



Report

A lack of shade-tolerant plant species in the species-pool of urban parks results in degradation of ecosystem services under tree canopies

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Abstract: The herbaceous vegetation layer in urban parks provides ecosystem services that include places for people to sit on the ground, prevention of mud and dust formation, prevention of soil erosion, and flood prevention via increased rain infiltration. Species composition in green spaces in urban areas varies owing to differences in their histories. In newly developed parks on reclaimed land, shade-tolerant native species that grow on the forest floor in 'satoyama', or remnant vegetation, may be absent from the species pool, leading to concerns that the ecosystem services of the forest-floor vegetation may be degraded. In this study, we measured the ecological traits of the species pool (shade and trampling tolerance at the species-pool level) in various parks, and analysed their effects on the ground-surface leaf area index. Because trampling also affects vegetation in parks, we used soil penetration-resistance values to account for its effects. A lack of shade-tolerant species in the species pool reduced the leaf area index of forest-floor plant communities. The shade-tolerant species detected in our surveys included native species such as *Houttuynia cordata*, *Ophiopogon japonicus*, *Oplismenus undulatifolius*, *Paederia foetida*, *Pleioblastus chino*, and sedges. Species pools in parks with 'satoyama' typically included these species. Species pools containing shade-tolerant native species are important for improving ecosystem services beneath tree canopies, and we recommend conserving historical 'satoyama' to prevent the loss of native shade-tolerant floras when renovating or creating parks.

Keywords: extreme value statistics, leaf area index, satoyama traditional vegetation, shade tolerance, trampling tolerance

Introduction

Ground vegetation in urban parks includes open lawns, grasslands and forest-floor vegetation. By preventing bare ground, it provides places for people to sit (Fig. 1a), allows visitors to enter parks immediately after rainfall without encountering muddy ground, prevents dust and soil erosion, and promotes rainwater infiltration to prevent flooding (Monteiro 2017; Ito et al. 2020).

The species pool of a community at a given site is the set of species that can reach the site through seeds, rhizomes or other propagules and potentially become community members (Grime 1998; Zobel et al. 1998; Tanaka and Koike 2011; Spasojevic et al. 2018). Attempts have begun to predict the dominance of individual species in communities from the ecological traits of species in the

pool (Koike 2001; Shipley et al. 2006; Koike 2010; Tanaka and Koike 2011). Reduced functional diversity of a species pool is also considered to decrease community productivity and substantially affect ecosystem services (Hector et al. 1999; Balvanera et al. 2006).

Urban areas contain green spaces with differing species compositions that reflect their histories (Johnson et al. 2018). Some species are unlikely to expand their distributions rapidly within urban green spaces. These include ant-dispersed sedges and violets (Handel 1978; Kjellsson 1991; Ohkawara and Higashi 1994; Ness et al. 2004; Tanaka and Tokuda 2016), dwarf bamboos that reproduce primarily vegetatively through rhizomes, and species dispersed by food-caching animals whose principal seed dispersers cannot inhabit cities (Komuro and Koike

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Fig. 1. (a) People resting at a woodland edge at midday in summer. (b) A herbaceous community at a woodland edge in a park on reclaimed land with no remnant satoyama (Kiba Park).

2005). Such species are likely to be missing from species pools in newly established vegetation (Westoby et al. 1996; Komuro and Koike 2005), raising concerns about the loss of ecosystem services. Figure 1b shows a park established on reclaimed land. In such parks, vegetation is absent from shaded sites beneath the canopy, and the shade-tolerance limit of weedy species growing in sunny, disturbed habitats appears to determine the limit of ground vegetation itself. Forest-floor vegetation may fail to develop because shade-tolerant species cannot reach these sites and are consequently absent from the species pool.

In this study, we surveyed ecological traits of species pools (shade tolerance and trampling tolerance) in various parks, including parks on reclaimed land and parks containing satoyama, the traditional rural landscape, persisting since the early modern period. We analysed their effects on leaf area index, which is closely related to the ecosystem services of ground vegetation. A higher leaf area index means less exposed soil surface; thus, leaf area index is used as a proxy for ecosystem services such as erosion prevention (Xu et al. 2020). Shade tolerance is an important species trait for plant growth under light-limited canopy conditions. However, because vegetation in parks is also degraded by trampling (Morimoto and Masuda 1975; Maenaka and Okubo 1986; Cole 1995), we considered

trampling tolerance (Maenaka and Okubo 1986) as well as shade tolerance. Parks contain a mixture of woodland and grassland, and woodland edges receive seeds and rhizomes from both habitats. Along short light gradients extending from open grassland through woodland edges into woodland interiors, diverse communities develop in response to light conditions while sharing a species pool. The dominance of sun-loving species declines on the forest floor, where the effects of missing shade-tolerant species should therefore be easier to detect. We used woodland edges in urban parks to test whether a reduction in species-pool shade tolerance caused by the absence of shade-tolerant species reduces leaf area index beneath the canopy as a proxy for ecosystem services.

