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Spatial and functional niche overlap between invasive *Ligustrum lucidum* and
native woody species in an urban shrine forest in Japan

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analyzed the data and wrote the paper together. KK and YN helped with field work. MO conducted
spatial analysis using R software. MH provided facilities for chemical analysis. All authors have
approved publication of the final draft.

Abstract (250max)

Preventing invasion of exotic species into urban forests is important for sustaining native species diversity. In Japan, *Ligustrum lucidum*, an invasive tree, has become wide spread in urban areas. Here, we investigated the spread of *L. lucidum* in a semi-natural, urban shrine forest to infer which native species' preferred habitats may be affected. *L. lucidum* was most abundant near the artificially created forest edge where canopy trees were pruned regularly. Spatial distribution of *L. lucidum* overlapped with those of two native species (*Cinnamomum japonicum*, *Quercus glauca*), but was segregated from the other three native species. We also compared leaf functional traits between *L. lucidum* and the native species to infer functional niche overlap. *L. lucidum* exhibited greater plasticity of leaf functional traits compared to native species and its leaf functional traits were similar with *Ci. japonicum*, *Ilex rotunda* and *Q. glauca*, but not with *Camelia japonica* and *Ternstroemia gymnanthera*. Our results suggest that, currently, the preferred habitat and realized functional niche of *L. lucidum* overlaps with those of *Ci. japonicum* and *Q. glauca*. High plasticity of leaf functional traits contributing to shade tolerance may allow *L. lucidum* to expand its spatial distribution in this forest, affecting other native species in the future. Our results emphasize the importance of removing invasive species during early stages of invasion while their distribution is still relatively confined and negative effects on native species are limited.

Keywords: functional traits, invasive species, plasticity, preferred habitat, spatial distribution

Introduction

Preventing invasion of exotic species into urban forests is important for sustaining native species diversity (Alvey 2006). Compared to fast-growing herbaceous species, the threat of biological invasion by exotic trees is not as widely recognized due to their slow growth and reproductive rates (Richardson 2011). Invasive trees can alter community structure as well as ecosystem function (Lamarque et al. 2011), and more than 357 trees have been identified as invasive world-wide (Richardson and Rejmanek 2011). The nature of ecological invasions and impacts of invasive species are “idiosyncratic and context-dependent” (Moles et al. 2008), affected by environmental conditions as well as interactions between invasive and native species (Huston 2004; Vila and Weiner 2004). This means that we must accumulate empirical knowledge to identify potentially aggressive invaders and predict long-term outcomes of invasion by exotic trees.

Here, we present a case-study of urban forest invasion by *Ligustrum lucidum* Ait. (glossy privet), a bird-dispersed, evergreen tree native to China. *L. lucidum* is globally distributed as an ornamental tree, but has become invasive in parts of Asia, North and South America, Australia and New Zealand (Cronk and Fuller 1995; Hoyos et al. 2010; Reichard 1994). In Japan, *L. lucidum* was first introduced for use in urban greening in the late 19th century (Meiji Era), because of its fast-growing, drought-tolerant characteristics (Kameyama et al. 2012). First reports of invasion into urban forests date back to 1956 (Hashimoto et al. 2005; Yoshinaga and Kameyama 2001). Since then, it has become wide spread in urban areas (Hashimoto et al. 2005; Yoshinaga and Kameyama 2001).

Its preferred habitat overlaps with several native evergreen trees (Ito and Fujiwara 2007). It is not clear, however, which native species will be affected by *L. lucidum* invasion.

L. lucidum invades and grows quickly in forest edge environments (Aragon and Groom 2003; Yoshinaga and Kameyama 2001), but can also establish and survive in the shaded understory (Osugi and Ishii 2009), suggesting it may have high phenotypic plasticity, a characteristic that allows invasive species to establish, survive and spread in a wide range of new environments (Davidson et al. 2011; Funk 2008; Ghalambor et al. 2007). While invasive alien species may exhibit high plasticity of morphological and physiological traits contributing to plant performance under variable environmental conditions and resource availabilities (Richards et al. 2006), plasticity per se may not contribute directly to plant growth and success in alien environments (Dawson et al. 2012). Thus the role of phenotypic plasticity in ecological invasion is still under debate. In addition, it is difficult to measure phenotypic plasticity from short-term observations (Ishii et al 2018).

Leaf functional traits represent ecological strategies of plants for light capture and have been used to identify functional groups in a plant community or to compare ecological characteristics of invasive and native species (e.g., Cadotte et al. 2009; Ordonez et al. 2010). Intra-specific variation of leaf functional traits reflects plasticity of species' response to variable environmental conditions, namely light, and has been used to infer plasticity of photosynthetic and growth-related traits (Ishii et al. 2018; Valladares et al. 2007). For example, *Rhododendron ponticum* L. exhibited greater plasticity

of leaf functional traits in relation to light availability in Belgium, where it is invasive, than in Spain where it is native (Niinemets et al. 2003).

Here, we investigated the spread of *L. lucidum* in a semi-natural, urban shrine forest in Japan to infer its preferred habitat. We compared its spatial distribution with that of five native species to infer spatial niche overlap. We also compared leaf functional traits between *L. lucidum* and the native species to quantify phenotypic plasticity and infer functional niche overlap. We combine results of spatial analyses and trait variation to infer which native species' preferred habitats may be affected by *L. lucidum* invasion.

Study site and Methods

The study was conducted in the semi-natural, evergreen broadleaf forest at Nishinomiya Shrine in Nishinomiya City, southeastern Hyogo Prefecture, Japan (34°44'N, 135°20'E, 3.4 m asl). The 4.2-ha shrine area is located in a highly urbanized landscape including roads, railroad, houses, and buildings (Fig. 1). The forest canopy is dominated by *Cinnamomum camphora* Sieb. planted more than 100 years ago. The trees on the western edge are pruned regularly to prevent branches from growing into neighboring houses. To maintain a semi-natural state, other areas of the forest are not managed including the northern edge adjacent to a road and the eastern and southern edges adjacent to the shrine grounds. Therefore, tree recruitment is entirely from natural seed dispersal, creating

semi-natural conditions and dominance of the sub-canopy by native evergreen trees, such as *Ilex rotunda* Tunb., *Quercus glauca* Thunb., *Camellia japonica* L., and *Cinnamomum japonicum* Sieb. In 1961, the Hyogo Prefectural Government designated 1.3 ha of the forested area as a cultural heritage site representing late-successional forest vegetation of the region. See Ishii et al, (2016) for a detailed description of stand structure and species composition. Based on the Japan Meteorological Agency Database, mean annual temperature and precipitation in Nishinomiya City were 17.1°C and 1402 mm for 2008–2017.

