

Article

Effect of Anthropogenic Disturbance on Floristic Homogenization in the Floodplain Landscape: Insights from the Taxonomic and Functional Perspectives

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Abstract: Anthropogenic disturbances pose significant threats to biodiversity. However, limited information has been acquired regarding the degree of impact human disturbance has on the β -diversity of plant assemblages, especially in threatened ecosystems (e.g., floodplains). In the present study, the effects of anthropogenic disturbance on plant communities of floodplain areas (the Miya River, Mie Prefecture, Japan) were analyzed. The taxonomic and functional β -diversity among different degradation levels were compared, and the differences were assessed by tests for homogeneity in multivariate dispersions. In addition, the effects of non-native species and environmental factors on β -diversity were analyzed. As revealed from the results, anthropogenic disturbance led to taxonomic homogenization at a regional scale. The increase in non-native invasions tended to improve homogenization, whereas at a low degradation level, the occurrence of non-natives species was usually related to taxonomic differentiation. Furthermore, though the increase in non-natives and environmental parameters significantly affected the β -diversity of the floodplain area, environmental factors may be of more crucial importance than biotic interactions in shaping species assemblages in this study. The previously mentioned result is likely to be dependent on the research scale and the extent to which floodplains are disturbed. Given the significant importance of floodplains, the significance of looking at floodplains in the different levels of degradation was highlighted, and both invasion of non-native species and environmental factors should be considered to gain insights into the response of ecosystems to anthropogenic disturbance. The findings of this study suggested that conservation programs in floodplain areas should place more emphasis on the preservation of natural processes and forest resources.

Keywords: anthropogenic disturbance; floodplain; β -diversity; floristic homogenization; non-native species; functional traits

1. Introduction

Floristic homogenization has been defined as the rise in the spatial and temporal similarity of floras [1]. Overall, such loss of plant β -diversity in ecological processes is generally attributed to the local extinction of native species and wide spread of non-natives [2,3]. Since floristic homogenization can destroy the biodiversity in ecology and evolution processes and even affect human wellbeing [4,5], how β -diversity is changing and how it relates to human disturbances should be elucidated for regional biodiversity planning and, more broadly, for the field of conservation biogeography [6,7].

Humans have an adverse effect on natural habitats due to various activities, including urbanization, deforestation, roads, farming, and change of environmental conditions [8]. Therefore, anthropogenic disturbance was considered one of the most important and rapid human-driven factors that lead to

habitat degradation and biodiversity loss [9]. Habitat heterogeneity and fragmentation are considered to be the main consequences of human disturbance [10]. With the development of built-up areas, large natural habitats were transformed into several isolated patches with different biotic and abiotic conditions, which affect species distribution patterns and composition by the filter on ecological demand and dispersal ability of species [11]. Moreover, anthropogenic disturbance could induce habitat degradation by changing soil, hydrological conditions, biogeochemical cycles, and temperature regime, which resulted in the replacement of diverse plant assemblages by widespread, tolerant species [11,12]. Combination of the previously mentioned factors can cause floristic dissimilarity to be overall reduced in disturbed environments. Thus, over the past two decades, the effect of anthropogenic disturbance on floristic homogenization has become an emerging hotspot in ecology [13–16]. Thus far, studies on floristic homogenization have been primarily conducted by comparing the plant assemblages at different urbanization and habitat disturbance levels [15,17–21]. However, existing studies have achieved divergent results. Some of the studies reported a decrease in β -diversity with the increase in anthropogenic disturbance, while others detected an increase or even no change at all [18,19,21]. In any case, species invasions and extinctions are the main causes of biotic homogenization, whilst other habitat alterations that come with human disturbance (e.g., the habitat's heterogeneity and fragmentation, land-use change as well as the intensity and time span of urban sprawl) are factors critically contributing to floristic homogenization [22,23]. However, a comparison of floristic similarity among sites at different disturbance levels has been commonly performed after removing the effect of environmental factors [14,18,24]. Thus far, the association of environmental factors and human disturbance to floristic similarity has been rarely studied at a small-scale, which may hinder the management of urban landscape and habitats.