Methods

We selected 12 parks in Tokyo and Kanagawa Prefecture to include both parks containing satoyama that has persisted since the early modern Edo period and may have retained its flora in their species pools, and parks on land reclaimed since the modern period whose species pools consist entirely of introduced species (Table 1).

Historical satoyama and recently developed, artificially planted areas often coexist within a single park. Clonal plants that were unintentionally introduced in the root balls of planted park trees and have slowly expanded from them

Table 1. Parks surveyed. Rapid Survey Maps indicate land use in the early modernisation period. Landscapes with a mixture of woodland, rice paddies and cultivated fields were classified as satoyama (Historical Agricultural Environment Browsing System, <https://habs.rad.naro.go.jp/>, accessed 15 July 2022).

Park	City / ward	Area (m ²)	Opened	Landform	Rapid Survey Map	Park type	Transects
Isogo Umi-no-Mieru Park	Yokohama	8 306	2007	Artificial deck	Sea	Neighbourhood	4
Kuraki Park	Yokohama	230 762	1973	Hills	Satoyama	Comprehensive	6
Tomioka General Park	Yokohama	219 208	1975	Hills; reclaimed land	Satoyama; sea	Comprehensive	6
Toyosu Park	Koto	24 303	2006	Reclaimed land	Sea	Neighbourhood	6
Kiba Park	Koto	238 711	1992	Delta	Timber ponds, etc.	Comprehensive	4
Kameido Chuo Park	Koto	103 027	1980	Delta	Lowland paddies	Comprehensive	9
Minamihonjuku Park	Yokohama	49 790	2019	Hills	Satoyama	District	5
Konandai Chuo Park	Yokohama	41 400	1980	Hills	Satoyama	District	3
Kodomo Shizen Park	Yokohama	464 118	1972	Hills	Satoyama	Regional	15
Konandai Nishi Park	Yokohama	26 016	1983	Hills	Satoyama	Neighbourhood	2
Negishi Forest Park	Yokohama	193 102	1977	Hills	Fields; racecourse	Comprehensive	8
Shikinomori Park	Yokohama	453 000	1988	Hills	Satoyama	Scenic	18

can also be observed. The species pool considered here is a list of species whose propagules or clones can reach the site and potentially become members of its community (Grime 1998; Zobel et al. 1998; Tanaka and Koike 2011). A large spatial scale may be appropriate when only species with long seed-dispersal distances are involved, but a smaller scale is necessary when species with short seed-dispersal distances are present. In particular, ant-dispersed species, such as sedges and violets common on forest floors, disperse over distances of approximately 0.2–2 m (Handel 1978; Kjellsson 1991; Ohkawara and Higashi 1994; Ness et al. 2004; Tanaka and Tokuda 2016). Dwarf bamboos, which reproduce mainly through rhizomes, expand clonally at approximately 1 m per year (Tomimatsu et al. 2020). As populations expand over time (Skellam 1951), the spatial scale appropriate for a species pool increases with the time scale considered (Levin 1992). Because urban parks undergo frequent renovation (Hirata and Tachibana 2020), we adopted a spatial scale of 10 m, corresponding to approximately 10 years of spread by forest-floor species expanding at about 1 m per year. We assumed that spatially separated survey sites did not share the same species pool, even within a park. We therefore surveyed straight, 10-m transects centred on woodland edges, extending 5 m into woodland and 5 m into open grassland. Each transect was treated as one species pool, for which ecological traits were determined. This design includes species from both open habitats and beneath the canopy in each species pool.