In 2003, a 0.65 ha contiguous research plot was established in the forest consisting of 65 sub-plots ($10 \times 10 \text{ m}^2$), where all trees and shrubs taller than 1.3 m were measured for height and diameter at breast height (DBH, 1.3 m above ground) (Fig. 1). In 2019, we mapped the location of all measured individuals within a $40 \times 100 \text{ m}$ rectangular area facing the western forest edge and re-measured both DBH and height.

Five native evergreen trees, *Ca. japonica*, *Ci. japonicum*, *I. rotunda*, *Q. glauca* and *Ternstroemia gymnanthera* were selected for comparison with *L. lucidum*. *Ca. japonica* is shade-tolerant (Wu et al. 2013), while the other four species are moderately shade-tolerant (Yaguchi 2013). Fruits and seeds of *Ca. japonica* and *Q. glauca* are mainly gravity-dispersed, while the other three species are bird-dispersed (Abe et al. 2006; Xu et al. 2015).

Leaf functional traits

To measure leaf functional traits, we selected several trees of each species covering the range of sizes and light environments of the populations (Table 1). From each tree, we sampled branches (about 30cm long) including multiple leaf cohorts from the crown periphery. Samples were taken from upper and lower crown positions to cover the range of intra-crown light environments, i.e., both sun and shade leaves. We quantified the light environment of each sample branch using hemispherical photographs taken with a digital camera equipped with a fish-eye lens (Theta m15, Ricoh Co. Ltd., Tokyo, Japan) attached to a pole pruner. The hemispherical photographs were analyzed using Gap Light Analyzer (ver 2.0, Simon Frazer University, Burnaby BC, Canada) to obtain canopy openness (%), a measure of light availability.

The sample branches were cut with a pole pruner, cut again under water, covered with a plastic bag and transported to the laboratory. The sample branches were kept under darkness for more than two hours before measurement of leaf photosynthesis. From each sample branch, we randomly chose one current-year leaf for photosynthesis measurement using the LI-6400 portable gas exchange measurement system (Li-Cor, Lincoln, NE, USA) fitted with a LED light source (LI-6400-02B). Air temperature and CO₂ concentration in the cuvette were adjusted to 20°C and 400 µmol mol⁻¹, respectively. Net photosynthetic rate of the attached leaf was measured starting at 500 µmol m⁻² s⁻¹ photosynthetic photon flux density and was gradually increased until the light-saturated maximum

rate of net photosynthesis ($A_{\max}$) was reached. Due to time-constraints, we could only measure photosynthesis for two representative leaves (sun and shade), covering the range of intra-crown light environments of each tree. However, because our experimental units were individual trees and we compared bulk traits among species, we were able to obtain statistically significant results.

After photosynthesis measurements, we randomly chose five current-year leaves from each sample branch and measured leaf thickness using a digital thickness meter (QuickMini, Mitsutoyo Co. Tokyo, Japan). These leaves were then scanned using a flatbed scanner (CanoScan LiDE220, Canon Ltd., Tokyo Japan). The scanned leaf images were analyzed using image analysis software (Image J, National Institute of Health, USA) to obtain individual leaf area. These leaves were then oven-dried to constant mass at 65°C to obtain leaf mass and calculate leaf mass per area (LMA). These dried leaves (five current-year leaves from each branch) were ground to fine powder, mixed and about 50 mg was used for analysis of mass-based N content (%) using a CN coder (MT-700, Yanako Analytical Technologies, Tokyo, Japan). The amount of powder used for the measurement was adjusted to be proportional to the total for each species to prevent underestimation of standard errors.

Statistical analysis

The spatial distribution of each species reflects their respective realized niches in relation to various spatially heterogeneous factors, e.g., edaphic conditions, seed dispersal and regeneration pattern,

suitable sites for establishment and growth. On the other hand, observed leaf functional traits reflect species' respective realized niches related to leaf function, mainly photosynthetic production and carbon gain (growth). We applied analyses of spatial point patterns to infer spatial niche overlap between *L. lucidum* and the five native species. We first calculated the distance of each tree from the intensively managed western edge. The spatial distribution pattern of each species was analyzed using the pair correlation function, $g(r)$ (Loosemore and Ford 2006).

$$g(r) = \rho(r) / \lambda^2$$

Where λ is mean density of stems in the plot and $\rho(r)$ is the product density (Dale 2000). The value of $g(r)$ indicates whether an observed spatial point pattern is spatially random ($g(r) = 1$), clustered ($g(r) > 1$), or regular ($0 < g(r) < 1$).

We used the L -function with marked points, to analyze the spatial pattern of *L. lucidum* in relation to each of the four native species. The L -function is a square-root transformation of Ripley's K -function (Loosemore and Ford 2006; Ripley 1979).

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r.$$

Where, r denotes distance between trees. $L(r)$ can be used to test whether spatial association between marked points are random ($L(r) = 0$), sympatric ($L(r) > 0$), or exclusive ($L(r) < 0$). All spatial analyses were conducted using the `Kmulti` and `pcf` functions of the `spatstat` package in R version 3.6.1. Confidence intervals (95%) were calculated using simulations of 1000 randomized realizations.

We chose not to consider tree size in our spatial analysis for two reasons: 1) all six species are sub-canopy trees so variability in light environment among trees is unlikely to be dependent on tree size; 2) tree sizes are continuous, so stratification of trees into size-classes could be arbitrary and biased. An unbiased analysis would involve incorporation of competition models, which is beyond the scope of this study.

We analyzed leaf functional traits in relation to canopy openness to infer trait variation (plasticity) of each species. Mean values were compared in an analysis of covariance (ANCOVA) with species as the main effect and canopy openness as covariate. Multiple comparisons were conducted using Tukey's HSD. Species' bulk traits were analyzed using principle components analysis (PCA). We defined functional trait plasticity of each species as the range of the first and second PCA axes. We interpreted overlap between *L. lucidum* and the five native species' leaf functional traits on the PCA plane as functional niche overlap. PCA analysis was conducted using JMP ver 12.0.

