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Community Attributes Predict the Relationship between Habitat Invasibility and Land Use Types in an Agricultural and Forest Landscape

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Abstract: Finding ecosystem or community level indicators for habitat invasibility may provide natural resource managers with environmentally friendly measures to control alien plant invasion; yet, ecosystem invasibility remains understudied. Here, we investigated alien plant invasion into various ecosystems representing different land use types in a subtropical peri-urban area of south China. Four invasive alien species were found from five out of the six ecosystems. Lower plant diversity in both the overstory and understory was consistently associated with more severe alien plant invasion to the ecosystems. The highest total abundance and plot occurrence of the invasive plants were found in the agroforestry ecosystem representing the highest disturbance. At plot scale, an increase in invasion severity was associated with a significant decrease in overstory stem density, species richness, and diversity, but with a significant increase in overstory plant dominance. The understory community attributes in response to the increase in invasion severity followed similar patterns, except that the stem density increased with invasion severity. Higher canopy openness and thus lower leaf area index and greater understory radiation were associated with higher invasion severity of invasive plants to the understory habitat. For predicting total abundance of the invasive species, the most important variable is land use type, while for the abundance of *Lantana camara* and *Mikania micrantha*, the most important predictor variable is overstory Berger–Parker index and canopy openness, respectively. Canopy structure and understory gap light regimes were among the most important factors determining the abundance of the worst invasive plant *Mikania micrantha*. Our results demonstrate that land use types with varying disturbance regimes determine the spatial heterogeneity in plant diversity and community structure, which predicts alien plant invasion and habitat invasibility; and that the severity of alien plant invasion in turn is a good indicator of habitat disturbance across the ecosystems.

Keywords: habitat invasibility; resident community; invasive alien plant; invasion severity; land use type; canopy structure

1. Introduction

Plant invasion has been recognized as one of the major factors threatening biodiversity, ecosystem health, and ecosystem services, and one of the major economic costs to the agricultural and forestry sectors [1–3]. Predicting and controlling alien plant invasion will help maintain biodiversity and prevent the local ecosystems from ecological and economic losses. However, limited knowledge of the indicators of alien plant invasion and the interactions between invasive plants and the resident communities has been an obstacle to achieving this goal. Although plant invasion is a common phenomenon across the terrestrial ecosystems, the invasibility of a particular ecosystem, which is defined as the vulnerability of its associated habitat and biological community to invasion [4,5], is dependent on various biotic and abiotic factors, such as species diversity and composition, community structure, land use types, soil functioning, and disturbance regimes [6–9]. At ecosystem scale, finding the indicators of alien plant invasion may be crucial for forest and natural resource managers. Such indicators can provide ecosystem managers with environmentally friendly measures to control invasive plants, such that conventional approaches such as chemical methods by herbicides and mechanical methods that either pollute the soils or incur tremendous workforce can be avoided.

Habitat heterogeneity provides plants with diverse niches and is conducive to the growth and distribution of the resident plant species as well as the invasive ones [10]. Species diversity, composition, and the structure of the resident community establish and shape the micro-habitats [11] and consequently affect the colonization of alien invasive plants [12,13]. Various mechanisms have been proposed to explain plant invasion and habitat invasibility. Studies on the biodiversity–ecosystem functioning relationships have demonstrated that higher plant diversity will increase the resistance of a resident ecosystem to alien plant invasion [14,15]. The biotic resistance hypothesis is commonly used to explain the negative relationship between native plant diversity and habitat invasibility [16]. As an important mechanism of the biotic resistance hypothesis, the resource use complementarity effect suggests that different plant species use different types and quantities of environmental resources [17]. The native individuals reduce the invasibility of the resident community by fully occupying resource niches, so that there are less ecological niches and resources available for alien plants to become successful invaders [18,19]. Alternatively, alien plants will be suppressed by the resident community through niche filling or competitive exclusion during vegetation recovery [20]. However, the relationships between plant diversity and invasibility may be scale dependent [21,22], and positive diversity–invasibility relationships have been reported in a number of cases [23–25].

A growing number of studies have demonstrated that land use types and human activities have a major effect on the success of alien plant invasion [26–29], yet the interactions between the resident plant community structure and the severity of alien plant invasion remains understudied. As land use types represent human disturbance of various intensity [28], examining the relationships between alien plant invasion and environmental factors across various land uses will reveal how resident communities respond to alien plant invasion, thus providing management and conservation implications for the local ecosystems. During the past decades, the Pearl River Delta of south China has experienced rapid development due to industrialization and urbanization driven by both international as well as domestic investment [30,31]. However, such an incomplete urbanization, or peri-urbanization [32], has left a mosaic of agricultural and forest landscapes with some industrial establishments in the peri-urban fringes of the area. Here, we examined several such land use types in relation to alien plant invasion with the objective of answering the following questions: (1) How do invaded and uninvaded communities differ in stand structure, species composition, and diversity? (2) Are land use types and management regimes the major determinants for alien plant invasion at the ecosystem level? (3) Are species diversity, composition, functional diversity, and canopy and gap light parameters significantly associated with alien plant invasion severity? (4) What are the most important biotic or abiotic factors determining the severity of alien plant invasion?

2. Materials and Methods

2.1. Study Area

Our study area was located in the peri-urban fringe of Dongguan (113°31′–114°15′ E, 22°39′–23°09′ N), a rapidly developing region in the southeast part of the Pearl River Delta of South China [33]. Dongguan is situated between the two metropolitan cities, Shenzhen to the south and Guangzhou to the north. The area has a subtropical monsoon climate. Mean annual temperature is 23.1 °C, with the maximum temperature of 37.8 °C in July and the minimum temperature of 3.1 °C in January. Mean annual precipitation is 1819 mm, approximately 80% of which concentrated during April to September to form a rainy season [34].

Major land uses in the peri-urban fringes of Dongguan form diverse agricultural and forest landscapes, including protected natural forests, forest farms, orchards, and paddy fields. Most of the forest farms and orchards have been withdrawn from production and converted to noncommercial ecological forests by planting native trees.