Field surveys were conducted during the growing seasons of 2020 and 2021, from late April, when spring leaf expansion was complete, to September, when cherries (*Cerasus* spp.) began shedding their leaves. We established

84 transects in total across the 12 urban parks in the Tokyo metropolitan region (Table 1). Because planted species occur among woodland trees and canopy species composition is complex, canopy conditions were measured directly using hemispherical photographs, and canopy species were not recorded. Transects were distributed throughout each park at intervals of at least 10 m, although some were adjacent where sufficient separation was difficult. A 50 cm x 50 cm quadrat was established at every metre along each transect and treated as a local community; these are hereafter termed 50-cm quadrats. Each transect contained 11 quadrats, including both ends, giving 924 quadrats across the 84 transects.

Species dominance within each quadrat was measured by the point-quadrat method. A 15-cm pin was inserted vertically towards the ground 100 times, at 0.5-cm intervals along the line through the centre of the 50-cm quadrat, and the number of contacts with plants was recorded. The mean number of contacts per pin insertion corresponds to ground-level leaf area index, assuming horizontal leaves. Plants were identified to species wherever possible, but some could only be identified to genus because reproductive organs were absent. Woody saplings were pooled, as were dwarf turf grasses, which are frequently planted and include horticultural cultivars. The latter group comprised dwarf species such as *Zoysia* spp., *Cynodon dactylon* (L.) Pers. var. *dactylon*, *Stenotaphrum secundatum* (Walt.) Kuntze and *Eremochloa ophiuroides* (Munro) Hack.; it excluded *Lolium* spp. and *Poa* spp., which are sold as Western-style turf grasses but differ in growth form.

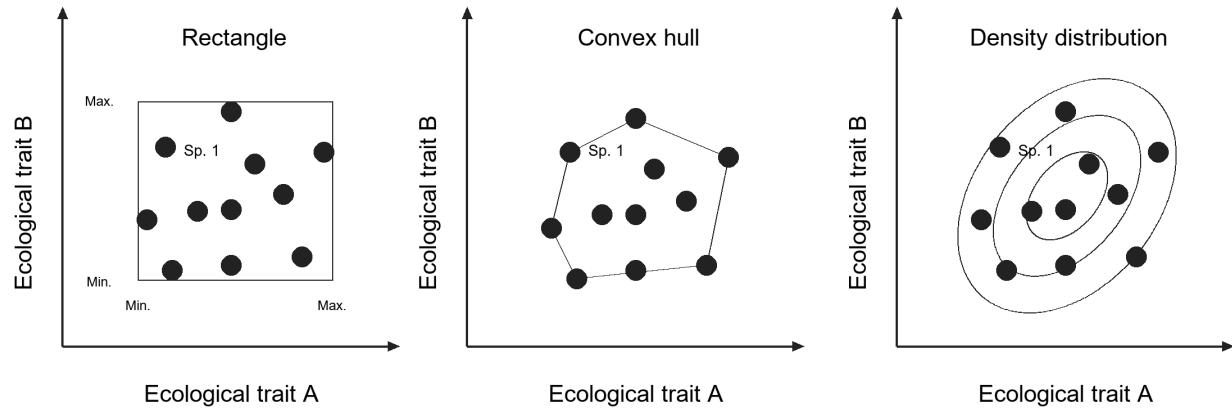


Fig. 2. Schematic representation of a species pool. Species occupy positions in a space defined by ecological traits (ecological trait space). The number of species represents diversity, and the extent of their distribution represents functional diversity (Spasojevic et al. 2018). The position and extent of a species pool can be quantified by representing the overall distribution as a rectangle, convex hull or density distribution. Community-weighted mean functional traits (Valencia et al. 2015), weighted by species dominance, are traits of a community, not of a species pool.

To measure light conditions, a hemispherical photograph was taken with a fisheye lens (Olympus Tough TG-6) above the vegetation, at a height of approximately 30 cm, at the centre of each 50-cm quadrat during the vegetation survey. Canopy openness was measured using ImageJ. Penetration resistance was measured at the same point with a Yamanaka-type soil hardness meter as an indicator of trampling.