Results

Spatial distribution

Compared with the five native species, the spatial distribution of *L. lucidum* was skewed toward the intensively managed, western forest edge (Fig. 2, 3). Analyses of spatial pattern indicated that *L.*

lucidum was clustered at all spatial scales (Fig. 4). *Ci. japonicum*, *Q. glauca*, *Ca. japonica* and *I. rotunda* were clustered at scales less than ca. 6, 4, 5 and 9 m, respectively. *T. gymnanthera* was randomly distributed at scales less than 2 m, but clustered at ca. 3, 5 and 9 m. Pair-wise analyses of the spatial distributions indicated that *L. lucidum* was sympatrically distributed (spatially overlapping) in relation to *Ci. japonicum* and *Q. glauca* at scales greater than 6 m, whereas it was exclusively distributed (spatially segregated) in relation to *T. gymnanthera*, *Ca. japonica* and *I. rotunda* at all spatial scales (Fig. 5).

Leaf functional traits

Within the range of light environments sampled, leaf thickness and LMA were both positively correlated with canopy openness for all species except *I. rotunda* (Fig. 6). The response of these traits to canopy openness was greatest for *L. lucidum* as indicated by the steepest regression slope. The $A_{\max}$ and N_{mass} of *L. lucidum* were higher than those of native species ($F = 9.72$, $P < 0.01$ and $F = 37.1$, $P < 0.01$, respectively) with the exception of *I. rotunda* for $A_{\max}$ (Table 2). The $A_{\max}$ of *I. rotunda* was comparable to that of *L. lucidum*, but only at higher levels of canopy openness. For *I. rotunda*, both $A_{\max}$ and N_{mass} were positively correlated with canopy openness, whereas both traits were high at all levels of canopy openness for *L. lucidum*.

Results of PCA indicated that the first principle component (PC 1) explained 57.8% of the

variation in leaf functional traits. PC 1 was positively correlated with leaf thickness and LMA ($r = 0.78$ and 0.75 , respectively), while negatively correlated with $A_{\max}$ and N_{mass} ($r = -0.66$ and -0.83 , respectively) (Fig 7). PC 2 explained 24.9% of the variation and was positively correlated with all four measures of leaf functional traits ($r = 0.50, 0.43, 0.68$ and 0.32 for leaf thickness, LMA, $A_{\max}$ and N_{mass} , respectively). Plasticity of functional traits, as measured by the ranges of PC 1 and 2 values, was greatest for *L. lucidum*. As a result, the observed range of leaf functional traits on the PCA plane for *L. lucidum* overlapped with those of *Ci. japonicum*, *Q. glauca* and *I. rotunda* but not with *T. gymnanthera* and *Ca. japonica*.

Discussion

As with many invasive species, *L. lucidum* invades into forests from artificially created edges (Aragon and Groom 2003; Yoshinaga and Kameyama 2001). Because its seeds are bird-dispersed, *L. lucidum* could potentially be dispersed over a wide area of the shrine forest. Spatial distribution of *L. lucidum*, however, was markedly skewed toward the forest edge, suggesting that the highly disturbed, open environment of the western forest edge, where trees are pruned regularly, had created favorable conditions for establishment by *L. lucidum*. The spatial distribution of *L. lucidum* in this forest overlapped with those of two native species, *Ci. japonicum* and *Q. glauca*, suggesting their preferred habitats are similar. This suggests spatial niche overlap between *L. lucidum* and these two native

species, which could be attributed to multiple factors such as, patterns of seed dispersal and establishment, edaphic conditions contributing to growth, etc. In addition, leaf functional traits of *L. lucidum* overlapped with these two native species, suggesting functional niche overlap.

Of the three native species whose spatial distribution did not overlap with *L. lucidum*, *I. rotunda* and *T. gymnanthera* were spatially segregated from *L. lucidum*. *T. gymnanthera* was randomly distributed in the forest, which may have dispersed chances of spatial overlap with *L. lucidum*. Leaf functional traits of these two native species, however, overlapped with that of *L. lucidum*. *L. lucidum* exhibited broad functional niche with regard to the leaf functional traits examined. High A_{max} across a wide range of canopy openness may contribute to its regeneration and establishment in the shaded forest interior (Aragon and Groom 2003; Osugi and Ishii 2009). A few individuals of *L. lucidum* have already established in the interior part of this forest (Fig. 2) suggesting that if *L. lucidum* spreads its distribution from forest edge to interior, it could potentially invade preferred habitats of *T. gymnanthera* and *I. rotunda*. *Ca. japonica* was distributed in clusters in the forest interior and as a result, its spatial distribution did not overlap with that of *L. lucidum*. In addition, *Ca. japonica* had thicker leaves and lower A_{max} and N_{mass} compared to *L. lucidum*, such that their leaf functional traits did not overlap. Segregation of realized spatial/functional niches between these two species suggests their preferred habitats are different.

Phenotypic plasticity allows individual plants to acclimate to various environments

(Valladares et al. 2007). However, it is still under debate whether or not high phenotypic plasticity is advantageous for ecological invasions (Davidson et al. 2011; Palacio-Lopez and Gianoli 2011). Although the number of trees and range of light environments sampled in this study were limited, our results suggested *L. lucidum* has high plasticity of leaf functional traits, especially morphological traits, namely leaf thickness and LMA (Fig. 6). Although to a lesser extent, the native species also exhibited plasticity of these traits in response to light availability. Within the range of light environments sampled, *I. rotunda* had low morphological plasticity, but plasticity of photosynthetic traits ($A_{\max}$ and N_{mass}) was high. These results suggested contrasting strategies for light acclimation among the study species. Bulk analysis of leaf traits using PCA showed that functional niche of *L. lucidum* overlapped with those of multiple native species (Fig. 7). Plasticity is adaptive if it contributes to fitness of a species in variable environments (Funk 2008). We inferred that plasticity of leaf functional traits of *L. lucidum* is adaptive because it could contribute to high photosynthetic performance under variable light environments, which could potentially increase fitness via greater growth and reproduction. This could ultimately allow *L. lucidum* to expand its distribution in this forest, leading to invasion of preferred habitats of various native species.

Conclusions

Because ecological invasions and impacts of invasive species on native ecosystems are so variable

(Moles et al. 2008), we must accumulate case studies of interactions between native and invasive species in order to predict which native species will be affected ecological invasion. Using spatial analysis, we inferred how *L. lucidum* is invading this forest and how it may potentially overlap with the preferred habitats of the native species. Bulk analyses of leaf functional traits allowed objective and quantitative inference of species' respective functional niches with regard to light environment. Although *L. lucidum* is currently concentrated near the intensively managed, western forest edge, we inferred that this represents the initial phase of invasion. Our results and those of previous studies suggest that *L. lucidum* is capable of expanding into the forest interior, invading preferred habitats of currently unaffected native species, such as *Ca. japonica*. We also showed that spatial and functional trait analyses are useful for identifying which native species are affected by invasive species. We conclude that, in order to manage urban forests in near-natural state and conserve native species diversity, invasive alien species like *L. lucidum* should be removed during early stages of invasion while their distribution is still relatively confined and negative effects to native species are limited.