2.2. Sampling Design and Data Collection

We selected six sites in the peri-urban fringe of Dongguan for our study. Each of the sampling sites corresponded to one ecosystem representing a unique land use type (Table 1). In each of the six land use types, we set up five rectangular plots separated by at least 20 m. Each plot was 20 × 50 m and was further divided into ten 100-m^2 contiguous square quadrats for field data collection. All the trees ≥ 1 cm in every quadrat were tallied and recorded by species identity, diameter at breast height (DBH), and tree height. Understory plant census was carried out in five 1 × 1-m sub-quadrats within each 100-m^2 quadrat.

Table 1. Summary of site characteristics. The size of arrows increases with greater disturbance.

Attribute	Ecosystem					
	1	2	3	4	5	6
Location	114°13′23″ E 22°53′09″ N	114°14′40″ E 22°53′12″ N	113°48′06″ E 22°55′20″ N	113°46′18″ E 22°51′41″ N	113°47′50″ E 22°50′51″ N	113°46′53″ E 22°50′42″ N
Land use types	Nature reserve	Forest park	Coniferous-broadleaf forest	Naturally-regenerated forest	Artificially-rehabilitated forest	Agroforestry ecosystem
Management regime	Natural	Natural	Semi-natural	Semi-natural	Managed	Managed
Disturbance regime	Strictly protected					
Elevation (m)	246.4	581.2	59.6	62.5	57.2	68.7
Aspect	NW	NE	SW	SW	SW	NW
Slope (°)	25	15	7	5	6	8
Plot area (m^2)	5000	5000	5000	5000	5000	5000
Number of quadrats	50	50	50	50	50	50

We measured canopy openness, leaf area index (LAI), and understory radiation in all the quadrats using hemispherical photography. Hemispherical photography is a photogrammetric technique that involves field image acquisition using a digital camera and image analysis with a computer program. We took a hemispherical photograph at the center of each 100-m^2 quadrat, using a Nikon 4500 Coolpix® digital camera fitted with a Nikkor FC-E8 fisheye converter. The camera was mounted on a tripod 1.65 m above the ground and pointed upwards to the sky. All the hemispherical images were acquired at 2272 × 1704 pixels and saved as fine quality JPEG format. To ensure uniform light conditions and minimize glare from direct sunlight, photographs were taken in the afternoon under overcast conditions and still air [35,36]. After the hemispherical images were downloaded, we analyzed all the images using WinScanopy Pro 2008 (Regent Instruments Inc. Quebec, QC, Canada) to extract canopy openness, leaf area index (LAI) and understory radiation parameters, i.e., direct photosynthetically-active photon flux density (direct $PPFD_{under}$) and diffuse photosynthetically-active photon flux density (diffuse $PPFD_{under}$). These parameters represent canopy structure and gap light regimes that might affect understory plant patterns and invasive alien plant invasion.

2.3. Data Analysis

We constructed five primary datasets based on the field data: (1) a dataset with canopy tree abundance; (2) a dataset with all understory plants, as well as (3) one with the invasive alien plants removed; (4) a dataset with only invasive plants, and (5) a dataset with canopy openness, LAI and understory radiation data. With the canopy plant dataset and understory plant dataset with invasive alien plants removed, we calculated six community metrics by quadrat, i.e., number of stems or stem density (stems per 100-m^2 quadrat), species richness, Berger–Parker index, Shannon–Wiener index, functional richness, and functional dispersion, to generate secondary datasets. Both Berger–Parker and Shannon–Wiener indices are indicators of community structural diversity [37]. From the invasive plant dataset, we defined an invasion severity gradient according to the total abundance of invasive alien plants in each quadrat. The invasion severity gradient was defined in five classes as follows: 1 = Uninvaded; 2 = Low (1 stem); 3 = Medium (2–5 stems); 4 = High (≥6 stems). Our final step was to merge the secondary datasets of diversity metrics with invasive plant abundance, LAI and gap light variables into one integrated dataset. The values of one grouping variable for land use types and one for invasion severity were also assigned to each quadrat of the integrated dataset.

We generated multiple rank–abundance plots to contrast the differences in species richness and abundance patterns across land use types for the forest canopy and the understory. Rank–abundance plot, also called diversity–dominance curve, visualizes the community dominance and evenness as well as species richness of an ecosystem in a two-dimensional graph. A steeper curve indicates greater community dominance and less evenness of species patterns in an ecosystem [37,38].

To evaluate the effects of diversity metrics of both the canopy and understory communities on understory plant invasion, we tested the changes in diversity metrics for significance across invasion severity gradients using Kruskal–Wallis test. Kruskal–Wallis test, a nonparametric alternative to one-way analysis of variance (ANOVA), is the appropriate method for comparing two or more independent samples or groups of equal or different sample sizes, especially for field ecology data [39].

To assess the differences in species composition of both the canopy and understory communities across the invasion severity gradient, we performed multi-response permutation procedures (MRPP) on the plot-by-species datasets of both the canopy and understory plants.

To detect plant species with significant indicator values, which represent faithfulness to a particular invasion severity class, we performed indicator species analysis (ISA) using the Dufrêne and Legendre method [40]. The method combines information on the concentration of species abundance in a particular group (relative abundance, RA) and the faithfulness of occurrence of a species in a particular group (relative frequency, RF). The indicator value for a given species in a particular invasion severity class is then calculated by multiplying RA and RF and the result is expressed as a percentage [40]. Statistical significance of the highest indicator value of a given species across the invasion severity classes was evaluated using randomization method.

To determine which biotic or abiotic factors have the greatest impact on understory alien plant invasion, we performed Random Forest to visualize variable importance. Random Forest is a data mining technique developed by Breiman and can handle multiple categorical variables and quantitative variables in one analysis [41,42]. Sixteen quantitative variables including overstory and understory diversity metrics, canopy structure and gap light attributes, as well as two categorical variables, land use types and management regimes, were used as predictor variables in the Random Forest regression model, while the abundance of invasive alien plants were used as response variables. The Random Forest regression model produces bar charts showing the predictor variable importance for the given response variable.