In the analysis, shade tolerance as a species trait was defined using the light conditions (canopy openness) of the darkest 50-cm quadrat in which a species occurred along the light gradient from open grassland to woodland within each transect. This value was taken as the species' minimum canopy openness for that transect. The minimum of these values across all transects occupied by a species was then taken as its shade-tolerance value (Koike 2001). However, species occurring on more transects tend to have lower minimum openness simply because the number of occupied transects differs among species. To remove this effect, we used extreme value statistics, as employed in civil engineering to predict river discharge during a once-in-100-years flood (Gumbel 1954), to estimate the minimum openness assuming occurrence on five transects, and used this estimate as the species' shade tolerance. Specifically, we assumed a Gumbel distribution, widely used for the frequency distribution of maxima, and estimated its parameters using probabilistic modelling in Stan 2.21. We obtained an interval estimate of minimum openness and used its median as the species' shade-tolerance value (Appendix 1, Code 1). We also visually checked the suitability of the Gumbel assumption using a plot that linearises its cumulative distribution, a

method traditionally used in flood prediction. Because the Gumbel distribution here treats maxima, minimum openness was estimated as the maximum of $-\ln(\text{openness})$. Preliminary analyses showed that the cumulative distribution was linearised after logarithmic transformation but not for untransformed openness, so openness was transformed using natural logarithms. These analyses were performed for species occurring on at least four transects. Trampling was analysed similarly for the same species: an interval estimate of maximum penetration resistance assuming occurrence on five transects was used as the species' trampling tolerance.

As described above, shade tolerance as a species trait represents the light conditions of the darkest site at which a species can occur. Likewise, shade tolerance as a species-pool trait was defined as the value of the most shade-tolerant species among all species occurring in a pool (one transect). The loss of shade-tolerant species reduces the shade tolerance of the pool, making this a possible indicator of functional diversity. Species-pool trampling tolerance was similarly defined as the value of the most trampling-tolerant species among all species in the pool. This approach represents the extent of a species pool within multidimensional ecological trait space as a rectangle bounded by minima and maxima, and describes species-pool traits using extreme values (Fig. 2). Studies of alien species in various ecosystems show that adding a single alien species with an extreme ecological trait relative to the native species pool can completely alter a region's climax ecosystem. Examples include *Bischofia javanica* Blume, which replaces native climax forests in the Ogasawara Islands and becomes monodominant (Koike

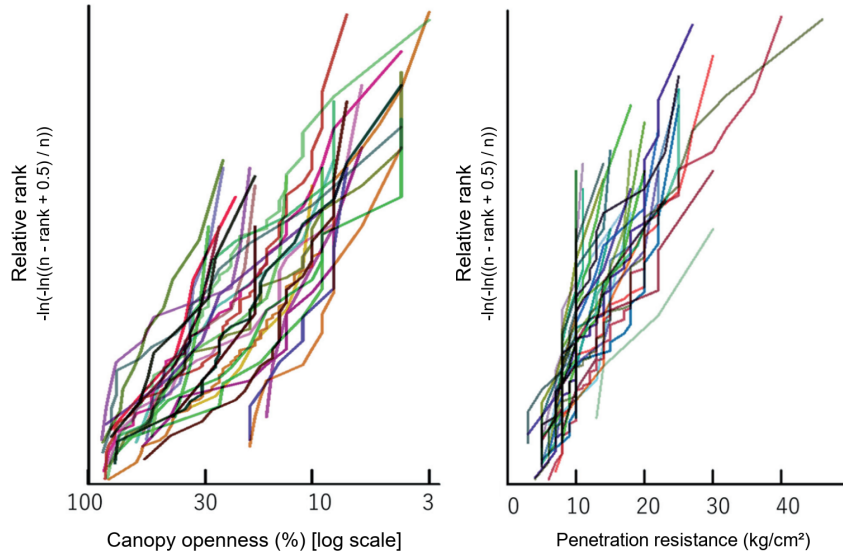


Fig. 3. Extreme value plots used to determine shade tolerance (left) and trampling tolerance (right). Each polyline represents one species; lines are longer for species with more samples and shorter for those with fewer samples. Species plotted farther to the right have higher shade or trampling tolerance. The cumulative Gumbel distribution is plotted on a linearising scale; an approximately straight line supports use of the Gumbel distribution (Gumbel 1954).

Table 2. Minimum canopy openness (%) and maximum soil penetration resistance (kg cm^{-2}) measured on each transect in parks with and without satoyama (Table 1).