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Table 1. Sizes and light environments of the sample trees ($n = 5\sim 6$ for each species) and total number of individuals in the research plot and for each species. Species are listed in order of increasing distance of spatial distribution from forest edge (Fig. 3).

Species	DBH (cm)	Height (m)	Canopy openness (%)	Total individuals
<i>L. lucidum</i>	4.13~7.83	4.43~9.04	5.4~26.4	58
<i>Ci. japonicum</i>	2.76~5.90	3.09~10.05	6.48~21.41	84
<i>Q. glauca</i>	2.45~6.78	3.30~10.66	5.51~17.12	166
<i>T. gymnanthera</i>	3.03~8.42	3.96~10.12	4.95~14.48	112
<i>Ca. japonica</i>	3.79~9.01	4.05~10.52	6.30~18.51	206
<i>I. rotunda</i>	2.31~6.23	3.43~10.15	6.88~24.15	55

All measurements were taken in 2019.

Table 2. Leaf functional traits (mean $\pm$ one standard error) of the study species.

Species	Thickness (mm)	LMA (g m^{-2})	A_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	N_{mass} (%)
<i>L. lucidum</i>	0.34 ± 0.01 bc	103.4 ± 3.9 b	8.58 ± 0.57 a	2.89 ± 0.09 a
<i>Ci. japonicum</i>	0.24 ± 0.01 d	102.8 ± 4.5 b	4.76 ± 0.67 b	2.00 ± 0.11 b
<i>Q. glauca</i>	0.33 ± 0.01 c	101.9 ± 4.0 b	6.00 ± 0.61 b	1.97 ± 0.09 b
<i>T. gymnanthera</i>	0.45 ± 0.01 a	112.8 ± 4.7 ab	6.61 ± 0.72 b	1.12 ± 0.11 c
<i>Ca. japonica</i>	0.39 ± 0.01 b	125.4 ± 4.0 a	4.14 ± 0.58 b	1.35 ± 0.10 c
<i>I. rotunda</i>	0.26 ± 0.01 d	67.2 ± 4.9 c	8.85 ± 0.70 a	2.09 ± 0.12 b

Means with the same letter are not significantly different (ANOVA, $P < 0.05$)

Figure captions

Fig. 1. Aerial view and map of Nishinomiya Shrine in southeastern Hyogo Prefecture, Japan. The evergreen broadleaved forest is located on the north and west sides of the shrine grounds. A 0.65 ha contiguous research plot was established comprising 65 sub-plots (10×10 m). Of these tree locations were mapped for the 40×100 m area (filled squares).

Fig. 2. Stem map (all trees taller than 1.3 m) of the 40×100 m area of the shrine forest.

Fig. 3. Box-whisker plot of the distance of individual trees of each species from the intensively managed, western forest edge. Box length is the inter-quartile range. Lines and X inside boxes represent median and mean distances, respectively. Bars represent 10 and 90 percentiles. Circles are trees outside this range. Species are listed in order of increasing mean distance from forest edge. Letter indicate significantly different means ($P < 0.05$, ANOVA and Tukey's HSD).

Fig. 4. Spatial distribution pattern of each species in the shrine forest (solid lines). The horizontal line indicates $g(r) = 1$. Dotted lines indicate 95% confidence interval for null hypothesis of for Poisson random distribution. Positive and negative deviations outside the confidence intervals indicate clustered and regular distribution patterns, respectively. Species order follows that of Fig. 3.

Fig. 5. Spatial distribution pattern of *L. lucidum* in relation to each of the five native species (solid lines). Dotted lines indicate 95% confidence interval for null hypothesis of for Poisson random distribution. Positive and negative deviations outside the confidence intervals indicate sympatric and exclusive distribution patterns, respectively. Species order follows that of Fig. 3.

Fig. 6. Leaf traits in relation to canopy openness for *L. lucidum* and five native species. Data points for N_{mass} , LMA and thickness are the mean of five leaves at each sampling position, while A_{max} is the mean of ten measurements taken at light saturation for one leaf. All standard errors were less than 3%. Lines indicate significant regressions ($P < 0.05$).

Fig. 7. Results of principle component analysis of leaf functional traits of *L. lucidum* and the five native species. Arrows indicate correlation vectors showing correlation coefficients of each trait in relation to PC1 and PC2.