Though increasing studies have reported the impact of human disturbance on flora homogenization, the emphasis of the existing studies was primarily placed on taxonomic homogenization. However, homogenization can be also manifested in increased similarity in the trait composition, a process known as functional homogenization, which is arousing gradual attention [25–27]. Traits are crucial indicators to determine biodiversity as impacted by their roles of shaping species distribution patterns [28], promoting ecosystem stability and functioning [5], as well as determining responses to environmental changes [29]. For instance, common environmental changes caused by human disturbance include elevated temperature, drought, and alkaline and eutrophic soils; these changes could potentially act as biotic environmental stressors or filters, impacting plants depending on the traits they have evolved to utilize external environments (e.g., moisture preference, nutrition requirement, dispersal strategy, leaf traits, and lifeform) [30,31]. Since functional traits often reflect the requirements of vegetation for the environment and show close relationships with human disturbance [32], trait-based approaches should be conducted in combination with species-based approaches to comprehensively study the relationship between anthropogenic disturbances and floristic homogenization.

Floodplain areas are one of the most significantly threatened ecosystems that exhibit susceptibility to anthropogenic impacts [33]; research involving riparian plant assemblages may be highly conducive to connecting local floras' responses to degradation level with β -diversity. However, it is noteworthy that limited studies assessing the impacts of anthropogenic disturbance on the β -diversity of plant communities have been conducted in riparian areas [6,18,34]. Floodplain areas encompass the space between the running water and the floodplain, where vegetation is subject to natural disturbance, such as flooding, sediment, and inundation [35]. However, as an attraction of urbanization and human activities, riparian areas and plant assemblages come under the pressure of artificial disturbances [36,37]. To be specific, anthropogenic disturbance in floodplain areas is associated with the expansion of impervious surfaces, which alters hydrological and sediment regimes, increases the frequency of flood events, and inhibits the infiltration of rainfall, thus causing natural floodplain habitats to be lost and degraded [38,39]. On the other hand, humans impose intensive pressures on floodplain areas. Some of the most apparent types of disturbance consist of soil compaction, water and soil pollution,

trampling of vegetation, and introduction of non-native species [40,41]. Moreover, anthropogenic disturbance disrupts the heterogeneity of the floodplain landscape by construction of hardening banks and recreational spaces, and destruction of floodplain forests, which in turn alters the composition and diversity of plant assemblages [42,43]. It has been increasingly evidenced that anthropogenic disturbance affects biodiversity, whereas most of the relevant studies have focused on residential areas or parks [14,17,44]. Hence, it is necessary and urgent to elucidate the sustainable developing systems in the floodplain areas to better support their ecological services (e.g., providing heterogeneous habitats and maintaining biodiversity) [45].

Thus, this study analyzed floristic homogenization in the floodplain landscape to explore the responses of β -diversity to the invasion of non-natives and environmental factors. The focus was on all the shrubs and herbaceous species that occur in the sampling sites, since the previously mentioned layers contain the majority of species richness in riparian ecosystems and exhibit the susceptibility to environmental change [46,47]. This study aimed to understand the effects of anthropogenic disturbance on patterns of taxonomic and functional homogenization in shrub and herbaceous assemblages in the floodplain area. The following objectives were set: (1) to examine whether human disturbance induces floristic homogenization, (2) to identify whether the increase in non-native species generates floristic homogenization, and (3) to determine the effects of the environmental matrix (LULC parameters and human disturbance) on floristic homogenization. This study predicted (1) floristic homogenization driven by the high level of human disturbance, (2) floristic homogenization associated with increased non-native species, and (3) the environmental matrix may affect the taxonomic and functional β -diversity of plant assemblages.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Mie Prefecture (Central Japan). We selected the floodplain area of the Miya River for this study (Figure 1). The Miya River originates from Mt. Ōdaigahara and flows into the Ise Bay. It is officially classified as a Class 1 river by the Japanese government and is one of four Class 1 rivers that flow solely through Mie Prefecture. This river exhibits a 91 km length and a basin area of approximately 920 km². The average annual temperature is 15 °C, and the mean annual precipitation is about 1847.8 mm (average at the Obata observation station for 2002–2018, which is located in this study area). The Miya River basin is composed of Ise City, Tamaki Town, Watarai Town, Taki Town, Ōdai Town, and Taiki Town. The population of this river basin is approximately 140,000, primarily concentrated in Ise City. The land-use status in the Miya River basin is nearly 84% mountainous areas, about 8% farmland, about 4% urban (e.g., homestead), and approximately 4% other areas (Ministry of Land, Infrastructure, Transport, and Tourism, 2016). The urban area is concentrated in Ise City in the lower reaches. The source basin and upper reaches are designated as national parks and county parks, respectively, and the forest area ratio is high.