Rank-abundance curve analysis, Kruskal–Wallis test, and Random Forest modeling were performed with Statistica 8.0 (Statsoft, Inc., Tulsa, OK, USA), while MRPP and ISA, as well as the calculation of community metrics, were performed with PC-ORD 7.0 (MjM Software, Gleneden Beach, OR, USA).

3. Results

3.1. Effect of Land Use and Species Composition on Plant Invasion

The six ecosystems representing various land use types differed in management and disturbance regimes (Table 1), species richness, total abundance (Table 2), and community structure (Figure 1). A decreasing trend in species richness from natural forest through the agroforestry ecosystem was associated with increasing disturbance. The strictly protected natural forest has 68 species in the overstory and 192 species in the understory, while the most-disturbed agroforestry ecosystem has 25 species in the overstory and 82 native species in the understory (Table 2). Lower plant diversity in both the overstory and understory was consistently associated with more severe alien plant invasion to the ecosystems as indicated by the total number of invasive plant individuals and the number of subplots invaded by the invasive plants (Table 2).

Table 2. Alien plant invasion status of the six heterogeneous ecosystems. Ecosystems representing various land use types are coded as: 1 = Nature reserve; 2 = Forest park; 3 = Coniferous-broadleaf forest; 4 = Naturally-regenerated forest; 5 = Artificially-rehabilitated forest; 6 = Agroforestry ecosystem. Abbreviations for invasive plants: EUPCAT = *Eupatorium catarium*; LANCAM = *Lantana camara*; MIKMIC = *Mikania micrantha*; RHYREP = *Rhynehelytrum repens*.

Attribute	Ecosystem					
	1	2	3	4	5	6
Number of species						
Overstory	68	45	42	43	33	25
Understory	192	147	90	102	91	85
Number of stems						
Overstory	1292	1315	1116	737	762	367
Understory	5723	3645	3685	6242	4946	9446
Number of subplots with invasive plants	uninvaded	2	5	8	30	45
Invasive plant species	None	EUPCAT LANCAM	LANCAM MIKMIC	MIKMIC	LANCAM MIKMIC	LANCAM MIKMIC RHYREP
Total number of invasive plant individuals	None	2	9	18	62	286

At ecosystem level, alien plant invasion intensified with disturbance and stand history. No invasive plants were found in the natural broadleaf ecosystem in the Yinpingshan Nature Reserve, but even in the natural forest in a neighboring forest park with moderate disturbance from tourist visits, two invasive plant individuals were found from the sampling plots there. Of all the four invasive alien plant species (Table 2), *Mikania micrantha*, a fast-growing, perennial vine from the Compositae family, is one of the world's worst alien invasive weeds [43]. It has ruined forests and agricultural ecosystems and caused tremendous economic losses across tropical and subtropical China [44]. Except for the two natural forest ecosystems, *Mikania micrantha* occurred in all the other ecosystems. Alien plant invasion severity was associated with the disturbance regimes. The total number of invasive plants increased with disturbance at the ecosystem level (Table 2). The highest total abundance and plot occurrence of the invasive alien plants were found in the agroforestry ecosystem with the highest disturbance. Species richness is a good indicator for alien plant invasion at the ecosystem level. The uninvaded forest ecosystem had the highest species diversity with 68 overstory species and 192 understory plant species, while the severely invaded agroforestry ecosystem had only 25 overstory species and 86 understory resident plant species (excluding the invasive alien plants; Table 2).

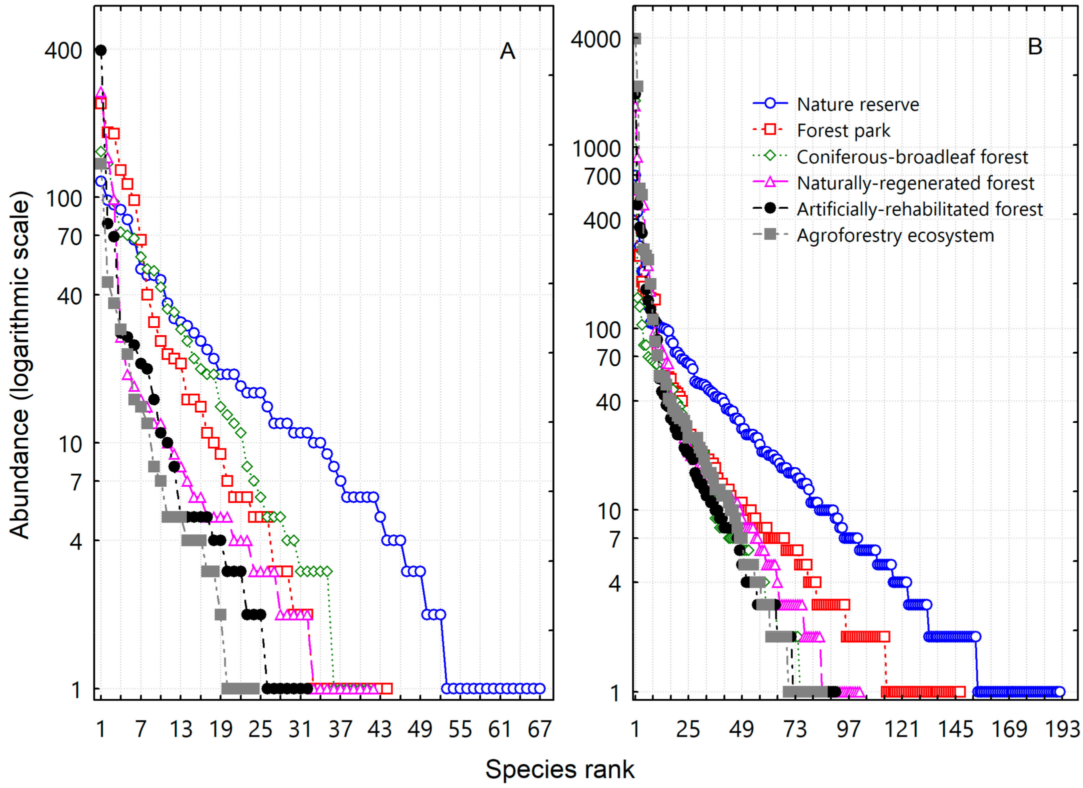

Figure 1. Rank–abundance curves showing plant diversity and dominance patterns of the six ecosystems representing various land use types for both the overstory (**A**) and the understory (**B**).