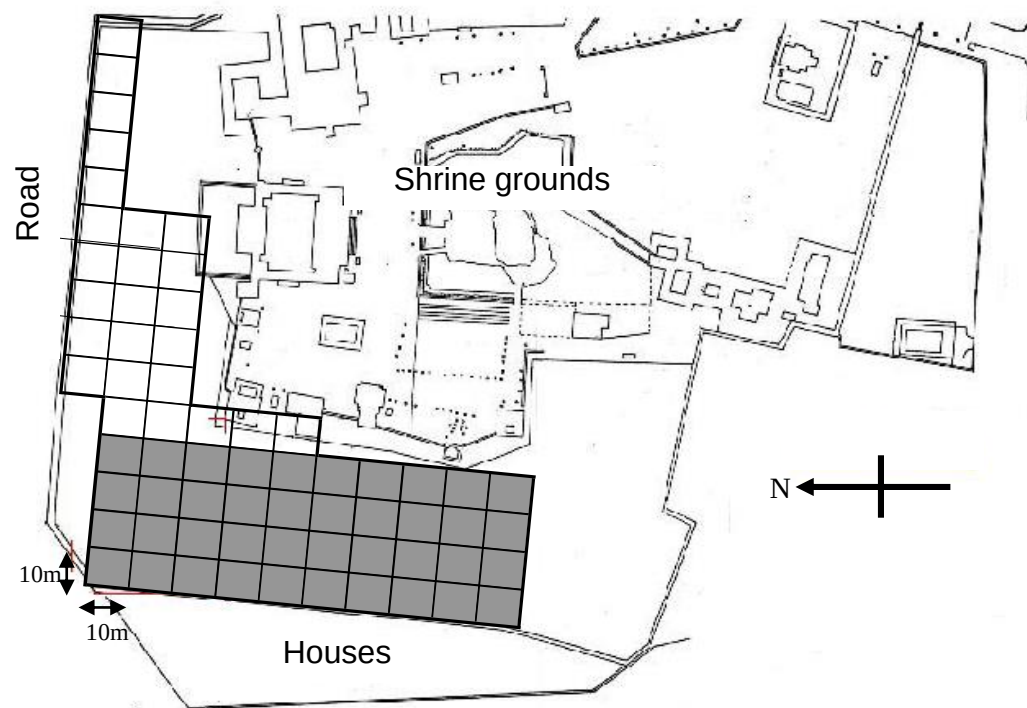
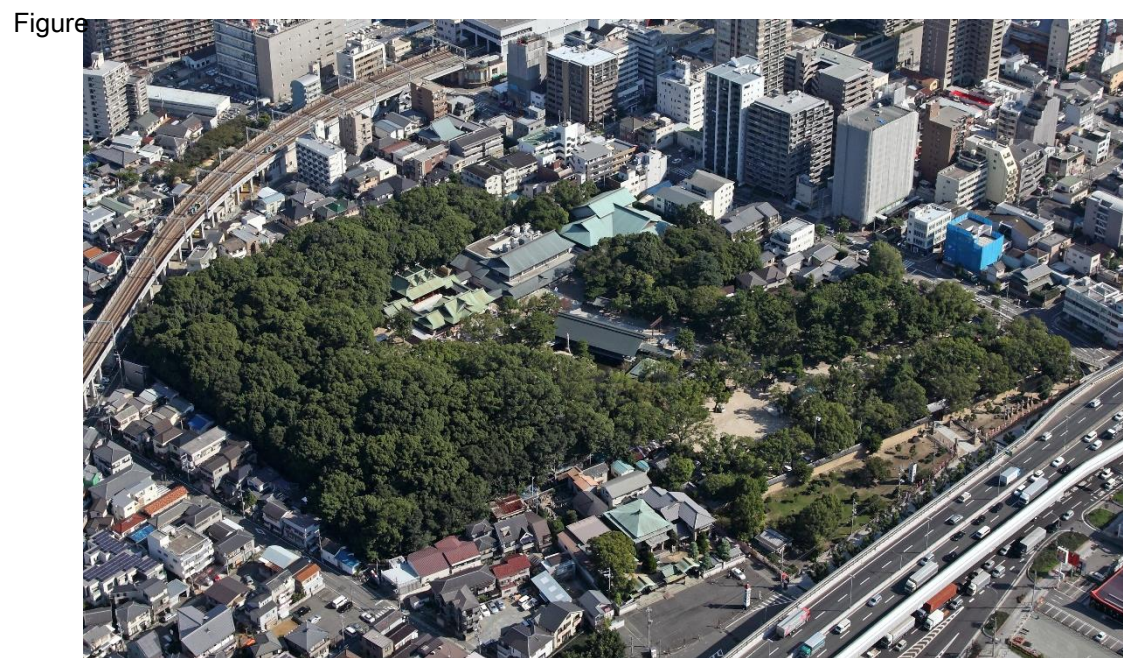