Environmental value	With satoyama	Without satoyama
Minimum canopy openness per transect (%)		
Median	13	10
First quartile	9	6
Third quartile	17.5	18
Maximum soil penetration resistance per transect (kg cm^{-2})		
Median	18	18
First quartile	12.5	14
Third quartile	21	20

2001); *Pinus* spp., which have converted climax herbaceous and shrub vegetation in the Southern Hemisphere into forests (Richardson et al. 1994); and *Melaleuca quinquenervia* (Cav.) S.T.Blake, which has converted herbaceous wetlands in Florida and elsewhere into forests (Turner et al. 1998). Across communities in satoyama landscapes, from weed communities to evergreen broad-leaved forests, maximum dominance occurred at extreme values (maxima or minima) of key ecological traits, whereas maximum dominance at intermediate trait values was not observed (Tanaka and Koike 2011). Extreme values are therefore preferable to means for describing the position of a species pool in ecological trait space. Whether the maximum or minimum affects an ecosystem depends on how the trait functions within it. Convex hulls and multidimensional density distributions can describe species-pool extent in more detail (Fig. 2), but

convex hulls require simultaneous consideration of multiple ecological traits and make the description of the region more complex. Further work is also needed on multidimensional density distributions suitable for representing species pools that do not have long tails, as normal distributions do, and that readily accommodate extreme trait values.

To compare species-pool traits between parks with and without remnant satoyama, we used probabilistic modelling in Stan to compare mean shade tolerance ($\ln$ canopy openness) and trampling tolerance (penetration resistance), treating park as a random effect (Appendix 1, Code 2). To compare the probability of occurrence of shade-tolerant plants on transects in the two park types, we assumed that the frequency distribution of park-level occurrence probabilities followed a beta distribution within each type. Probabilistic modelling in Stan was used to obtain the

Table 3. Shade tolerance estimated by extreme value statistics as minimum canopy openness for occurrence on five transects, and trampling tolerance estimated as maximum soil penetration resistance. Percentiles for minimum canopy openness were calculated after transformation to $-\ln(\text{openness})$ and then back-transformed; Q1/Q3 is therefore reported as the counterpart of the interquartile range. Lower minimum canopy openness indicates greater shade tolerance; higher maximum penetration resistance indicates greater trampling tolerance. Q1, first quartile; Q3, third quartile; IQR, interquartile range.

Species	Minimum canopy openness (%)				Maximum penetration resistance (kg cm ⁻²)			
	Median	Q1	Q3	Q1/Q3	Median	Q1	Q3	IQR
<i>Houttuynia cordata</i> Thunb.	6.3	8.6	4.2	2.0	10.4	10.0	10.8	0.9
<i>Ophiopogon japonicus</i> (Thunb.) Ker Gawl.	6.6	7.6	5.6	1.4	14.4	13.2	15.7	2.6
<i>Oplismenus undulatifolius</i> (Ard.) Roem. et Schult.	6.8	8.8	5.3	1.6	11.5	10.5	12.7	2.2
<i>Paederia foetida</i> L.	7.7	10.9	5.0	2.2	15.7	13.8	19.1	5.3
<i>Pleioblastus chino</i> (Franch. et Sav.) Makino	7.9	9.3	6.6	1.4	21.4	18.5	25.1	6.6
<i>Carex</i> spp.	8.4	10.2	6.5	1.6	13.8	12.8	14.8	2.0
Woody saplings	8.9	10.8	6.5	1.6	10.9	9.9	12.8	2.9
Dwarf turf grasses	9.9	10.8	9.2	1.2	19.8	19.3	20.4	1.1
<i>Cyperus rotundus</i> L.	10.3	17.2	5.1	3.4	20.0	17.2	23.9	6.7
<i>Gamochaeta coarctata</i> (Willd.) Kerguelen	11.9	13.7	10.0	1.4	15.3	14.3	16.3	2.0
<i>Taraxacum</i> spp.	11.9	13.4	10.2	1.3	15.7	14.8	16.7	1.9
<i>Potentilla indica</i> (Andrews) Th. Wolf	12.0	17.4	7.1	2.4	14.9	13.2	18.2	5.0
<i>Oxalis corniculata</i> L.	12.5	13.9	10.9	1.3	13.0	12.4	13.7	1.3
<i>Erigeron sumatrensis</i> Retz.	14.7	18.3	10.9	1.7	13.6	12.0	15.2	3.2
<i>Plantago asiatica</i> L.	15.7	17	14.4	1.2	18.8	18.1	19.4	1.3
<i>Lysimachia japonica</i> Thunb.	15.9	19.4	12.2	1.6	10.0	9.3	10.9	1.6
<i>Poa annua</i> L.	17.7	19.4	16.0	1.2	18.3	17.5	19.1	1.6
<i>Trifolium dubium</i> Sibth.	18.8	23.2	14.1	1.6	10.4	9.7	11.2	1.5
<i>Paspalum</i> spp.	19.2	27.3	10.8	2.5	30.9	25.2	39.6	14.4
<i>Potentilla heptichigo</i> Yonek. et H. Ohashi	21.4	23.7	18.8	1.3	12.5	11.9	13.3	1.4
<i>Veronica persica</i> Poir.	21.7	25.4	17.4	1.5	13.8	12.6	15.2	2.5
<i>Trifolium repens</i> L.	22.3	23.7	20.6	1.2	15.7	15.2	16.3	1.1
<i>Erigeron philadelphicus</i> L.	22.8	28.7	16	1.8	18.5	16.4	21.8	5.4
<i>Sisyrinchium rosulatum</i> E.P. Bicknell	24.2	29.8	18.6	1.6	11.1	10.0	12.4	2.5
<i>Eleusine indica</i> (L.) Gaertn.	26.4	29.8	22.1	1.3	21.9	18.0	28.9	10.8
<i>Juncus tenuis</i> Willd.	27	30.1	23.7	1.3	15.5	14.2	17.5	3.3
<i>Digitaria ciliaris</i> (Retz.) Koeler	27.8	34.3	20.4	1.7	18.8	16.3	21.2	4.9
<i>Hydrocotyle sibthorpioides</i> Lam.	37.2	41.9	31.7	1.3	12.1	10.7	13.7	3.0

