Beta diversity was negatively related to patch area (Fig. 2e). The beta diversity of nonanimal-dispersed species increased with increasing isolation from other forests, while that of animal-dispersed species was not related to the isolation index (Fig. 2f). Overall, the beta diversity of animal-dispersed species was lower in the seedling stage than in the tree stage, while that of nonanimal-dispersed species was higher in the seedling stage (Fig. 2g).

3.2. Relationships between community composition and urban forest characteristics

The community composition of saplings and seedlings was congruent with that of trees, clustering into four groups according to district (Fig. 1, illustrated as different point shapes in Fig. 3). The Procrustes analysis showed a strong consistency of community composition between trees and seedlings ($m^2 = 0.694$; $r = 0.553$, $P < 0.001$), trees and saplings ($m^2 = 0.329$; $r = 0.819$, $P < 0.001$) and seedlings and saplings ($m^2 = 0.712$; $r = 0.537$, $P < 0.001$) (Fig. 3a). For animal-dispersed species, there was a significant consistency of community composition between trees and seedlings ($m^2 = 0.497$; $r = 0.709$, $P = 0.006$), trees and saplings ($m^2 = 0.361$; $r = 0.799$, $P < 0.001$) and seedlings and saplings ($m^2 = 0.348$; $r = 0.807$, $P < 0.001$) (Fig. 3b). However, for nonanimal-dispersed species, there was no congruence between trees and seedlings ($m^2 = 0.886$; $r = 0.337$, $P = 0.255$) or seedlings and saplings ($m^2 = 0.818$; $r = 0.426$, $P = 0.090$). There was, however, congruence between trees and saplings ($m^2 = 0.710$; $r = 0.538$, $P = 0.029$) (Fig. 3c).

The congruence of community composition across plant life stages was influenced by forest area and isolation (Table 2). According to the Procrustes analysis, the community composition of animal-dispersed plants was similar across the three life stages in both small and large forests, as well as in highly isolated forests. However, for nonanimal-dispersed plants, congruence of community composition across all life stages was detected in only large forest patches. In small patches or highly isolated forests, the community composition of nonanimal-dispersed plants was similar between trees and seedlings but not between trees and saplings or seedlings and saplings. In less-isolated forests, there was no community composition congruence among life stages for both animal- and nonanimal-dispersed species, except between seedlings and saplings in animal-dispersed communities (Table 2).

4. Discussion

In the forest patches of the mega-city of Wuhan, we found that plant choice during reforestation interventions, fragmentation of forest patches, and the seed dispersal mode of plants explain the species diversity and composition of trees, as well as that of naturally regenerating seedling and sapling assemblages. Our results showed that urban forests in Wuhan were reforested with a more diverse set of animal-dispersed species than wind-dispersed species, and these plants have a legacy

Table C

Sample coverage and species abundance and richness by seed dispersal mode at three life stages in 28 forest patches in Wuhan, China.