Fig. 1

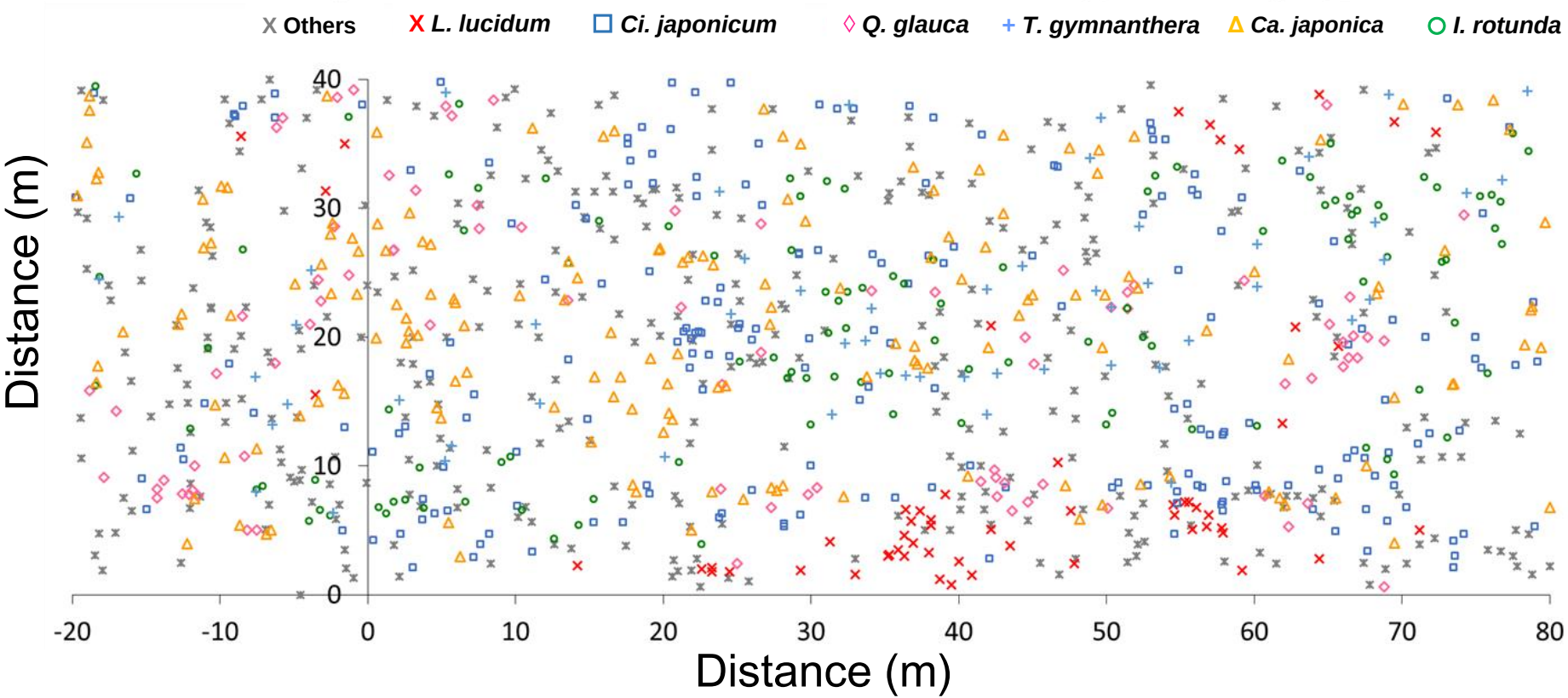


Fig. 2

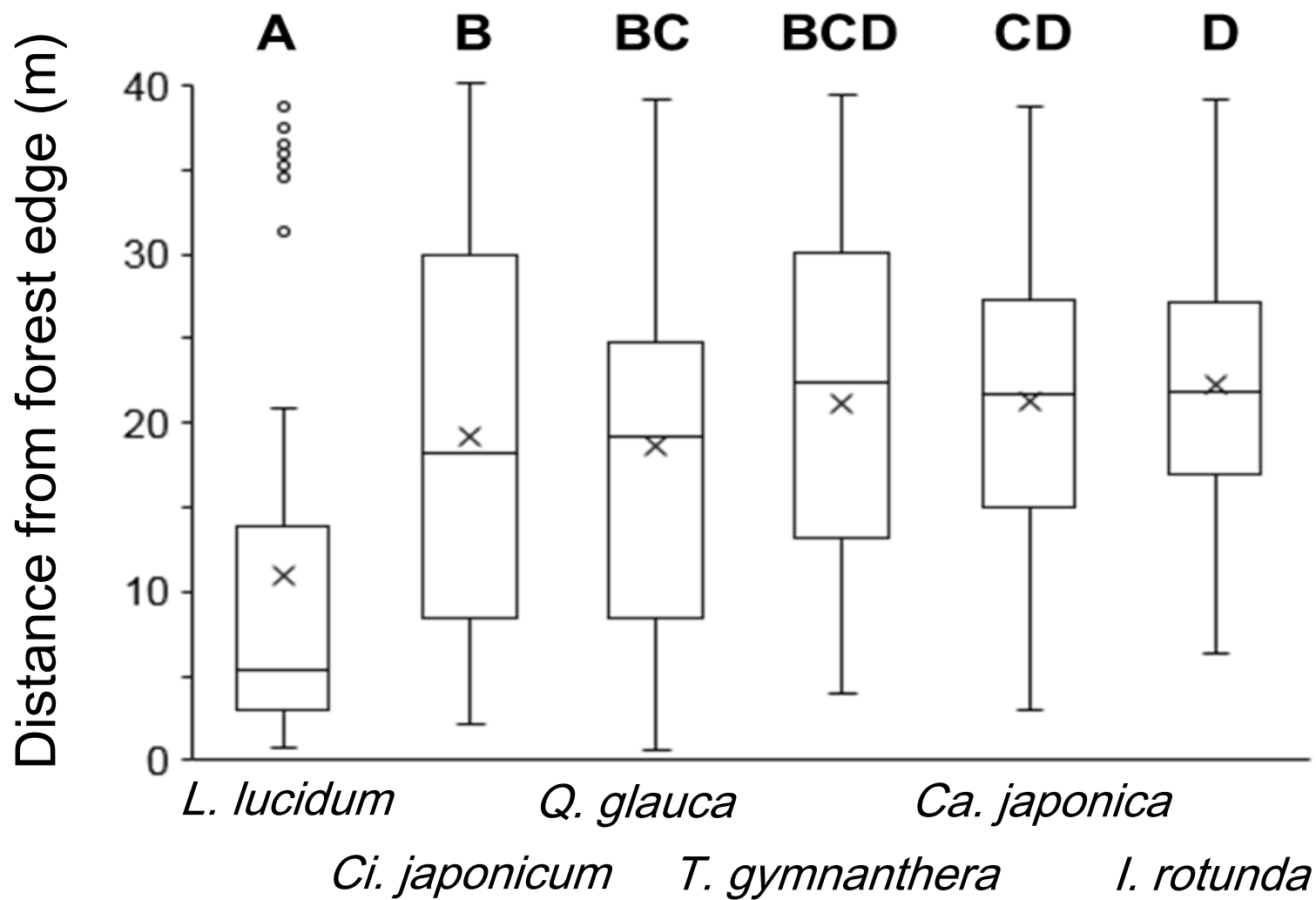


