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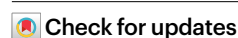
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Response and sensitivity of urban plants with different seed dispersal modes

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Spontaneous plants, those not planted by people or remaining from before urbanization, are vital to urban biodiversity. Their distribution in urban systems is affected by seed dispersal mode and environmental factors such as natural dispersal limitation and habitat quality factors. We assessed four seed dispersal modes in 16 cities in Yunnan province, the most biodiverse province in China. Autochory, in which plants eject seeds or otherwise power their seeds' dispersal, was the dominant seed dispersal mode of urban spontaneous plants in most cities (13 out of 16), whereas hydrochory, or passive seed dispersal by water, was the least frequent. Our research showed spontaneous plants in urban ecosystems adopt convergent strategies to address environmental stressors. The number of urban plants was significantly higher in colder and more-humid climates but decreased with increased dispersal limitations and reduced habitat quality. Sensitivities to these factors varied, with autochory especially sensitive to dispersal limitation and hydrochory sensitive to habitat quality and climate. Findings suggest improving habitat quality and creating green corridors would enhance conservation efforts for urban biodiversity.

The seed dispersal mode is a crucial trait that determines the response of species to environmental changes and is therefore considered as a main driver of biodiversity patterns¹. Urban areas are complex systems characterized by a myriad of environmental factors that affect the distribution of plant species². The land-use and disturbance characteristics of urban regions are complex, and the highly intricate factors that influence the seed dispersal of species, such as climate, altitude and urbanization, make the pattern even more complex³. Moreover, the response of a species to these environmental factors is also affected by seed dispersal mode⁴. For example, plants with self-dispersal modes

(including gravity and explosive dispersal, hereafter autochory) are typically more sensitive to habitat fragmentation and urbanization than species that rely on wind dispersal (that is, anemochory)⁵. This disparity may lead anemochory to have a higher chance to become widespread and dominant in urban environments than species that rely on autochory^{6,7}. Additionally, plant species that highly rely on specific habitats, such as water dispersers (that is, hydrochory), are particularly susceptible to watery habitat loss⁸, whereas species dispersed by animals (that is, zoochory) are affected by local fauna populations and diversity^{9,10}. Therefore, the disparate responses of species with

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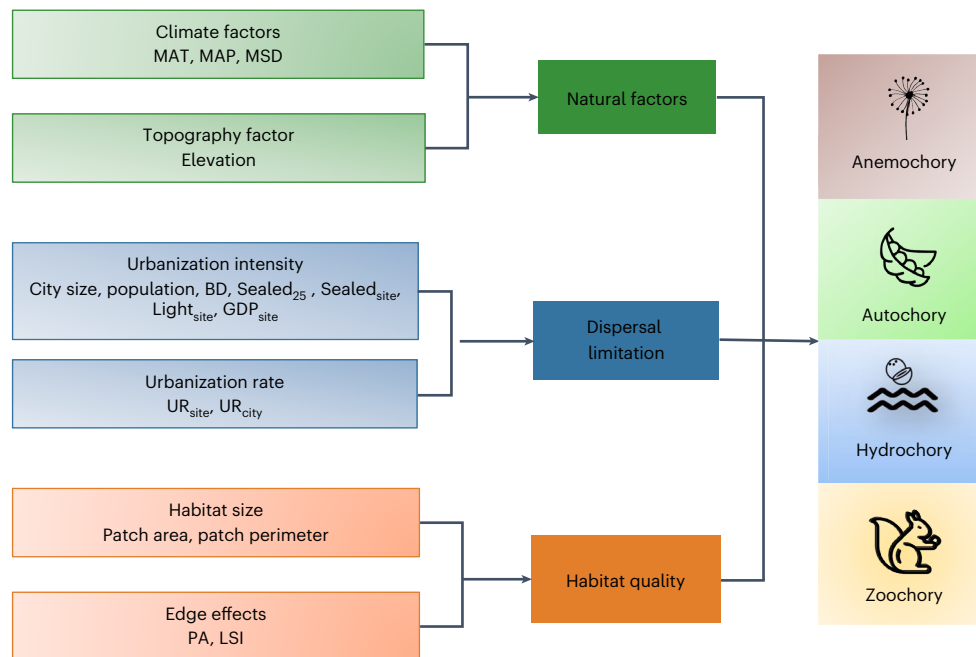


Fig. 1 | The conceptual framework of urban spontaneous plants with different seed dispersal modes and corresponding drivers of species richness. The conceptual framework of urban spontaneous plants with different seed dispersal modes and corresponding drivers of species richness. MAT, mean annual temperature; MAP, mean annual precipitation; MSD, mean annual duration of sunshine; Sealed₂₅, the proportion of impervious surface within a radius of 25 m

around the patch; Sealed_{site}, the proportion of impervious surface within site; Light_{site}, nighttime light intensity in each site; GDP_{site}, gross domestic product in each site; UR_{site}, urbanization rate in each site; UR_{city}, urbanization rate in each city; BD, distance of patches from city boundary; PA, perimeter-area ratio; LSI, landscape shape index.