3.2. Relationships of Alien Plant Invasion to Community Attributes

At plot scale, an increase in invasion severity is associated with the significant decrease in overstory stem density (Figure 2A), species richness (Figure 2B), Shannon–Wiener index (Figure 2D), and functional diversity (Figure 2E,F), but with the significant increase in dominance as indicated by Berger–Parker index (Figure 2C). The understory community parameters in response to the increase in invasion severity followed similar patterns (Figure 3B–F) with the overstory community, except that the stem density increased with invasion severity in the understory (Figure 2A).

Canopy structure and understory gap light regimes significantly varied across an invasion severity gradient. Higher canopy openness and thus greater understory radiation were associated with higher invasion severity of alien plants to the understory habitat (Figure 4A,C,D), whereas the changes in leaf area index were negatively associated with invasion severity (Figure 4B).

Species composition in both the overstory and understory of the six ecosystems significantly differed across the severity classes by overall comparison (Table 3). By pairwise comparison, except for the Low vs. Medium severity classes, significant differences were found in all other pairs (Table 3).

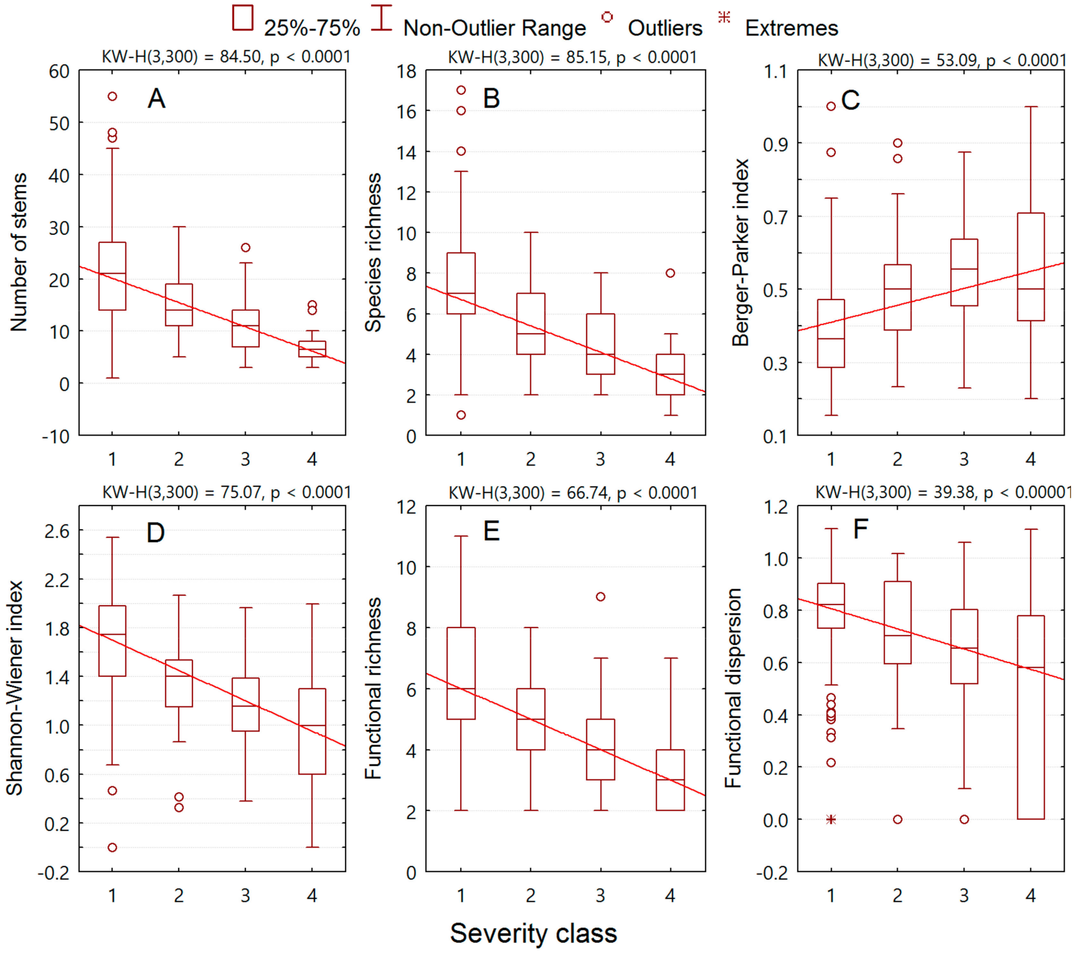

Figure 2. Changes of overstory community parameters (**A**–**F**) in relation to invasion severity. A linear fit to the medians was plotted to show the trend of change. The invasion severity classes are defined according to the total number of invasive plant individuals found in a subplot, as follows: 1 = Uninvaded; 2 = Low (1 stem); 3 = Medium (2–5 stems); 4 = High (≥6 stems).

Table 3. Multi-response permutation procedures (MRPP) to test for significance of variation in both overstory and understory plant species composition across heterogeneous habitats represented by invasion severity classes. The invasion severity classes are as follows: Uninvaded, Low (1 stem), Medium, and High (≥6 stems). *T* is a statistic describing the separation between groupings, while *A* represents within-group homogeneity. *P* is the *p*-value for significance calculated using randomization method.