The Miya River basin can be roughly split into the source part, the upper part of the mountain, the middle part of the hill, and the lower part of the plain. Moreover, vegetation, climate, and land-use also exhibit different characteristics according to the differences in these areas (Ministry of Land, Infrastructure, Transport, and Tourism, 2016). The source reach is characterized by continuous mountain areas with an average altitude of more than 500 m. *Fagus crenata* Blume, *Tsuga sieboldii* Carr., and *Cryptomeria japonica* (L.f.) D. Don are the dominant species, forming a forest landscape. The upper reach winds its way through the V-shaped valley in the low mountains, achieving an average altitude range of 100–500 m. The riparian areas in the middle reach are formed in the hills, with an average altitude of approximately 300 m. The middle reach of the Miya River is narrow and composed of a continuous forested strip, gravel floodplain, and cultivated areas. The dominant plant species include *Chamaecyparis obtuse* (Siebold & Zucc.) Endl. and *Cryptomeria japonica*. The lower reach with an altitude below 100 m above sea level is characterized by vast agricultural landscapes and the core urban area of

Ise City. In the lower reach area, the floodplain has been frequently employed as a recreational space. Moreover, to protect residents from flooding, most of the floodplain area in the lower reach has been reinforced. The plant species that dominated in this area were *Phragmites australis* (Cav.) Trin. ex Steud. and *Phragmites japonica* Steud.