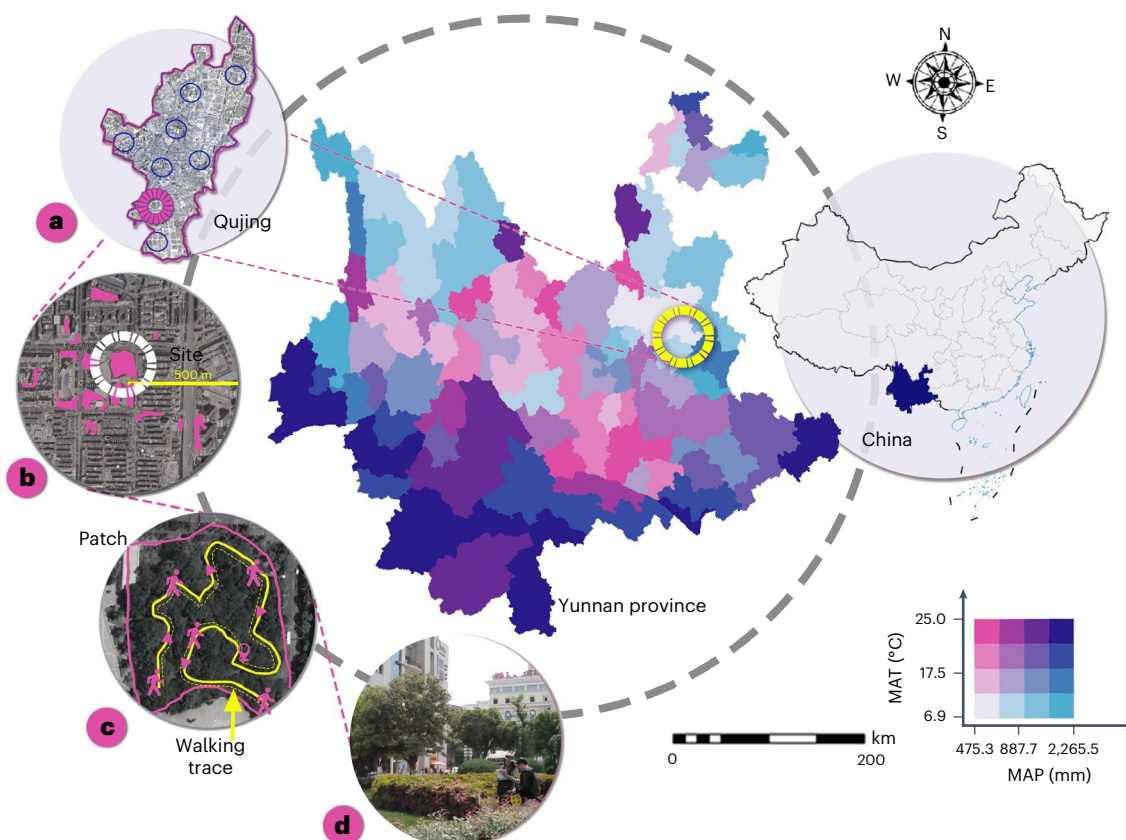


Fig. 2 | The sampling sites and patches in the 16 prefecture-level cities in Yunnan province, China. Sampling strategy in the 16 prefecture-level cities in Yunnan province, China. **a**, In each prefecture-level city (example city of Qujing), sampling sites were established at set intervals from the city's center. **b**, At

each site, more than three green patches were randomly sampled for a survey of species diversity. **c,d**, The walking trace (**c**) and photo (**d**) are shown for an example patch.