Groups Compared	Overstory			Understory		
	T	*A*	*P*	*T*	*A*	*P*
Overall comparison	−36.170	0.048	$<10^{-7}$	−22.590	0.029	$<10^{-7}$
Pairwise comparison						
Uninvaded vs. Low	−12.478	0.012	$<10^{-6}$	−10.422	0.010	$<10^{-5}$
Uninvaded vs. Medium	−24.299	0.021	$<10^{-7}$	−20.265	0.018	$<10^{-7}$
Uninvaded vs. High	−38.944	0.036	$<10^{-7}$	−17.436	0.016	$<10^{-7}$
Low vs. Medium	−1.053	0.005	0.131	−0.086	0.0004	0.380
Low vs. High	−14.579	0.111	$<10^{-5}$	−5.013	0.030	0.001
Medium vs. High	−7.709	0.049	0.001	−3.134	0.016	0.011

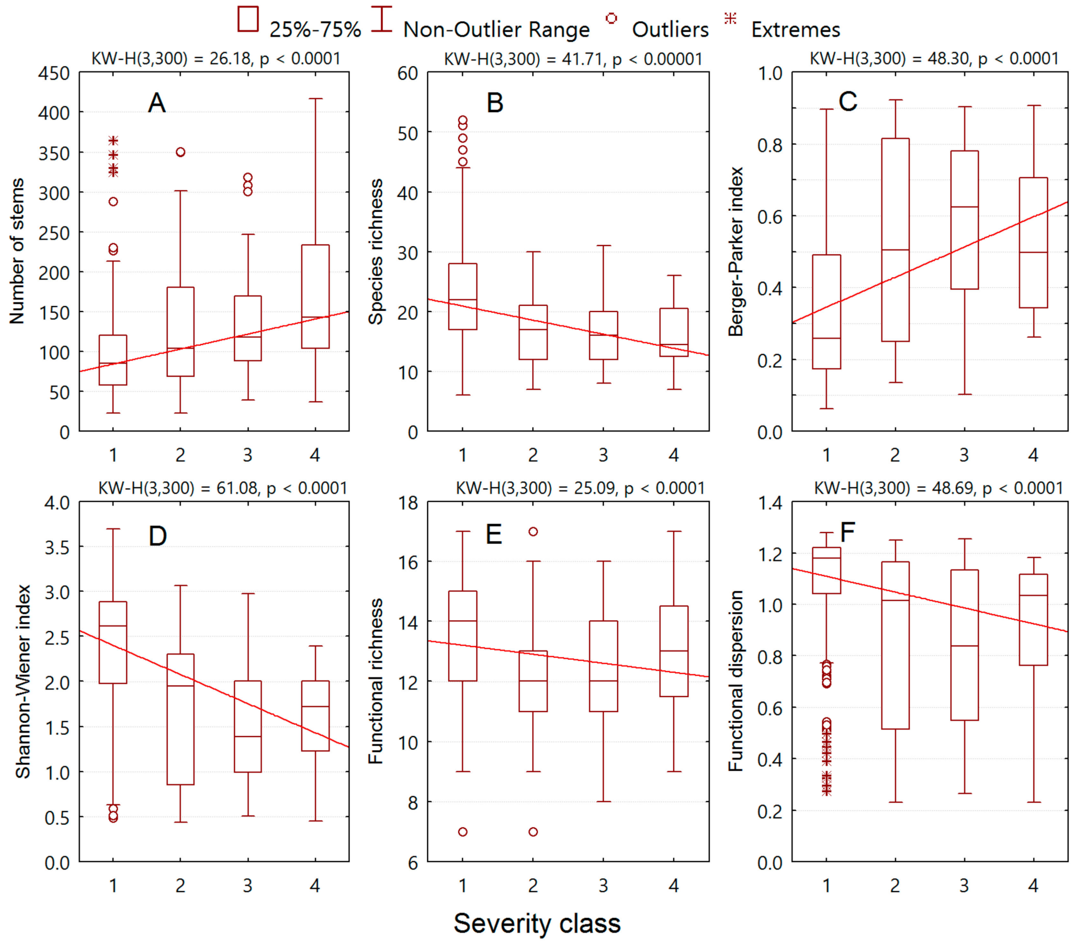

Figure 3. Changes of understory community parameters (**A**–**F**) in relation to invasion severity. A linear fit to the medians was plotted to show the trend of change. The invasion severity classes are defined according to the total number of invasive plant individuals found in a subplot, as follows: 1 = Uninvaded; 2 = Low (1 stem); 3 = Medium (2–5 stems); 4 = High (≥6 stems).