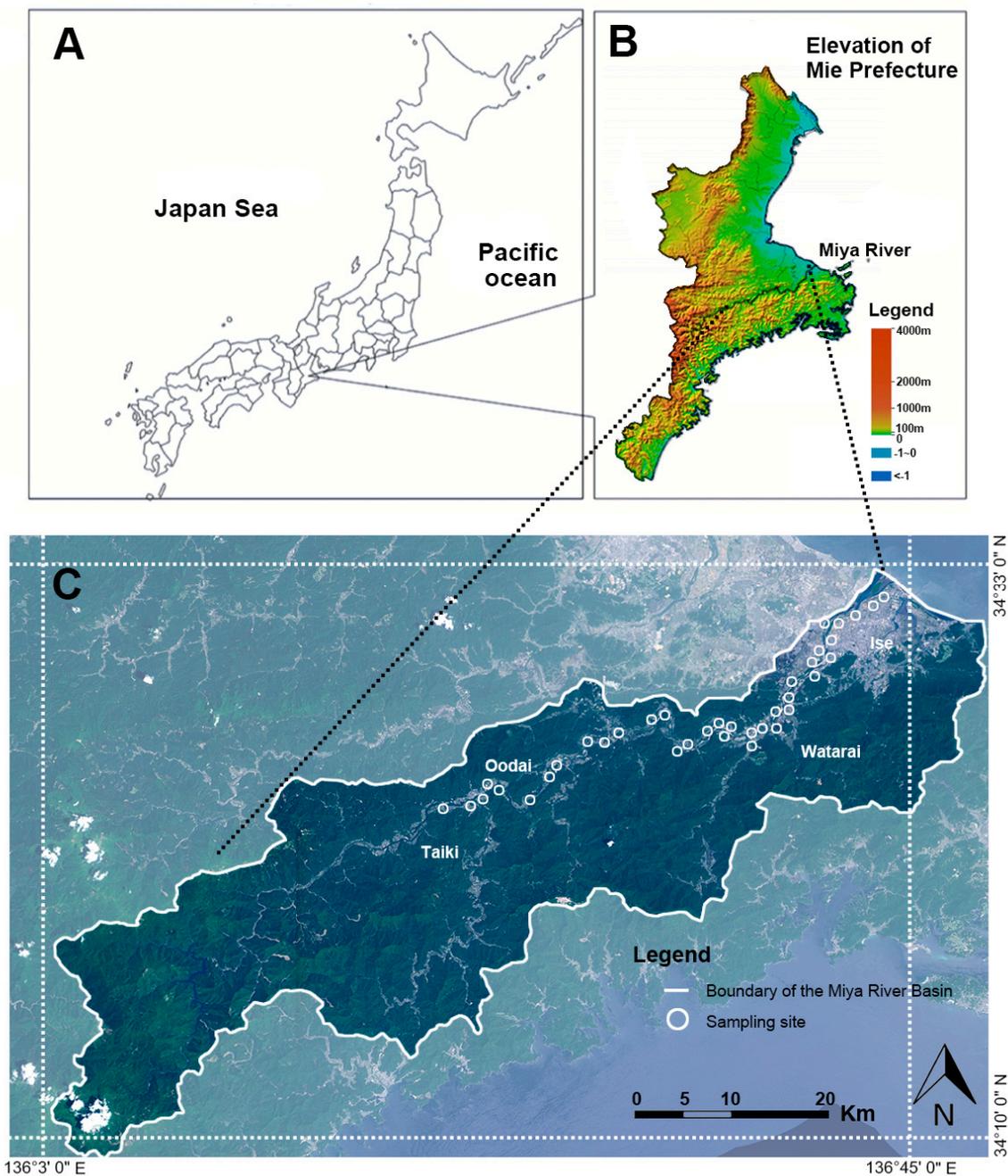


Figure 1. (A) Location of the Mie Prefecture. (B) Location of the Miya River and elevation map of the Mie Prefecture. (C) Area of the Miya River basin and the location of sampling plots.

2.2. Field Sampling

Ideally, the extant and historical vegetation data should be used to compare the effect of anthropogenic disturbance on the variation of floras. Since these data are usually unavailable, sampling sites with different degradation levels are commonly compared to determine a spatial change in plant communities. Therefore, this approach was applied in the present study. First of all, the lower, middle,

and upper reaches of the Miya River basin were selected as the study area, because these areas can reflect the variation of anthropogenic disturbance. The lower reach of the Miya River is located within Ise City, subject to the modification of riparian land cover and human activities. The middle and upper reaches of the Miya River are embellished by paddy fields, tea fields, as well as peasant households. Secondly, to obtain unbiased and spatially well-represented sampling sites, a 1/25,000 digital land condition map (geospatial information authority of Japan, 2014) was used as the base layer, and the basin area was divided into 74 squares with an area of 1km² (each square was considered as a potential representation of a sampling site). The sampling sites were selected according to land condition (riparian lowland), size (floodplain width >50 m), and vegetation structure (vegetation cover >80% and excluded bare ground). In this step, the satellite image (1:5000), and 1/25,000 vegetation map downloaded from J-IBIS (Japan Integrated Biodiversity Information System, 2013; <https://www.biodic.go.jp/index.html>) were used as Supplementary Materials. Then, a total of 49 floodplain areas were selected according to previously mentioned criteria. Meanwhile, to eliminate the influence of inaccessibility and significant differences in environmental conditions, we conducted a field reconnaissance survey to ensure the appropriateness of the 49 floodplains. Finally, 36 sampling sites were selected from the upper to lower reaches. Among the 13 eliminated floodplains, 9 floodplains were forbidden to access and 4 floodplains were excluded for inadequate vegetation coverage. In some parts of the floodplain areas, riparian lowlands were transformed into major beds, thus major beds and waterside lowlands of the floodplain area were selected as the primary sampling area (Figure 2).