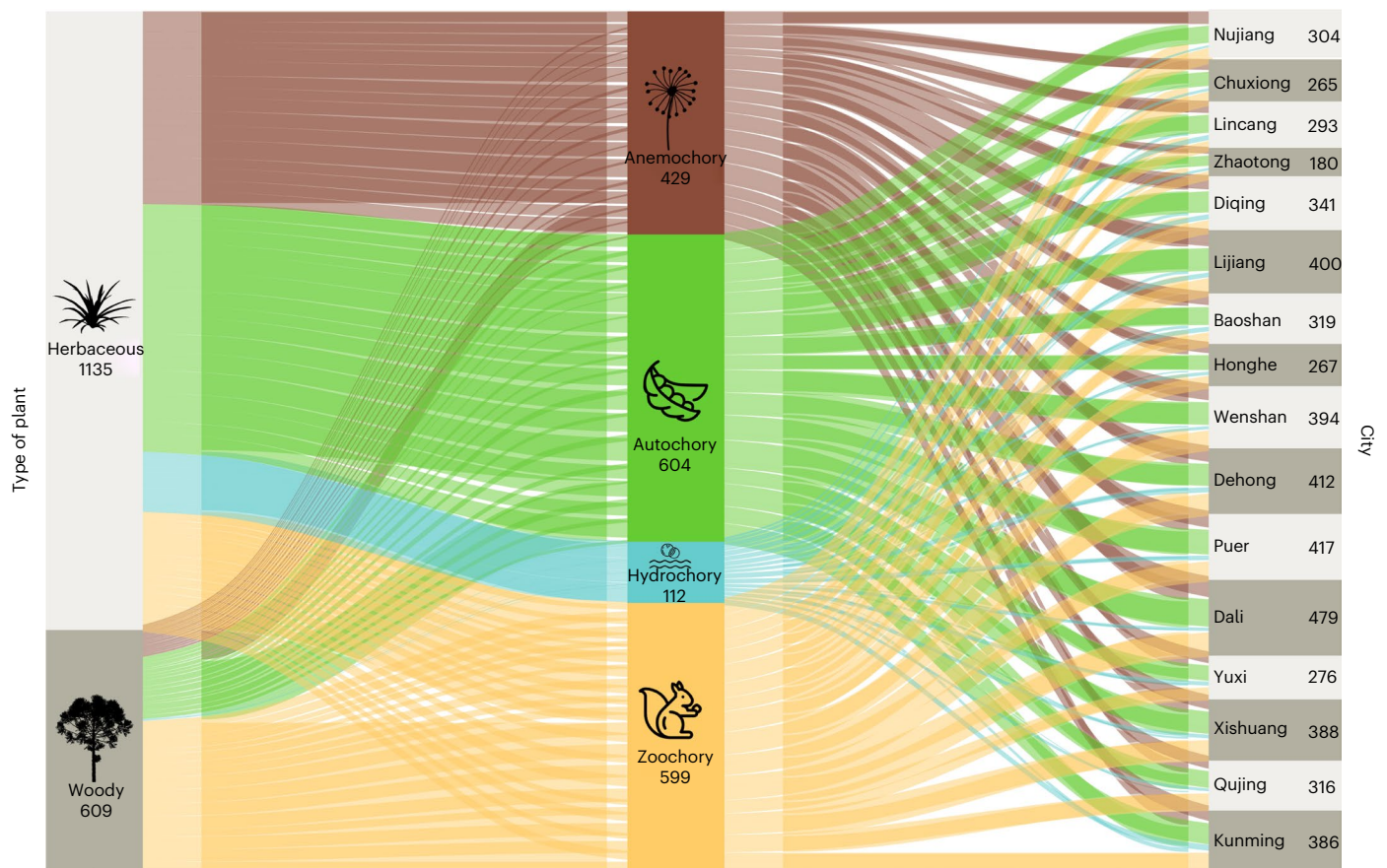


Fig. 3 | Sankey chart of species composition in 16 cities surveyed in Yunnan province, China. The number represents spontaneous species richness. Different colors represent various seed dispersal modes, while alternating greyscale shading widths indicate the magnitude of species richness.

different seed dispersal modes are considered as the main driver of local biodiversity patterns^{11,12}. Nonetheless, we lack a comprehensive understanding of the diversity patterns and drivers of plants with different dispersal modes in urban environments.

Beyond dispersal capability, successful dispersal to a new habitat is also affected by environmental factors¹³. Several classic theories and framework have postulated that dispersal is affected by the size of the habitat (the species–area relationships^{14,15}), the distance between habitat islands and species pools (the island biogeography theory¹⁶), the degree of isolation (metapopulation theory¹⁷), urban–rural gradient¹⁸, edge effects and matrix properties (the patch–matrix perspective¹⁹). Furthermore, the response of plants to environmental changes may have ‘lag effect’, resulting in ‘extinction debt’ or ‘invasion debt’^{20–22}, therefore the historical process can also affect biodiversity pattern²³. At the regional scale, species dispersal is also affected by climatic and topographic factors, such as temperature, precipitation and elevation²⁴. Whereas numerous studies have assessed factors that affect species dispersal, it remains unknown how these factors interact, and a comprehensive investigation into urban ecosystems is lacking.

Urban spontaneous plants form an important part of urban vegetation. They are not intentionally planted yet are also not part of the remaining natural vegetation, as they have established throughout urban environments on their own accord²⁵. These plants can rapidly respond to disturbances, making them effective indicators for the urbanization process²⁶. In recent years, urban spontaneous plants have gained increasing attention as the optimal material and life landmark for enhancing resilience and sustainability of native plant communities^{27–29}. To help elucidate the mechanisms of species dispersal, we use urban spontaneous plants as a model species group to integrate

urbanization characteristics and climatic factors in urban ecosystems. Using a survey of spontaneous plants in 16 prefecture-level cities in Yunnan province, the most biodiverse province of China, we systematically analyze the relative contribution of three types of environmental driver (Fig. 1; natural factors, dispersal limitation and habitat quality) to diversity patterns of spontaneous plants with different seed dispersal modes. Our aims are: (1) to clarify the composition pattern of the life form and seed dispersal modes of urban spontaneous plants in 16 prefecture-level cities in Yunnan province, China; (2) to explore the differences in sensitivity among spontaneous plants with different dispersal modes to environmental factor; (3) to disentangle the relative contribution of environmental factors to diversity patterns of spontaneous plants with different seed dispersal modes.

Results

Across the 16 major cities surveyed in Yunnan province, we recorded 1,744 spontaneous plants species (including infraspecific taxa, such as 14 subspecies, 57 varieties and 6 forms) of 916 genera and 175 families (Fig. 2). Whereas the genetic similarity between subspecies and varieties is relatively high, different forms of the same species may still have varied responses to different levels of urbanization. As a result, in this study, these forms were treated as separate species. Of all species, 1,135 were herbaceous (65.1%) and 609 were woody plants (34.9%). Autochory was the most frequent seed dispersal mode (604 species, 34.6%), followed by zoochory (599, 34.4%), anemochory (429, 24.6%) and hydrochory (112, 6.4%). Plant species richness among the 16 surveyed cities varied from 180 in Zhaotong city to 479 in Dali city. The species composition of Chuxiong city (34.3%), Dehong city (34.5%) and Qujing city (35.1%) was dominated by zoochory, whereas other cities

were all dominated by autochory ($\geq 33.5\%$). In addition, anemochory varied between 23.5% and 27.6%, and hydrochory constituted less than 10.9% of all species surveyed (Fig. 3).

The model showed natural factors (that is, MAT and MAP), dispersal limitation factors (BD) and habitat quality variables (patch area) significantly correlated with spontaneous plant diversity. The model included significant interaction terms with dispersal mode and patch area, LSI, BD, GDP_{site}, city size, UR_{city}, MAP and MAT, indicating substantial evidence for disparate responses of various dispersal modes to these variables (Table 1).