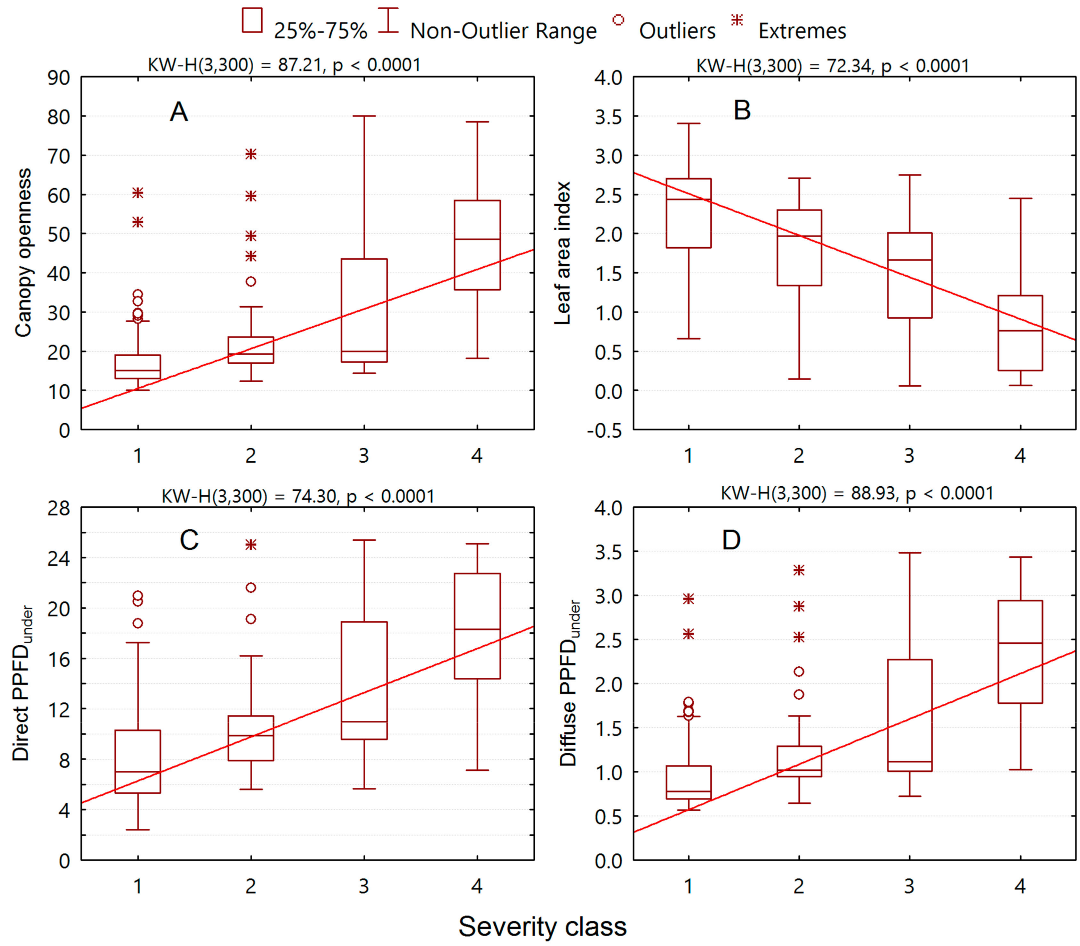

Figure 4. Changes of canopy structure (**A**,**B**) and understory photosynthetically-active photon flux density ($PPFD_{under}$; **C**,**D**) in relation to invasion severity. A linear fit to the medians was plotted to show the trend of change. The invasion severity classes are defined according to the total number of invasive plant individuals found in a subplot, as follows: 1 = Uninvaded; 2 = Low (1 stem); 3 = Medium (2–5 stems); 4 = High (≥6 stems).

3.3. Indicator Species of the Resident Community for Alien Plant Invasion

Eight understory species were detected as indicators of uninvaded habitats (Table 4). These are the common floristic elements native to the subtropical vegetation [42]. Twelve other species were detected as indicators of habitats with various invasion severities (Table 4). Two indicator species from the overstory corresponded with land use type. The fruit tree *Dimocarpus longan* from the agroforestry ecosystem was associated with habitats of high invasion severity, while the *Acacia mangium* from the artificially rehabilitated forest was associated with medium invasion severity (Table 4). Ten understory species indicative of habitats with low to high invasion severity are light-demanding plants that commonly occur in the open, under canopies with high openness, or in habitats with disturbance [45]. These understory species are similar in ecophysiological aspects with the invasive alien plants [45], especially the worst invasive plant *Mikania micrantha*.

Table 4. Plant species with a significant indicator value (IV) ≥ 20 for different invasion severity classes from both the overstory and understory resident communities. The invasion severity classes are as follows: Uninvaded, Low (1 stem), Medium, and High (≥6 stems).

Invasion Severity Class	Species	Growth Form	IV	*P*
Overstory				
Medium	*Acacia mangium*	Tree	22.8	0.0019
High	*Dimocarpus longan*	Tree	55.1	0.0001
Understory				
Uninvaded	*Adiantum flabellulatum*	Fern	34.7	0.0028
Uninvaded	*Wikstroemia nutans*	Shrub	26.1	0.0005
Uninvaded	*Tricalysia dubia*	Shrub	23.6	0.005
Uninvaded	*Rapanea neriifolia*	Shrub	22.5	0.0064
Uninvaded	*Itea chinensis*	Tree seedling	21.7	0.0065
Uninvaded	*Styrax suberifolia*	Tree seedling	21.4	0.0039
Uninvaded	*Gardenia jasminoides*	Shrub	20.6	0.0166
Uninvaded	*Smilax hypoglauca*	Climber shrub	20	0.0037
Low	*Psychotria rubra*	Tree seedling	29.1	0.0184
Low	*Litsea glutinosa*	Tree seedling	28.6	0.0029
Low	*Ficus hirta*	Shrub	24.7	0.0348
Medium	*Aporosa dioica*	Tree seedling	28.8	0.0077
High	*Lygodium japonicum*	Fern	58.7	0.0001
High	*Miscanthus sinensis*	graminoid	58.3	0.0001
High	*Blechnum orientale*	Fern	42.2	0.0002
High	*Hedyotis hedyotidea*	Climber shrub	34.3	0.0001
High	*Microstegium vagans*	Graminoid	32.2	0.0002
High	*Lindsaea heterophyllum*	Fern	21.5	0.0019

3.4. Major Drivers for the Alien Plant Invasion

The relative importance of major biotic and abiotic determinants for alien plant invasion were visualized by the bar plots with Random Forest (Figure 5), a data mining algorithm. The most important variable for predicting total abundance of all the invasive species was land use type (Figure 5A), while for the abundance of *Lantana camara* and *Mikania micrantha*, the most important predictor variables were overstory Berger–Parker index and canopy openness, respectively (Figure 5B,C). Other important predictors for alien plant invasion included leaf area index, understory diffuse PPFD, management regimes and density of overstory plant individuals for the total invasive plant abundance (Figure 5A); land use type, overstory functional dispersion, overstory species richness, overstory Shannon–Wiener index, understory functional dispersion, and management regimes for predicting the abundance of *Lantana camara* (Figure 5B); and land use type, understory diffuse PPFD, understory direct PPFD, and leaf area index for predicting the abundance of *Mikania micrantha* (Figure 5C). Although functional diversity of the understory plants significantly decreased with the invasion severity, surprisingly they were less important as compared with canopy structure and gap light variables for predicting invasive alien plant abundance, especially *Mikania micrantha* abundance. Canopy structure and understory gap light regimes are among the most important factors determining the abundance of the worst invasive plant *Mikania micrantha*.