	Sample coverage			Species abundance		Species richness	
	Tree	Sapling	Seedling	Animal-dispersed (Tree/Sapling/Seedling)	Nonanimal-dispersed (Tree/Sapling/Seedling)	Animal-dispersed (Tree/Sapling/Seedling)	Nonanimal-dispersed (Tree/Sapling/Seedling)
P01	0.95	0.96	0.98	483(112/136/235)	24(10/4/10)	19(11/12/12)	7(3/3/3)
P02	0.96	0.95	0.98	475(136/122/217)	104(82/4/18)	23(13/10/20)	10(7/3/4)
P03	0.97	0.94	0.99	339(87/93/159)	45(22/9/14)	16(6/11/14)	7(3/4/4)
P04	0.94	0.94	0.98	490(117/87/286)	66(38/13/15)	27(16/13/24)	9(8/5/5)
P05	0.96	0.92	0.95	270(109/77/84)	67(23/29/15)	22(7/12/15)	8(2/8/4)
P06	0.97	0.98	0.99	926(180/279/467)	188(127/38/23)	37(22/22/33)	10(7/8/7)
P07	0.98	0.92	0.97	476(100/88/288)	85(54/8/23)	28(14/19/25)	10(7/4/6)
P08	0.94	0.94	0.99	503(81/110/312)	44(16/7/21)	21(14/15/16)	11(5/5/5)
P09	0.99	0.97	0.95	351(93/77/181)	95(53/12/30)	29(14/10/26)	8(5/3/5)
P10	0.98	0.98	0.98	338(122/59/157)	352(137/142/73)	21(5/10/15)	11(6/8/9)
P11	0.99	0.97	0.99	1028(286/274/468)	478(160/149/169)	29(13/22/26)	13(6/10/10)
P12	0.94	0.94	0.97	199(44/49/106)	214(101/79/34)	27(17/16/17)	7(4/4/5)
P13	0.98	0.98	0.98	1428(392/499/537)	460(202/173/85)	39(22/28/36)	16(12/9/9)
P14	0.97	0.98	0.90	221(25/117/79)	334(146/182/6)	25(9/22/16)	9(4/4/4)
P15	0.95	0.97	0.94	282(54/115/113)	141(54/63/24)	25(14/16/18)	11(6/6/6)
P16	0.98	0.98	0.91	185(29/70/86)	247(121/107/19)	30(7/14/25)	9(5/6/7)
P17	0.97	0.98	0.91	284(25/159/100)	401(255/102/44)	25(11/14/23)	12(4/5/9)
P18	0.98	0.98	0.93	264(89/69/106)	330(130/185/15)	21(7/8/17)	10(7/7/5)
P19	0.95	0.95	0.98	412(115/80/217)	87(39/16/32)	22(15/13/18)	10(8/3/5)
P20	0.97	0.97	0.95	240(84/65/91)	196(61/99/36)	22(9/14/15)	8(5/5/6)
P21	0.98	0.90	0.97	332(95/43/194)	90(57/8/25)	24(11/11/20)	11(5/2/7)
P22	0.98	0.98	0.97	984(344/231/409)	226(103/60/63)	33(16/17/30)	16(8/7/13)
P23	0.98	0.98	0.99	878(292/217/369)	264(147/42/75)	34(18/22/25)	10(5/5/8)
P24	1.00	0.99	0.98	382(100/82/200)	98(56/5/37)	16(4/10/15)	8(4/3/4)
P25	0.99	0.99	0.99	1210(117/525/568)	829(410/201/218)	37(18/26/30)	25(12/17/18)
P26	0.98	0.94	0.97	295(5/24/266)	121(90/4/27)	19(3/6/15)	5(1/2/4)
P27	0.97	0.97	0.99	391(31/152/208)	290(162/51/77)	21(8/13/18)	12(5/5/9)
P28	0.99	0.99	0.99	1837(294/860/683)	2006(799/716/491)	53(28/43/46)	31(22/25/23)

Table D

Characteristics of dominant woody species in 28 forest patches in Wuhan, China.

Abundance Rank	Species name	Fruit type	Dispersal mode	Shade tolerance	Growth form	Reforestation
1	<i>Cinnamomum camphora</i>	fleshy	animal	shade-tolerance	tree	yes
2	<i>Pinus massoniana</i>	dry	wind	shade-intolerance	tree	yes
3	<i>Vitex negundo</i>	fleshy	animal	shade-intolerance	shrub	no
4	<i>Cunninghamia lanceolata</i>	dry	wind	shade-tolerance	tree	yes
5	<i>Quercus variabilis</i>	dry	animal	shade-intolerance	tree	yes
6	<i>Loropetalum chinense</i>	dry	gravity	shade-tolerance	shrub	no
7	<i>Lindera glauca</i>	fleshy	animal	shade-tolerance	shrub	no
8	<i>Ilex chinensis</i>	fleshy	animal	shade-tolerance	tree	yes
9	<i>Liquidambar formosana</i>	dry	wind	shade-intolerance	tree	yes
10	<i>Dalbergia hupeana</i>	dry	wind	shade-intolerance	tree	yes
11	<i>Cyclobalanopsis glauca</i>	dry	animal	shade-intolerance	tree	yes
12	<i>Quercus chenii</i>	dry	animal	shade-intolerance	tree	yes
13	<i>Quercus serrata</i>	dry	animal	shade-intolerance	tree	yes
14	<i>Quercus aliena</i>	dry	animal	shade-intolerance	tree	yes
15	<i>Celtis sinensis</i>	fleshy	animal	shade-tolerance	tree	yes
16	<i>Camellia japonica</i>	dry	animal	shade-tolerance	shrub	yes
17	<i>Rhus chinensis</i>	fleshy	animal	shade-intolerance	tree	no
18	<i>Serissa japonica</i>	fleshy	animal	shade-tolerance	shrub	no
19	<i>Castanopsis sclerophylla</i>	dry	animal	shade-tolerance	tree	yes
20	<i>Broussonetia papyrifera</i>	fleshy	animal	shade-intolerance	tree	yes