Results of contrasts showed that the effect of patch area differed significantly among all seed dispersal modes, except for non-significance difference between anemochory and autochory (Fig. 4). Specifically, patch area showed the strongest positive effects on the richness of hydrochory and the least effects on anemochory. The effect of LSI showed more negative effects on the richness of hydrochory than other seed dispersal modes. The negative effect of BD on richness was significantly stronger for hydrochory and zoochory, compared to that for autochory and anemochory. The positive effect of GDP_{site} on richness was stronger for zoochory than for any other seed dispersal modes. The effect of city size on richness exhibited significant variations between zoochory and autochory and between anemochory and autochory. Notably, autochory showed stronger negative response to city size compared to both zoochory and anemochory. The effect of UR_{city} on richness showed the weakest negative effects on the anemochory than any other seed dispersal modes. The positive association between MAP and hydrochory was the strongest compared with other seed dispersal modes. Lastly, hydrochory showed the highest significant negative association with MAT compared with the other three dispersal modes (Fig. 4).

Detailed assessment of the separate GLMM for different seed dispersal modes showed that the combination of habitat quality, dispersal limitation and climate factors explained the richness of each seed dispersal mode of spontaneous plants well (R_m^2 ranges between 0.46 and 0.56, R_c^2 ranges between 0.69 to 0.86). Anthropogenic factors (including habitat quality and dispersal limitation) were the dominant drivers for the richness of all categories, accounting for over 66.57% of the fixed effects for each seed dispersal mode. Habitat quality (expressed as patch area and LSI) explained 54.36% (anemochory), 46.29% (autochory), 40.33% (hydrochory) and 52.73% (zoochory) of the variation in the richness of each seed dispersal modes. In contrast, anthropogenically driven dispersal limitation (expressed as BD, Sealed₂₅, Sealed_{site}, Light_{site}, GDP_{site}, UR_{site}, city size and UR_{city}) explained the variance 16.44%–anemochory, 28.91%–autochory, 26.24%–hydrochory and 31.18%–zoochory, respectively. Natural factors (MAP and MAT) explained 29.19% (anemochory), 24.79% (autochory), 33.43% (hydrochory) and 16.09% (zoochory), respectively (Supplementary Table 1 and Fig. 5).

Discussion

Despite increased attention on spontaneous plants in urban ecosystem studies and the importance of seed dispersal in biodiversity patterns generally, our knowledge on the distribution pattern and drivers of spontaneous plants with different seed dispersal modes is still lacking. Our study investigated the diversity patterns of spontaneous plants with different seed dispersal modes in the 16 prefectural-level cities of Yunnan province, China, and the importance of drivers related to natural factors, dispersal limitation and habitat quality. Our study highlights that while the richness of species with different dispersal modes is generally correlated with a similar combination of external drivers, the sensitivities among different dispersal modes to these factors vary.

Given the varying properties of species with different seed dispersal modes, including their dispersal distance, seed mass, seed quantity and seed morphology³⁰, it is expected that some species are more susceptible to fragmentation than others^{7,12,13}. For example, self-dispersed

Table 1 | Model summary of the final generalized linear mixed-effects model (GLMM) including the main effects of habitat quality, dispersal limitation and climate factors and their interactions with seed dispersal modes of spontaneous plant species

	Main effects and interactions	χ^2	Df	Pr ($> \chi^2$)
Habitat quality	Dispersal modes	6,303.49	3	<0.001***
	Area	602.45	1	<0.001***
	Dispersal modes: area	87.13	3	<0.001***
	LSI	0.94	1	0.333
	Dispersal modes: LSI	18.29	3	<0.001***
Dispersal limitation	BD	0.89	1	0.345
	Dispersal modes: BD	14.31	3	<0.05*
	Sealed ₂₅	1.94	1	0.163
	Sealed _{site}	1.48	1	0.224
	Light _{site}	1.97	1	0.161
	GDP _{site}	0.30	1	0.584
	Dispersal modes: GDP_{site}	19.99	3	<0.001***
	City size	16.74	1	<0.001***
	Dispersal modes: city size	11.92	3	<0.05*
	UR _{site}	0.00	1	0.945
	UR _{city}	2.49	1	0.114
	Dispersal modes: UR_{city}	48.79	3	<0.001***
Climate factor	MAP	30.62	1	<0.001
	Dispersal modes: MAP	38.59	3	<0.001***
	MAT	10.13	1	<0.005**
	Dispersal modes: MAT	35.62	3	<0.001***

Note: Df, the degrees of freedom for error; Pr, p values; bold text in the table means significance ($p < 0.05$); *, $p < 0.05$; **, $0.05 < p < 0.01$; ***, $0.01 < p < 0.001$.

species (autochory) may have more limitation in dispersal distance than wind-dispersed species (anemochory) and hence one may expect that autochory are more sensitive to fragmentation. Despite the highly fragmented landscape in urban systems, we found that species exhibiting autochory dispersal dominated the flora in most of the studied cities (13 out of 16 cities), whereas anemochory composed a relatively lower proportion in all cities. As expected, hydrochory comprised the smallest proportion of the urban floras, presumably due to urbanization-caused wetland habitat loss in urban areas⁸.