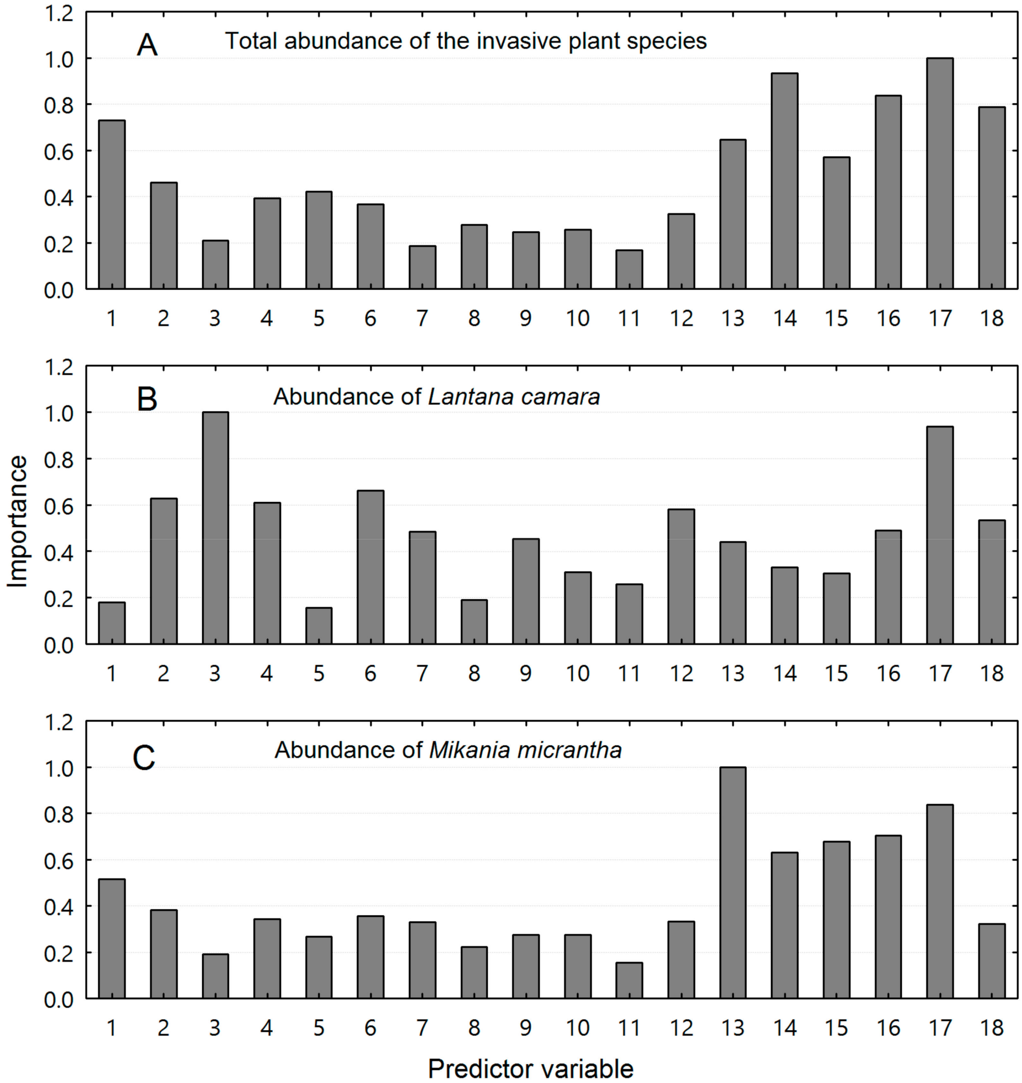

Figure 5. Predictor variable importance showing major biotic and abiotic factors influencing alien plant invasion. The bar plots are generated with Random Forest regression model, with overstory and understory diversity metrics, canopy structure and gap light attributes, land use types and management regimes as predictor variables, total abundance of invasive alien plants (**A**), the abundance of *Lantana camara* (**B**) and the abundance of *Mikania micrantha* (**C**) as response variables. Two other invasive alien species, *Eupatorium catarium* and *Rhynehelytrum repens* were excluded from analysis because they have either few occurrences in the quadrats or only few stems found in the survey. Response variables are given inside each graph panel. Predictor variable codes: 1 = overstory stem density; 2 = overstory species richness; 3 = overstory Berger–Parker index; 4 = overstory Shannon–Wiener index; 5 = overstory functional richness; 6 = overstory functional dispersion; 7 = understory stem density; 8 = understory species richness; 9 = understory Berger–Parker index; 10 = understory Shannon–Wiener index; 11 = understory functional richness; 12 = understory functional dispersion; 13 = canopy openness; 14 = leaf area index; 15 = understory direct PPFD; 16 = understory diffuse PPFD; 17 = land use type; 18 = management regime.

4. Discussion

Land use types of varying disturbance regimes had significant impacts on community structure, species composition and diversity, and these community parameters in turn changed with plant invasion severity. At ecosystem scale, an increasing trend of invasibility was observed from natural forest through the agroforestry ecosystem, corresponding to a decreasing trend of species richness in both the overstory and understory across these land use types. Canopy structure, understory light regimes, community structure, species composition, and plant diversity varied significantly in relation to plant invasion severity. We found that higher canopy openness, understory direct PPFD, and understory diffuse PPFD, as well as lower leaf area index (LAI) were associated with higher invasion severity.

Four invasive alien species were found from five out of the six ecosystems in the subtropical peri-urban area of south China. Lower plant diversity in both the overstory and understory of the resident ecosystems was consistently associated with more severe alien plant invasion to the ecosystems. The highest total abundance and plot occurrence of the invasive plants were found in the agroforestry ecosystem with the highest disturbance. At plot scale, an increase in invasion severity was associated with a significant decrease in overstory stem density, overstory and understory species richness, Shannon–Wiener index, and functional diversity, but with a significant increase in overstory and understory Berger–Parker dominance and understory stem density.