median of the frequency distribution of the mean occurrence probability for each type (Appendix 1, Code 3).

To examine the relationship between species pools lacking shade-tolerant species and the leaf area index of forest-floor ground vegetation, an indicator of ecosystem services, we fitted a Poisson generalised linear model (R 4.1.0). The response was the total number of contacts across all species in each 50-cm quadrat, based on 100 pin insertions. Explanatory variables describing the quadrat's physical environment were $\ln$ canopy openness and soil penetration resistance; those describing the biodiversity environment were species-pool shade tolerance ($\ln$ minimum openness) and species-pool trampling tolerance (maximum soil penetration resistance). Sunny park lawns

are often intensively managed through turf replacement, weeding and fertilisation. We therefore excluded quadrats outside woodlands with canopy openness greater than 50%, and analysed three datasets: quadrats with openness of 50% or less, encompassing woodland edges and interiors; quadrats with openness of 10% or less, representing dark forest floors; and quadrats with openness of 30% or less, approximately midway between 100% and 10% on a logarithmic scale.

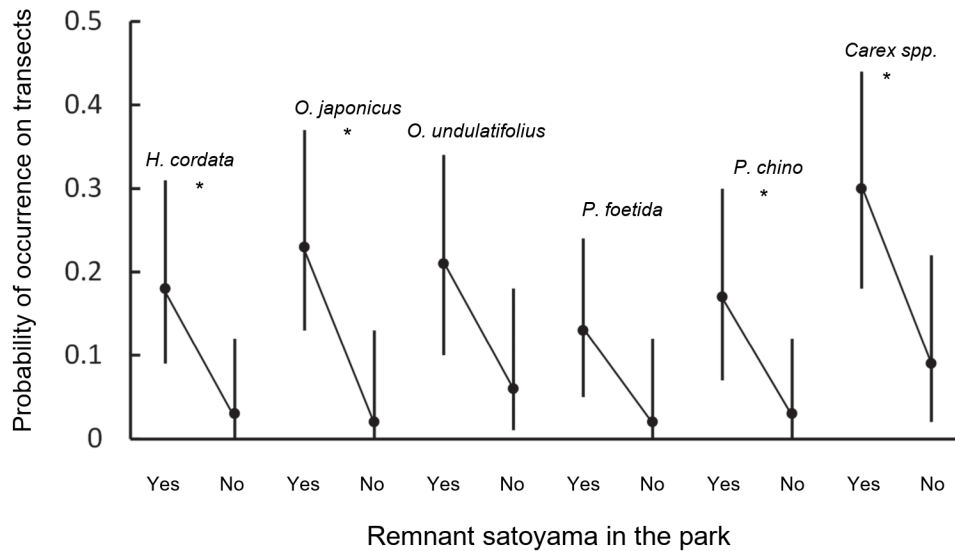


Fig. 4. Probability of occurrence on transects of shade-tolerant plants (Table 3; minimum canopy openness < 9%) in parks with and without satoyama (Table 1). Points and bars show the median and 95% range of the frequency distribution of mean park-level occurrence probability. * $P < 0.05$.