Habitat quality determines the extent that plants can obtain resources from the focal patches. Our results showed that larger patches contained higher richness in all groups of plants, following many other studies^{14,16,31}. However, trends differed significantly among the various groups, suggesting that the influence of patch area varies with different seed dispersal modes, which showed the strongest positive effects in hydrochory, followed by zoochory, autochory and, lastly, anemochory. Additionally, zoochory and anemochory responded more positively to LSI than hydrochory. The relative importance of habitat quality was the lowest for the richness of hydrochory, compared to species with other seed dispersal modes. Hence, though hydrochory appears most responsive to patch area, the explanatory power of this relationship was low. This disparity indicates the importance of

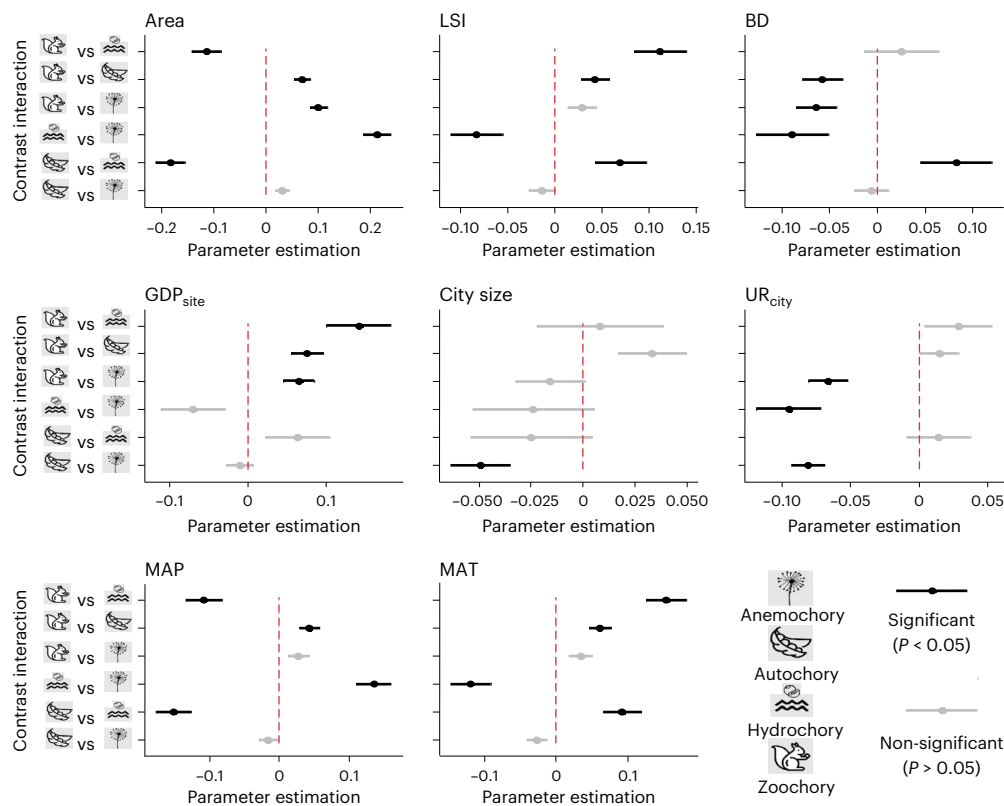


Fig. 4 | Contrast interactions estimate between different seed dispersal modes. Hydrochory showed the highest significant negative association with MAT compared with the other three dispersal modes.

conducting a comprehensive analysis, considering not only the driving factors and but also their relative contributions.

Given that the studied cities expand in concentric rings and are encompassed by natural mountains, our measure of distance to city BD conveyed not only the intensity of urbanization but also the difficulty of accessing the natural species pool²³. As hydrochory heavily relies on wet habitats^{1,12,32}, hydrochory showed decreased richness with increasing BD, contrasting to other seed dispersal modes. The diminishing presence of water bodies as we move towards city centers and the stronger dispersal barriers between water bodies in increasingly highly urbanized areas may contribute to the lower richness of hydrochory in urbanized regions³³. Indeed, spontaneous plants with different dispersal modes showed significantly decreased richness along increasing city size. Moreover, autochory demonstrated a more negative response to city size in comparison to anemochory, suggesting an elevated sensitivity to urbanization. As urbanization intensifies, there is a concurrent rise in fragmentation levels, indirectly affecting species with short dispersal range, such as autochory^{34,35}, and the processes may potentially amplify the sensitivity of short dispersal species to city size. For zoochory, we found the strongest positive effects of urbanization intensity, as represented by GDP_{site} on zoochory diversity. Zones with higher economic development may provide a more favorable environment for zoochory, as well-maintained urban parks and green spaces in these areas can support a diverse fauna to disperse seeds of zoochory.

Additionally, a higher urbanization rate (UR_{city} and UR_{site}) may lead to more frequent and unstable disturbances, potentially giving rise to 'extinction debt' or 'invasion debt' issues and affect biodiversity^{20,22}. Therefore, the current biodiversity pattern is jointly affected by both present status and historical process of urbanization²³. Collectively, our findings highlight urbanization rate as significantly shaping the richness of autochory and zoochory, while having the least impacts on

anemochory. Anemochory has long been regarded as possessing the capacity for sustained resistance to adverse environmental stressors with a longer dispersal range and a larger quantity of seeds, which makes them appear to be less sensitive to the current and historical urbanization process^{4,36}. Overall, our study underscores the significant impact of dispersal limitation on the diversity of spontaneous plants with different seed dispersal modes. We suggest that augmenting the number of wetland habitats in urban areas holds the potential to boost the richness of hydrochory. Additionally, the creation of corridors between urban and natural areas to reduce dispersal limitation emerges as a critical strategy for enhancing and conserving urban biodiversity.