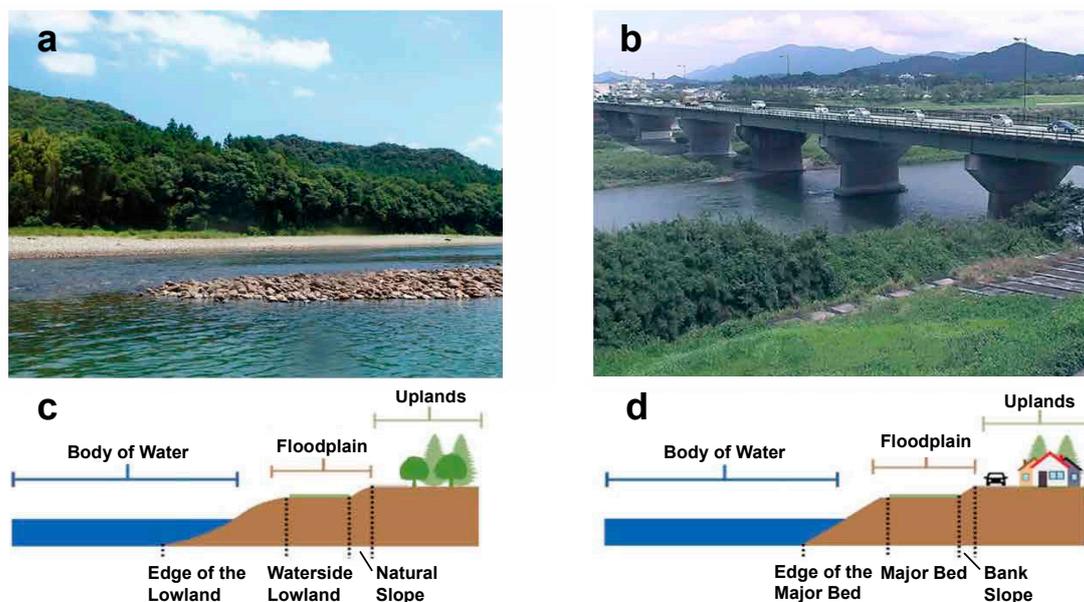


Figure 2. Examples of the sampling area. (a,b) example images of waterside lowland and major bed; (c,d) example section structure of waterside lowland and major bed.

A vegetation survey was carried out by using the line transect method [48]. In each of the selected sampling sites, 10 × 10 m sampling plots were positioned along transects perpendicular to the river at intervals of 50–100 m. According to the length of the shore, each sampling site contained one or two transects, aiming to establish the effort of transects proportionate to floodplain length. When the length of the sampling areas was not enough to accommodate the two transects, two sampling plots were established along the transect to ensure that each sampling site had two sampling plots. The shrubs were recorded in the 10 × 10 m plots, and the herbs and grasses were investigated in 5 smaller plots of 1 × 1 m, and randomly nested in the 10 × 10 m plot. In each plot, the name, coverage, and density of all shrubs and herbs were measured. The coverage of each plant was measured visually within each sampling plot according to a scale of 1–5: 1 = less than 5%, 2 = 5%–25%, 3 = 25%–50%, 4 = 50%–75%, 5 = 75%–100% [49]. The density of plant species was recorded by counting the number