The invasibility of the resident communities to alien plants are heavily affected by their resource availability [46]. Resource availability affects the growth and development of plants [47–49]. Higher overstory LAI reduces canopy openness, understory direct and diffuse PPFD, thus leading to lower temperature in the understory [50,51]. Invasive plants found in our study plots are light-demanding plants. Their performance and invasiveness were inhibited by lower light availability and temperature. Overstory plants with different preferences for light resource occupy different space in vertical direction in the community. In a community with higher diversity, trees might use space fully and intercept more light resources, such that less light is able to reach the understory. Similarly, a community with lower diversity in the overstory intercepts less light resource and there will be more light transmitted to the understory [50,52]. Lower stem density in the overstory increases the canopy openness and consequently increases the light resource transmitted to the understory to promote the growth of light-demanding plants, thus leading to higher ecological dominance and lower species diversity in the understory. According to the biotic resistance hypothesis, a community with higher diversity is more resistant to alien plant invasion [16]. The biotic resistance of the resident communities to invasive plants results largely from the resource complementarity effect and the sampling effect [53]. As the resource complementarity effect hypothesis proposed, different understory species complementarily use light and soil resource. A species-rich community use environmental resources more fully and less resource will be left for the alien plants [17]. According to the sampling effect, a species-diverse community is more likely to contain highly suppressive species to inhibit alien plant invasion by competing for resources [54,55] or by producing antagonistic substances [56]. Decreases in stem density and species diversity in the overstory may also increase plant invasion severity by reducing the effects of shading exclusion on invasive plants.

Multi-response permutation procedures (MRPP) reveal significant differences in species composition in both overstory and understory of the resident communities across plant invasion severity classes. Significant differences were also detected by pairwise comparison between the invasion severity classes, except for the Low vs. Medium classes. Overstory plants shape the micro-climate and plant species composition in the understory [50], while changes in understory species composition may lead to changes in species interactions, i.e., competition or facilitation [57], adding to the biotic factors that influence plant invasion severity. Indicator species analysis (ISA) provides a simple and intuitive method to calculate indicator values of specific species in the resident communities for indicating alien plant invasion severity. Conventional ISA usually treats indicator species as a response variable, such as indicator plants of a particular soil gradient [40,58]. Instead, here, we use ISA to find species from the resident community as predictors that are indicative of a particular invasion severity. Eight common understory plant species characteristic of the subtropical flora were detected as indicators of uninvaded habitats, which are characterized by high LAI, low canopy openness, and low understory light resource. Such habitats are resistant to invasion of the light-demanding alien plant species. Ten understory plant species and two overstory plant species were detected as indicators of the invaded habitats. *Dimocarpus longan* from the agroforestry ecosystem is the overstory fruit tree species indicative of high plant invasion severity, while *Acacia mangium* from the artificially rehabilitated forest is the overstory timber tree species indicative of medium plant invasion severity. The two ecosystems used to be intensively managed and later were left uncultivated to permit natural or artificially regeneration for noncommercial ecological purposes. All the ten understory species indicative of the invaded habitats are light-demanding plants, with similar habitat requirements to the invasive plants.

We found that land use type was the most important predictor for the total number of invasive plants. Land use type and management regimes exert influences on invasive plants in various ways. Changes in land use types from natural to managed types will alter resource availability and resource use by native plants [59–61]. Higher environmental resource availability due to plant exclusion by changes in land use types or management regimes will increase plant invasion severity. The most important predictor variables for the abundance of *Mikania micrantha* and *Lantana camara* were canopy openness and overstory Berger–Parker dominance index, respectively. *Mikania micrantha*, one of the most notorious "plant killers", is a climbing weed with high photosynthesis and growth rate [43,44]. Climbing plants is usually sensitive to light, heat, and moisture conditions [62]; therefore, canopy openness shaping the understory micro-climate became the most important driver for the invasion severity of *Mikania micrantha*. *Lantana camara*, a shrub species competing for space and resources against other standing plant individuals, might be chiefly affected by the crowding effect of other standing neighbors. Higher community dominance and thus lower diversity in the overstory might provide more space, and there might be less shading exclusion of *Lantana camara*.

As the indicators for disturbance and ecosystem history, land use types and management regimes of a forest ecosystem are associated with plant invasion in various ways [63,64]. Land use types and forest management regimes alter the distribution of environmental resources in an ecosystem both directly and indirectly through changed community structure and species composition [59]. Changes in site conditions and biotic interactions may transform habitat invasibility and the severity of alien plant invasion. For examples, anthropogenic irrigation, fertilization, and burning or fire control can alter soil moisture and nutrients that are fundamental resources for invasive plants [60,61]. Deforestation or reforestation during land use changes may eliminate or increase species diversity. Alterations in species composition and community structure may change the availability of environmental resources for alien plants. Changes in land use types and forest management regimes may also bring alien propagules to the resident community, raising possibilities of alien plant invasion [65]. Our study has identified indicators for habitat and community invasibility; however, further work such as control experiments still needs to be done to enhance our mechanistic understanding of the interactions between plant invasion and the biotic and abiotic indicators of habitat invasibility.

5. Conclusions

Finding indicators of alien plant invasion to the resident communities will provide forest managers an easy way to control plant invasion using ecosystem management methods. Indicators of different scales have been identified for predicting alien plant invasion and the invasion severity. Land use type is the ecosystem-scale indicator that reflects disturbance regimes and management regimes. The community-level indicators including species composition and diversity metrics varied significantly across invasion severity classes, while the species-level indicators were represented by certain species that were directly indicative of a particular invasion severity. Of all these indicators, land use type was the major indicator that encompassed, determined or shaped the other indicators. Our results demonstrate that land use types with varying disturbance regimes determine the spatial heterogeneity in plant biodiversity, species composition and community structure of the resident communities, which predicts alien plant invasion and habitat invasibility; and that the severity of alien plant invasion in turn is a good indicator of habitat disturbance across the ecosystems.

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