Through acting as the first-level environmental filter, climate factors influence the regional species pool and ultimately affect the biodiversity pattern³⁷. The results of our study demonstrate significant positive impacts of precipitation on all groups of spontaneous plants. Similar trends were also found in research on the diversity of urban vegetations in seven cities in the United States³⁸. Higher precipitation was also associated with increased urban plant richness across ten cities in Kazakhstan³⁹, 18 cities in China⁴⁰ and 117 urban yards from six metropolitan areas in the United States⁴¹. However, our study showed a significant negative impact of temperature on the richness of autochory and hydrochory. In contrast to MAP, species diversity reduced in cities with high MAT, presumably due to accompanying drought conditions^{38,42}. In addition, the divergent trends in climate factors revealed that hydrochory showed the strongest positive relationship with MAP and strongest negative relationship with MAT compared to plants with other seed dispersal modes. Evidently, lower precipitation and higher temperature jointly contribute to more arid environments, consequently impacting plant richness, particularly for hydrochory, which heavily relies on wet habitats. Furthermore, we infer that due to the restricted dispersal distance, autochory faces challenges in achieving long-distance migrations across climatic zones, rendering it more

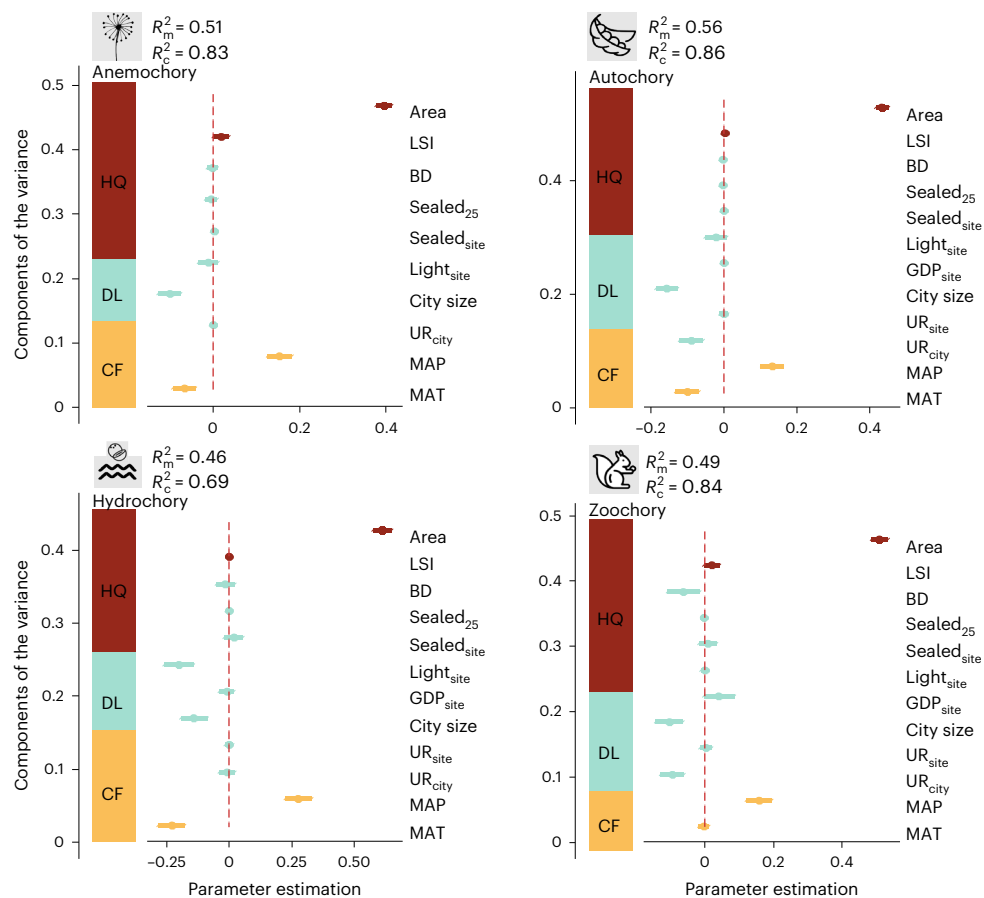


Fig. 5 | Averaged models for each seed dispersal mode. Parameter estimates and variance explained in the averaged model for each seed dispersal mode. Parameters are classified into three groups: habitat quality (HQ), dispersal limitation (DL) and climate factors (CF).

susceptible to the influence of climate compared to anemochory and zoochory. The findings of our study indicate that the ongoing rise in global temperatures may exacerbate the decline of plant diversity in urban areas and that hydrochory and autochory can be more sensitive than others. This underscores the need to implement effective conservation measures to preserve urban biodiversity in the face of climate change.

The study revealed significant interactions between seed dispersal modes and environmental factors. The divergent trends of environmental drivers among the different seed dispersal modes, indicating that different plant groups exhibit varied degrees of sensitivity to the environment. However, a more in-depth analysis of spontaneous plants with different seed dispersal modes showed that the drivers of diversity patterns within each group are similar, except GDP_{site} was not retained on the model of anemochory and autochory and UR_{site} was not retained on the model of anemochory. The natural factors (such as climate) and anthropogenic factors together shape the diversity pattern of urban spontaneous plants with different dispersal modes, however anthropogenic factors such as habitat quality and dispersal limitation played an overwhelming role. A study of urban plant diversity patterns in 110 cities globally revealed that anthropogenic features were the dominant driver⁴². Additionally, the combination of factors affecting different group of plants in urban areas aligns with observations in other studies, such as those conducted in Kunming city of China⁴³ and a study on vascular plants in 60 European cities⁴⁴. These results indicate that spontaneous plants in heavily disturbed artificial ecosystems such as urban areas tend to develop convergent strategies to cope with environmental stressors despite the various sensitivities among different dispersal modes to these factors. Therefore, to maximize the

conservation of urban biodiversity, in addition to improving habitat quality and reducing dispersal limitations, we should also consider the different dispersal modes of species, which require distinct management interventions.