Fig. 3

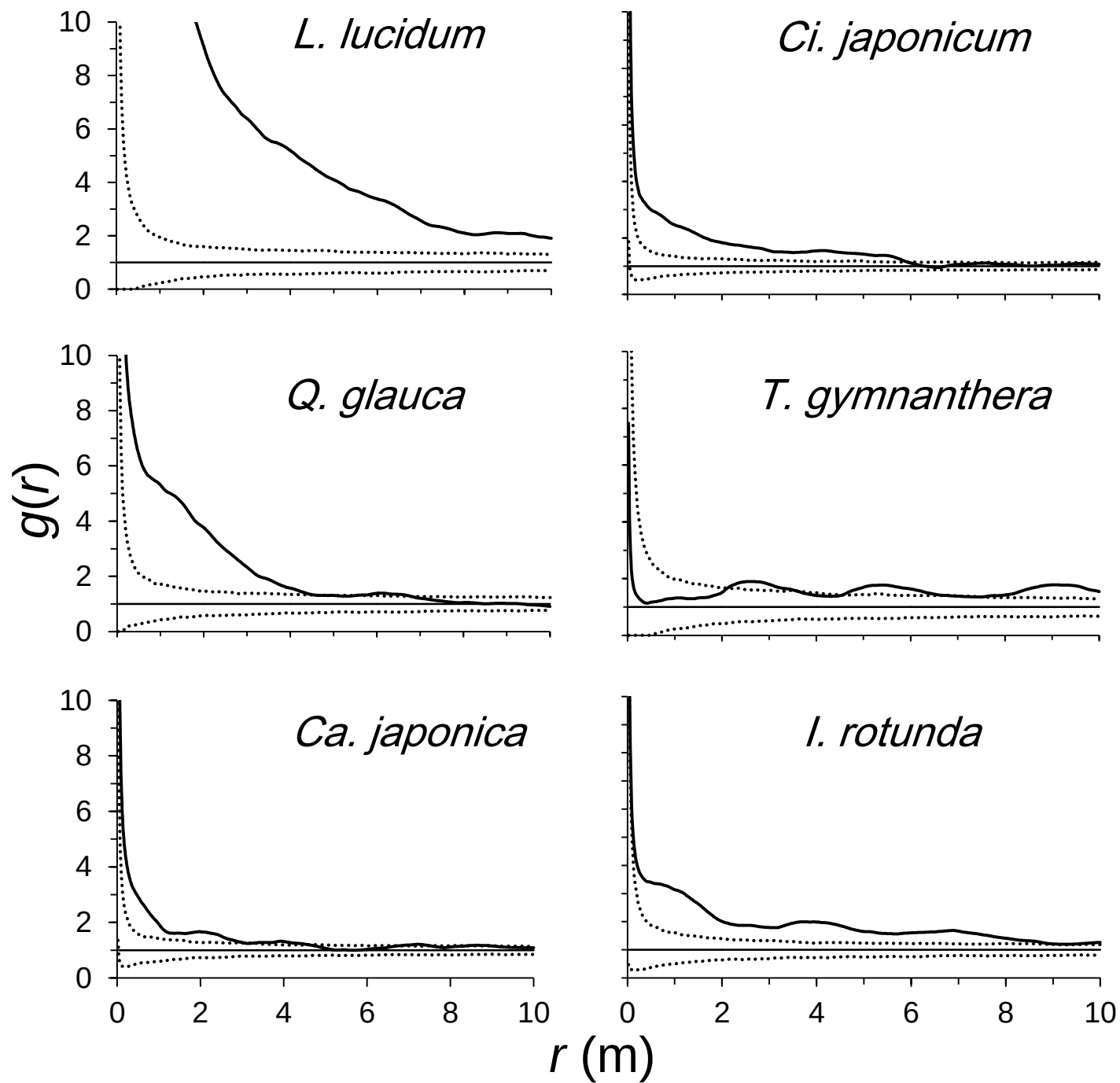


Fig. 4

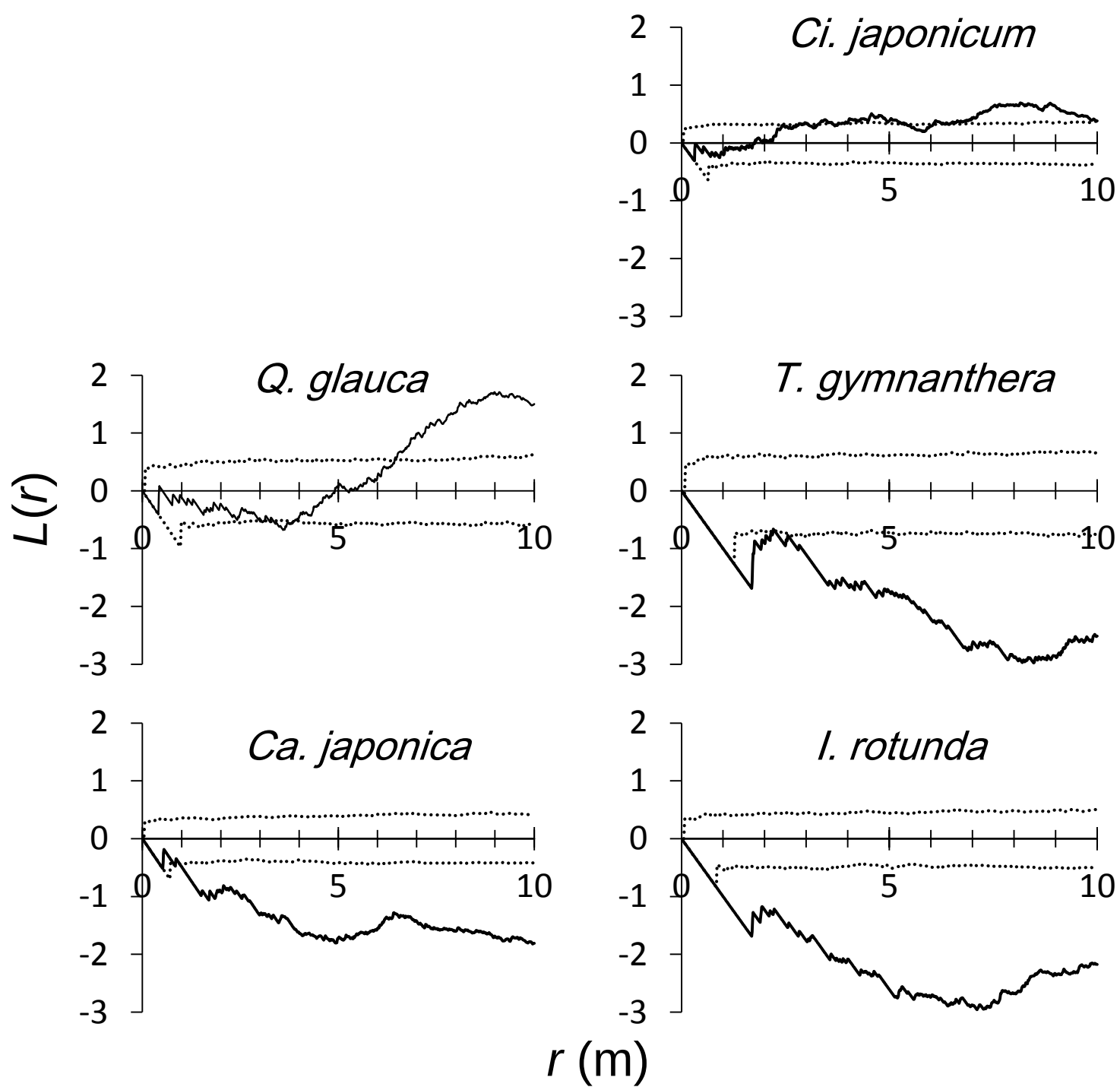