effect on the community composition of seedlings and saplings. The species diversity of woody plants was affected by forest area and isolation, mostly in line with expectations from island theory. Finally, animal-dispersed trees showed higher tolerance to urban forest fragmentation and were associated with a stronger legacy effect in natural regeneration, compared to nonanimal-dispersed trees.

4.1. Effect of reforestation interventions on urban forests

Reforestation is one of the widely used management measures for the restoration of degraded forests (Lamb, Erskine, & Parrotta, 2005; Hua et al., 2016). Following more than 30 years of recovery, the trees used in reforestation dominated at tree stage and contributed to dense tree

canopies in Wuhan forests, and the seedling and sapling assemblages reflected the natural regeneration of forest patches. Similar to the reforestation progress of other forests outside Wuhan but in central China (Yi et al., 2022), pioneering trees such as wind-dispersed species *P. massoniana* and *C. lanceolata* were widely used and across all sampled districts in Wuhan. However, a more diverse set of animal-dispersed plant species (e.g. *C. camphora*, *Q. aliena*, *Q. chenii*, *Q. variabilis*, *Q. serrata*) was used for reforestation among districts in Wuhan. This resulted in higher alpha and beta diversities of animal-dispersed species and greater differences in tree communities among districts.

During reforestation, mixed tree planting can provide greater benefits in restoring biodiversity than planting single species only (i.e. monoculture) (Hua et al., 2016; Huang et al., 2018). Although

monoculture was also the main reforestation practice in Wuhan's forests, similar to other reforestation programs across China (Hua et al., 2016; Yi et al., 2022), large forest patches are more likely to contain more small monoculture plots for different species candidates in reforestation. After at least 30 years of natural recovery, a high number of woody species was observed at tree stage in large-sized forest patches and resulted in high diversities in seedling and sapling assemblages. Across the three life stages, the congruence of the woody species community composition is indicative of the legacy effect of reforestation interventions.

The propagules of woody plants in remnant forests (e.g. soil seed bank) before reforestation can contribute to the natural regeneration of forests (Paul et al., 2012). However, there is no record of the original forest in Wuhan. In this study, some shrubs which had not been used for reforestation were found in Wuhan forest patches (Appendix D), indicating that the propagules from the original forest might have contributed to the natural regeneration of the reforested patches. However, the dominant animal-dispersed trees were originated from reforestation and remained even more dominant in seedlings and saplings, further confirming the legacy effect of reforestation interventions. This legacy effect from nonanimal-dispersed trees to seedlings was weaker than that from animal-dispersed trees. One reason for this might be that the dominant nonanimal-dispersed trees, *P. massoniana* and *C. lanceolata*, are shade-intolerant, and thus hardly recruit in high-density reforested patches. Overall, our results indicate that the choice of species for during reforestation, especially the selection of animal-dispersed trees, will have a lingering impact on urban forests (Williams, Hahs, & Vesik, 2015).

4.2. Effect of fragmentation and seed dispersal mode on urban forests

Decreased forest area caused by fragmentation reduced alpha diversity but increased beta diversity of woody species in Wuhan, which is consistent with results on true islands (Kohn & Walsh, 1994; Lu, Ding, & Xu, 2005) and in other fragmented forests (Phillips et al., 2018). Generally, large areas contain more habitats in which plants with different environmental requirements can coexist (MacArthur & Wilson, 1963; Fahrig, 2017). The similarity in community composition across plant life stages for both animal-dispersed species and nonanimal-dispersed species supports the conclusion that all species, no matter their seed dispersal mode, can achieve natural regeneration in large urban forests. In small forest patches, the community composition of animal-dispersed species showed similarities across all three plant life stages, while community similarity was displayed only between tree and seedling assemblages for nonanimal-dispersed species. The results indicate a shift in the community composition during regeneration at the sapling stage, particularly for nonanimal-dispersed species in small forests. This shift may be because small forest patches rarely provide enough microhabitats, such as canopy gaps, for shade-intolerant tree species to recruit.