Our study found that prediction variables, such as climate and GDP, collected at coarse spatial resolution, significantly contributed to variations in plant richness within green patches. However, those prediction variables derived from national datasets are known to lack precision in urban areas due to the heterogeneity of urban systems, introducing uncertainties into the models. Future large-scale research could benefit from incorporating urban-specific fine-scale data, such as urban surface temperatures and building density, to improve predictions of urban biodiversity. Additionally, using a Bayesian hierarchical model could help account for uncertainty in predictors by modeling them as true values with associated error terms⁴⁵.

Methods

Study area

Our study was carried out in Yunnan province, China (21° 8' 32" N–29° 15' 8" N, 97° 31' 39" E–106° 11' 47" E, total area 394,100 km²), which has complex topography with significant variation in altitude (77–6,740 m), temperature (average annual temperature 1.5–24 °C) and precipitation (total annual precipitation 580–2,700 mm) across its territory⁴⁶. Yunnan's diverse topography and elevational profiles create intricate meteorological climate dynamics across both horizontal and vertical gradients and result in a broad spectrum of climates. These range from extremely hot and moist zones (average temperature of 24 °C) at low elevations (below 100 m) to extremely cold zones (average temperature of 1.5 °C) at high elevations (up to 6,700 m) (ref. 47).

Additionally, Yunnan province can be categorized into seven distinct climate types from south to north: northern tropical, southern subtropical, mid-subtropical, northern subtropical, southern temperate, mid-temperate and alpine mountainous regions⁴⁸. These climate zones span nearly all major climate types found throughout China. Two of the world's 36 biodiversity hotspots—the mountains of Southwest China and Indo-Burma—partially drop within Yunnan province. Furthermore, the northwestern border of Yunnan is adjacent to the Himalayan biodiversity hotspot^{49,50}. The diverse natural environmental conditions contribute to Yunnan province status as the most biodiverse province in China. The province comprises more than 51.6% ($\geq 18,000$ species) of all higher plants recorded in China, despite occupying only 4.1% of the total territory area of China⁵¹. Additionally, the unique terrain and climate conditions of each city in Yunnan province have also led to distinct urbanization processes. These extensive and diverse environmental gradients present an exceptional place to study urban ecology. Spontaneous plants were sampled across all 16 prefecture-level cities, which are widely distributed along natural and urbanization gradients. In each city, sampling sites with a 500 m radius were established at about 2 km intervals from the city center to the outskirts. At each sampling site, more than three accessible green patches were randomly selected for a species richness survey (Fig. 2 and Supplementary Table 2). In total, 893 patches were surveyed in this study, with the mean patch area ranging from 0.15 ha to 2.9 ha in each city.

Data collection

Field surveys of spontaneous plant species were conducted during the growing season between April and October in 2017–2018 (one city), 2019 (eight cities) and 2022 (seven cities), following the sampling protocol by Gao et al., (2021; 2023). Our analysis focused solely on vascular spontaneous plant species within each patch. In this context, naturally occurring herbaceous plants, which have traditionally been described as 'weeds', 'ruderal plants' or 'escaped plants' and could be easily distinguished from the cultivated planted species. For woody plants, we classified spontaneous pioneer woody plants (such as *Broussonetia papyrifera* and *Buddleja officinalis*), and the seedlings of woody plants that can be clearly distinguished from cultivated plants in all urban manmade green patches were categorized as spontaneous species^{23,43}. Notably, trees of diameter breast height (DBH) ≥ 1 cm or shrubs of basal diameter ≥ 1 cm were excluded from further analysis to avoid potential bias. This exclusion is due to the frequent use of large woody saplings in urban greening, which makes it challenging to distinguish whether they were intentionally planted or occurred spontaneously. However, all woody plants growing on specific habitats such as abandoned lands, roofs and walls are usually naturally colonized and identified as spontaneous. Plant identification was conducted by the same researcher across all patches following identification standards specified in Chinese plant science data (<https://www.iplant.cn/>). The practice helped reduce identification bias. When encountering an uncertain species in the field, we took an in situ photograph (over 10,000 pictures) and take the specimen for subsequent experts' taxonomic identification in the laboratory. All the collected specimens were preserved as herbarium (in total 777 species), along with their digital scans, which can be partly used for future research and cross-validation of taxonomic classifications (the data are publicly available via figshare at <https://doi.org/10.6084/m9.figshare.27292317.v1>).

The seed dispersal modes of species are typically classified into four categories: anemochory, autochory, hydrochory or zoochory³². First, we determined the seed dispersal modes of the plant species by referring to published literature^{1,52,53}, International Network for Seed Based Restoration and Royal Botanic Gardens Kew (<https://ser-sid.org>). If not found in the literature or the database, a species' seed dispersal mode was determined based on fruit type and characteristics. For instance, species with fleshy fruits and nuts will attract

birds and other fruit-eating animal (such as bats and rodents) and are subsequently (accidentally) dispersed; these were categorized as zoochory. Seeds or fruits with special structures, such as mucilage or hooks, that adhere to animals for dispersion, as observed in *Bidens pilosa* and *Xanthium strumarium*, were also classified as zoochory. Adaptations representing wind dispersal include dust-like seeds (for example, the small and lightweight seeds, such as most of species in Asteraceae family), balloon-like structures (for example, genus *Koeleuteria*), winged structures (for example, genus *Acer*) or seeds with a tuft of hairs (as found in *Taraxacum* genus). Species with mechanisms such as seed pod explosion (where seeds are propelled when the fruit, often a capsule, bursts open, as seen in the *Echallium* genus) or seeds simply dropping to the ground due to their weight (as genus *Cocos*, were assigned to autochory. The seeds of hydrochorous species can float in water, allowing them to be carried to different locations by rivers and other water bodies. If multiple dispersal modes were addressed for the one species, only the main dispersal mode was used in our analysis. For instance, the seeds of *Cocos nucifera* can be dispersed by both gravity and water, but observations in urban areas suggest their dispersal there is mainly by gravity, resulting in an autochory classification in our research.