Results

The median of transect-level minimum canopy openness values, measured in the darkest 50-cm quadrat on each transect, was 13% in parks with satoyama and 10% in parks without it. No difference in environmental conditions was detected between the park types (Table 2). The median of transect-level maximum soil penetration resistance values, measured in the quadrat with the hardest soil, was 18 kg cm⁻² in both park types, again indicating no difference in environmental conditions. Seventy species were recorded in total (Appendix 2). Both log canopy openness and penetration resistance produced linearised plots in the extreme value analysis, supporting use of the Gumbel distribution (Fig. 3). *Houttuynia cordata* Thunb., *Ophiopogon japonicus* (Thunb.) Ker Gawl., *Oplismenus undulatifolius* (Ard.) Roem. et Schult., *Paederia foetida* L., *Pleioblastus chino* (Franch. et Sav.) Makino and *Carex* spp. had high shade tolerance, with minimum canopy openness of 9% or less (Table 3). *Trifolium repens* L., *Erigeron philadelphicus* L., *Sisyrinchium rosulatum* E.P.Bicknell, *Eleusine indica* (L.) Gaertn., *Juncus tenuis* Willd., *Digitaria ciliaris* (Retz.) Koeler and *Hydrocotyle sibthorpioides* Lam. had low shade tolerance, with minimum canopy openness of 20% or more. Trampling tolerance was high in *Paspalum* spp., *Eleusine indica*, *Pleioblastus chino*, *Cyperus rotundus* L. and dwarf turf grasses, whose maximum soil penetration resistance was at least 19 kg cm⁻² (Table 3). Maximum soil penetration resistance was below 12 kg cm⁻² in *Lysimachia japonica*

Thunb., *Houttuynia cordata*, *Trifolium dubium* Sibth., *Sisyrinchium rosulatum* and *Oplismenus undulatifolius*.

Mean minimum canopy openness as a measure of species-pool shade tolerance, calculated after natural-log transformation and then back-transformed, was 8.0% (95% range: 7.5%-8.5%) in parks with remnant satoyama and 9.7% (95% range: 9.0%-10.5%) in parks without it. Species-pool shade tolerance was significantly higher in parks with remnant satoyama ($P < 0.05$). Individual shade-tolerant species tended to have higher probabilities of occurring on transects in parks with satoyama (Fig. 4). Significant differences were detected for *Houttuynia cordata*, *Ophiopogon japonicus*, *Pleioblastus chino* and *Carex* spp. ($P < 0.05$).

For species-pool trampling tolerance, mean maximum penetration resistance was 20.0 kg cm⁻² (95% range: 17.9-22.2) in parks with remnant satoyama and 21.9 kg cm⁻² (95% range: 19.4-24.5) in parks without it. The difference was not significant ($P > 0.05$).

Light conditions in each 50-cm quadrat (ln canopy openness) positively affected the leaf area index of ground vegetation beneath park tree canopies, whereas trampling (soil penetration resistance) had a negative effect ($P < 0.05$; Table 4). In darker quadrats with canopy openness of 30% or less, leaf area index was greater where species pools contained shade-tolerant species, i.e., pools with lower ln minimum canopy openness ($P < 0.05$). Leaf area index was also greater in pools containing trampling-tolerant species, i.e., pools with higher maximum penetration resistance ($P <$

Table 4. Effects of the physical environment and species-pool ecological traits on quadrat leaf area index. Quadrat canopy openness was natural-log transformed. Species-pool shade tolerance was the natural logarithm of the value for the most shade-tolerant species on the transect. Because shade tolerance is measured as minimum openness permitting occurrence, smaller values indicate greater tolerance. Δ AIC is the difference in AIC between the full model and a model omitting only the variable concerned.

Dataset and variable	Estimate	Δ AIC
Canopy openness $\leq$ 50% (450 quadrats)		
Intercept	2.31**	
Quadrat canopy openness	0.598**	2234
Quadrat trampling	-0.0711**	2586
Species-pool shade tolerance	-0.0671	2
Species-pool trampling tolerance	0.0240**	39
Canopy openness $\leq$ 30% (230 quadrats)		
Intercept	4.02**	
Quadrat canopy openness	0.346**	199.6
Quadrat trampling	-0.0869**	1314
Species-pool shade tolerance	-0.703**	136.5
Species-pool trampling tolerance	0.0465**	33.6
Canopy openness $\leq$ 10% (41 quadrats)		
Intercept	2.80**	
Quadrat canopy openness	1.24**	118.2
Quadrat trampling	-0.134**	331
Species-pool shade tolerance	-1.33**	118.2
Species-pool trampling tolerance	0.0983*	4.2

**P < 0.01, *P < 0.05

0.05). However, the importance of trampling tolerance, assessed using Δ AIC, tended to be lower in the darkest quadrats (openness of 10% or less) than in the other, brighter quadrats.