Fig. 5

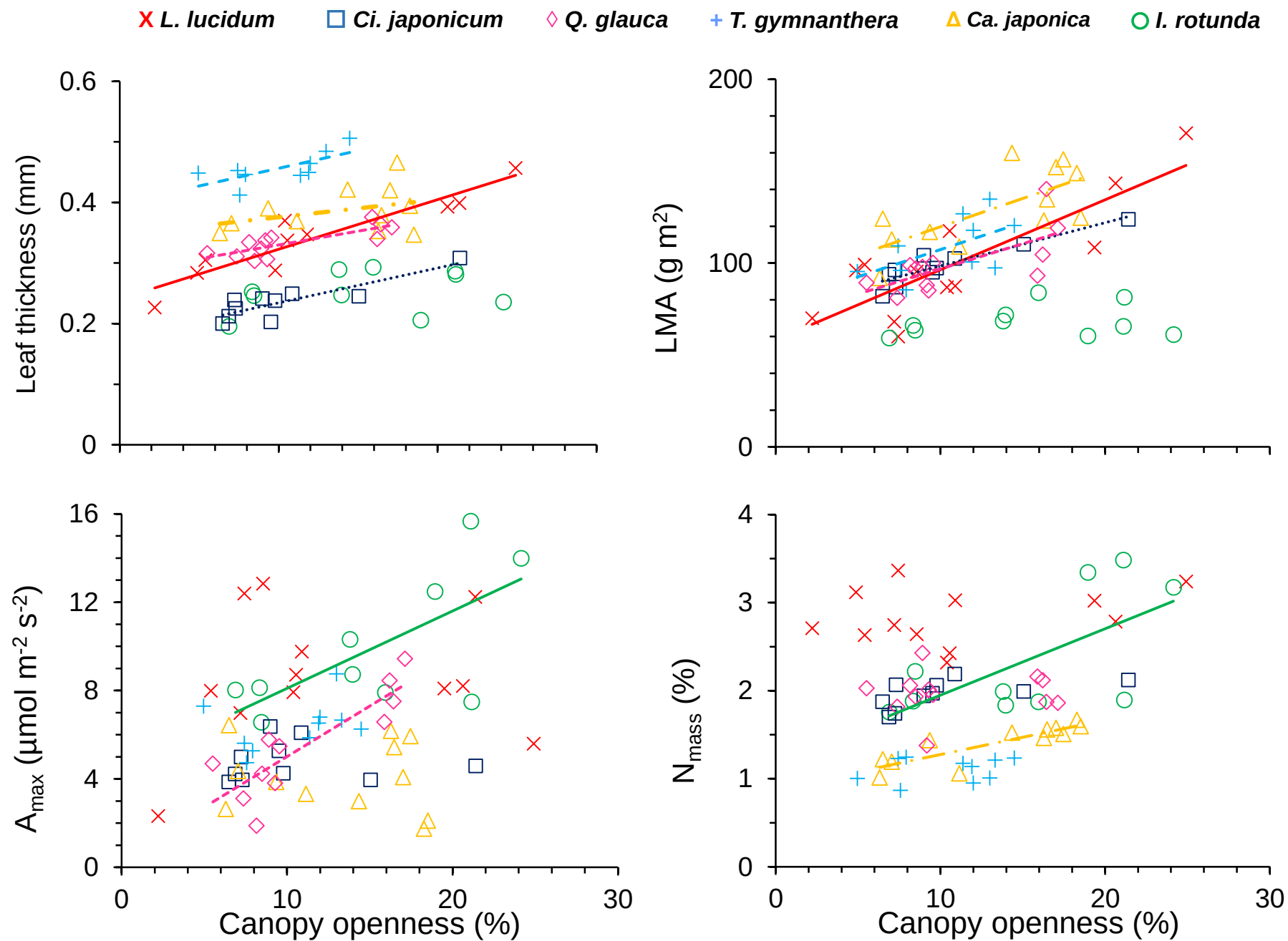


Fig. 6

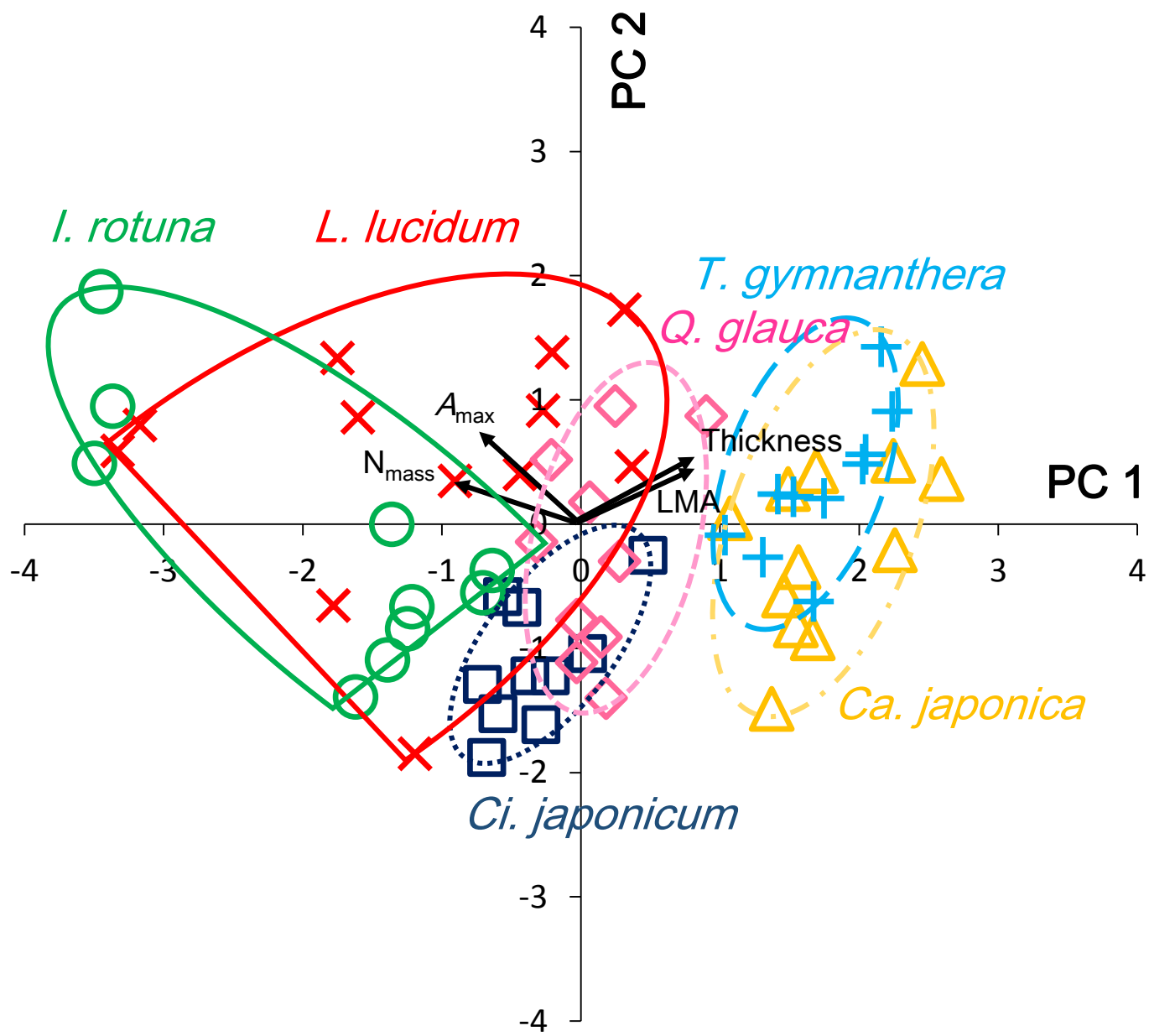


Fig. 7