The potential environmental drivers of species richness were divided into three groups: natural factors, dispersal limitation and habitat quality (Fig. 1). The natural environmental factors were sourced from the Resource and Environmental Science Data platform (mean value of 1960–2021, <https://www.resdc.cn/DOI/DOI.aspx?DOIID=96>, 1 km resolution), including MAT, MAP, mean annual duration of sunshine and elevation. The annual spatial interpolation dataset of Chinese meteorological elements is created using the Anusplin interpolation software, based on the annual values of various meteorological elements from over 2,400 stations across China. This dataset provides spatially interpolated meteorological data for each year since 1960. It features higher interpolation accuracy and smoother results, particularly excelling in describing the zonal distribution characteristics of meteorological elements. Habitat quality was represented by patches' properties, including patch area, patch perimeter, perimeter-area ratio and LSI ($LSI = \text{Perimeter} / (2\sqrt{\pi \times \text{Area}})$), which were calculated by ArcGIS 10.3⁵⁴. Dispersal limitation factors are mainly characterized by urbanization index, including urbanization intensity and urbanization rate²³. As urban areas are in rapid expansion, the frequency of habitat disturbances increases, subsequently intensifying species' dispersal limitations. Additionally, as the level of urbanization changes, the intensity of human management in corresponding urban areas also varies. For example, areas with higher gross domestic product often have more frequent practices such as weeding and fertilizing. To represent current urbanization intensity, we used Sealed₂₅⁴³, BD, Sealed_{site}, Light_{site}⁵⁵ (1 km resolution), GDP_{site}⁵⁶ (1 km resolution), city population and city size. City size was calculated by moving windows (1 km $\times$ 1 km, threshold = 50%, 2020); Population data were collected from 'Chinese population census yearbook 2020'. To estimate the Sealed₂₅ and Sealed_{site} the Maximum Likelihood Classification approach (a supervised classification in ArcGIS 10.3) was used to classify high-resolution aerial orthophotos of Google Earth (RGB, 2018, 0.14 m resolution). We represented urbanization rate by quantifying the sealed surface expansion rate of each city (that is, UR_{city} and UR_{site}) between 1990 and 2019 using land-cover data with a resolution of 30 m (ref. 57).

Data analysis

To check whether the responses of spontaneous plant richness to driving factors differ among dispersal modes, GLMMs were used to analyze the driving factors of the richness of species with the four seed dispersal modes: anemochory, autochory, hydrochory and zoochory. We fitted a model with species richness as the response variable, using a Poisson distribution and *glmer* function within R package lme4

(version 1.1–35.1)⁵⁸ with patch ID nested within site ID and site ID nested within city ID as random effect (1|patch ID/site ID/city ID). As fixed effects, we used all natural factors, dispersal limitation and habitat quality described above and the interaction between these factors and seed dispersal modes (hereafter called ‘full model’). To start, the independent variables were standardized and centered to ensure uniform dimensionality. To avoid collinearity, if the correlation coefficient between independent variables was greater than 0.7, only the variable of the highest correlation with the dependent variables was chosen for further modeling. After model construction, the variance inflation factor (VIF) of the model was checked, and variables with VIF greater than 5 were removed from the model sequentially until all variables had a VIF ≤ 5 ^{59–61}.

Residual diagnostics of models was then checked using the *simulateResiduals* function in R package DHARMa (version 0.4.6)⁶². The *Anova* function in the R package car (version 3.1–2) was employed to assess both the main effects and interaction effects in the full model. To assess differences in the response to predictor variables between dispersal modes, we used the *emtrends* function in the R package emmeans (version 1.10.1) to compare trend estimates of for the different dispersal modes⁶³.

To further explore the driving factors within a dispersal mode, we separately ran the same GLMM analysis described above for each group. The *dredge* function in the R package MuMIn (version 1.47.5) was used on each separate model, which created a suite of models with all possible combinations of the initial variables and sorted them according to the Akaike Information Criterion (AIC). We then conducted model averaging on all models with $\Delta AIC < 2$ using the function *model.avg*⁶⁴. We used the *r.squaredGLMM* function in the R package MuMIn to calculate R^2 , then manually performed variance decomposition to assess the relative contribution of each driving factor and the random effects^{37,65}. We ran all analyses using the software R 4.3.2⁶⁶.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data and codes that support the findings of this study are publicly available via figshare at <https://doi.org/10.6084/m9.figshare.27292317.v1> (ref. 67). Original photographs, collection numbers and scanned images of the herbarium specimens created during our study (currently housed at Kunming Institute of Botany) can also be obtained from the corresponding author upon request.

Code availability

The code that supports the findings of this study is available via figshare at <https://doi.org/10.6084/m9.figshare.27292317.v1> (ref. 67).

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Competing interests

The authors declare no competing interests.

Additional information

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