Forest fragmentation also influences the seed dispersal process and natural regeneration as forest patches become increasingly isolated (Wilson et al., 2016; Liu et al., 2018). In urban areas, high buildings and paved roads are common barriers so that seeds are rarely dispersed among patches without effective dispersal agents (Gelmi-Candusso & Hämäläinen, 2019). The beta diversity of animal-dispersed species was not related to the isolation index, indicating that generalist animal species regularly dispersed seeds across patches, which were then recruited efficiently. Generalist birds can disperse nearly all fleshy fruits and may be the most effective seed dispersal agents for animal-dispersed species in urban areas (Schneberg et al., 2020; Stanley & Arceo-Gómez, 2020). In Wuhan, the most common birds are light-vented bulbul (*Pycnonotus sinensis*), azure-winged magpie (*Cyanopica cyanus*), Chinese blackbird (*Turdus mandarinus*) and cinereous tit (*Parus cinereus*), all of which are generalists, likely promoting seed dispersal across patches and benefitting the associated plant regeneration. Furthermore, street trees, anthropogenic infrastructures, and small green areas can act as stepping

stones for seed dispersal by birds across barriers among and within forest patches (González-Varo et al., 2017; Gelmi-Candusso & Hämäläinen, 2019). In Wuhan, the fleshy-fruited tree *C. lanceolata* is not only used in reforestation but also as a street tree, potentially promoting its extreme domination in natural regeneration in forest patches.

In contrast, the beta diversity of nonanimal-dispersed species was positively related to the isolation index in seedlings and saplings, suggesting that high isolation could limit their natural regeneration. This may be due to seed dispersal limitation or habitat limitation for plant recruitment. Among nonanimal-dispersed species, gravity- and explosion-dispersed species are difficult to disperse across long distances or across patches (López-Martínez et al., 2013). Wind-dispersed species generally have a long dispersal distance, however, microenvironments such as eddies, turbulence, or downdrafts created by high buildings and forest edges likely capture their seeds and limit their long-distance dispersal in urban landscapes (Du, Mi, & Ma, 2012; Diogo, Fortunato, & Costa, 2015). In this study, however, we did not sample forest edge which might capture more seeds, especially those of wind-dispersed species than interior forests. As such, our design might underestimate the natural regeneration potential, particularly with respect to wind-dispersed species. These edge related effects as well as local processes such as seed and habitat limitation might further modulate natural regeneration patterns in urban forests (Piana et al., 2019). After seed dispersal, species require a suitable place to recruit. In highly-isolated forest patches, certain species required specific habitat conditions. In less-isolated forest patches, specific conditions may be less important if there is a high frequency of dispersal from other surrounding forests. This leads to both animal- and nonanimal-dispersed species showing a strong community shift across the three plant life stages.

We conclude that multiple factors influence the natural regeneration of urban forests. Reforestation interventions have long term effects on natural regeneration of urban forests which are additionally modulated by fragmentation and seed dispersal modes. Animal-dispersed plant species will become dominant in urban forests over time, while nonanimal-dispersed species will be lost when no additional conservation practices are applied. Nevertheless, our study highlights important factors contributing to the natural regeneration of urban forests at the landscape level. Future research on local processes such as seed production, seed dispersal and seedling recruitment across different microhabitats in each forest patch, could provide additional insight about whether weak recruitment of nonanimal-dispersed trees is mainly from seed or habitat limitations in fragmented urban forests. City managers aiming at establishing forests with high biodiversity in the long term need to be aware of the dispersal ability and recruitment potential of alternative plants in fragmented forests.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A

Table A

Appendix B

Fig. B

Appendix C

Table C4

Appendix D

Table D5

References

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