Discussion

The absence of shade-tolerant species from species pools was associated with lower leaf area index at woodland edges and on forest floors in parks (Table 4). The importance of species-pool shade tolerance decreased when relatively bright quadrats with canopy openness up to 50% were included (Table 4), probably because this dataset contained many quadrats where sun-loving species with low shade tolerance grew vigorously and produced a high leaf area index. Δ AIC indicates that trampling tolerance is important in relatively bright quadrats, whereas shade tolerance becomes relatively more important in dark quadrats (Table 4).

Even vegetation beneath tree canopies in urban parks may be used for sitting or by children running around. Our results suggest that the presence of shade-tolerant species may contribute to ecosystem services that prevent muddy conditions immediately after rain, dust during dry weather, and soil erosion, while promoting rainwater infiltration (Monteiro 2017; Ito et al. 2020). Although leaf area index is

frequently used as a proxy for ecosystem services (Xu et al. 2020), future comparative studies should also examine such aspects as comfort when sitting on the vegetation.

The shade-tolerant species detected here were native species, including *Houttuynia cordata*, *Ophiopogon japonicus*, *Oplismenus undulatifolius*, *Paederia foetida*, *Pleioblastus chino* and *Carex* spp. (Table 3). Species pools tended to contain shade-tolerant species in parks retaining satoyama from the early modern period. *Houttuynia cordata*, *Ophiopogon japonicus*, *Pleioblastus chino* and *Carex* spp., whose occurrence was significantly associated with remnant satoyama (Fig. 4), are all perennial herbs that reproduce vegetatively through rhizomes or clump growth. Their seed-dispersal distances are considered short: *Pleioblastus chino* does not ordinarily disperse by seed, *Houttuynia cordata* is thought to be gravity-dispersed, and *Carex* species are dispersed by ants and other agents (Handel 1978; Kjellsson 1991; Tanaka and Tokuda 2016). *Paederia foetida* and *Ophiopogon japonicus* are dispersed after ingestion by birds (Iijima and Sago 2005; Takatsuki 2023), while *Oplismenus undulatifolius* is thought to be dispersed by attachment to mammals and other animals. Nevertheless, even tree species dispersed by highly mobile birds colonise over distances of only about 300 m (Komuro

and Koike 2005), so movement between green spaces isolated by built-up areas is not easy. Species pools containing highly shade-tolerant native species are therefore important for improving ecosystem services beneath park tree canopies. During park renovation or establishment, historical satoyama within parks should be conserved to prevent the loss of native shade-tolerant species. Where its loss is unavoidable, measures such as conserving topsoil in blocks should be adopted (Nakamura et al. 2019).

Species-pool trampling tolerance was also important for the leaf area index of park ground vegetation (Table 4). Except for *Trifolium repens*, all species used as indicators of trampling tolerance in an earlier study (Maenaka and Okubo 1986) had maximum penetration resistance of at least 18.0 kg cm⁻² in this study (Table 3), indicating broad agreement in assessments of species' trampling tolerance. Maenaka and Okubo (1986) proposed managing trampled urban park lawns using naturally occurring wild plants. Our results support the use of *Pleiblastus chino* and wild dwarf turf grasses, which occur in well-preserved traditional grasslands of the phytosociological class *Miscanthetea sinensis* (Miyawaki 1986) and are highly trampling-tolerant. Feasibility studies are needed to conserve and develop grasslands using native species pools for use as urban park lawns, while avoiding destruction of semi-natural grasslands of *Miscanthetea sinensis* during park renovation and establishment.

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Appendices

- Appendix 1, Code 1. Stan program for extreme value statistics using the Gumbel distribution.
- Appendix 1, Code 2. Stan program for comparing ecological traits of species pools between parks with and without remnant satoyama.
- Appendix 1, Code 3. Stan program for comparing species occurrence probabilities on transects between parks with and without remnant satoyama.
- Appendix 2, Table 1. Survey data.