of individuals within a range of 1×1 m. Regarding clonal species, which have many stems for each individual, density was determined by dividing the total stem number by the mean number of stems per individual. Although tree species were recorded in the investigation process, they were excluded from further analyses for two reasons: (1) herbaceous and woody species respond differently to environmental change for the differences in turnover rate and longevity, therefore, adding tree data in vegetation analysis might lead to an inaccurate result in the current study; (2) trees in our study area may have an artificial character and there was no information available to distinguish planted trees from natural occurrences, thus the information that was involved in forest stand and management was not considered as an anthropogenic predictor for environment vegetation analysis. Plant species were identified to the species level in situ. For those species that could not be immediately identified, specimens were taken to the laboratory where they were identified by matching with a botanical guide and preserved herbarium specimens. Five soil samples were collected from five small plots that were randomly selected in each sampling plot at a depth of 0–40 cm to determine the soil texture. All soil samples were removed with a corer and were stored in labeled plastic bags immediately afterward.

2.3. Delineation of Sampling Area into Different Level of Habitat Degradation

The level of habitat degradation was delineated by calculating the Normalized Difference Vegetation Index (NDVI) [50] (Supplementary A). A 500-m buffer zone was set around each sampling site to calculate the NDVI. This index could be calculated by measuring the difference in reflectance between the red band (RED) and near-infrared band (NIR) of the satellite images. The NDVI ranges from -1.0 to $+1.0$, where positive values represent the increase in the amounts of green vegetation and negative values indicate the degradation of the habitat [51]. The NDVI was calculated by:

$$\text{NDVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED}} \quad (1)$$

where NIR denotes the near-infrared band digital number value; RED is the red band digital number value. The NDVI was calculated based on a Landsat ETM 7 satellite image (30-m resolution; <https://glovis.usgs.gov>, accessed 16 September 2019) with ArcGIS 10.2 software (ESRI, 2013, Redlands, CA, USA). The NDVI values of all sampling plots in the surrounding buffer zone were averaged. k-means clustering based on mean NDVI values was used to classify floodplains into different levels of habitat degradation—high, moderate, and low (Table 1). The NDVI was correlated with plant photosynthetic activity and was adopted as an indicator of habitat degradation, since NDVI values in highly disturbed areas are smaller than those in less disturbed areas [52,53]. Furthermore, the NDVI was reported to be a powerful proxy and screening tool for monitoring and assessment of riparian habitats [54].

Table 1. Number and location of floodplain areas selected at different degradation levels. Notes: the information of the population was derived from the Mie Prefectural Government.

Characteristic	High	Moderate	Low
Number of floodplains	13	11	12
Mean NDVI values	-0.11 – 0.17	0.17 – 0.4	0.4 – 0.58
Location of floodplains	Ise City (Miyagawatutumi Park, Love River Park, Miyagawashinsui Park)	Watarai Cho area, Tsumura Cho area, Souchi Cho area	Taiki Cho area, Ōdai Town, Kawazoe station area
Proportion of impervious surface (%)	25.47	12.97	5.31
Human population	96,387	15,439	11,603
Total number of plots	26	22	24

2.4. Functional Traits

Each plant species was identified as seven reproductive, physiological, and morphological trait groups. These functional traits could be adopted to measure the impact of environmental change and to quantify the effect of plant assemblages shift on ecosystem processes. Moreover, several environmental indices (Table 2) were selected for their representativeness as responses to natural and anthropogenic disturbances [31]. The plant height was measured in situ. Subsequently, the height data were transformed into five ordinal groups by performing a k-means clustering. Moreover, several surrogate traits were used to assess the ability of plant species to tolerate anthropogenic and hydrological disturbances [32]. For example, the wetness level was adopted as an indicator for the ability of plant species to address alteration of hydrological regimes, so it was linked to the probability of a plant species occurring in floodplain habitats. Shade tolerance is a crucial functional trait that significantly impacts plant community dynamics and is closely correlated with numerous plant traits (e.g., specific leaf area and photosynthetic rate) [55]. Shade tolerance was characterized since it can reflect the forest structure and dynamics in the floodplain area. On the other hand, shade tolerance could reflect the light demand of plant species since light intensity was closely related to human disturbance [56]. Fertility requirement was considered for high nutrition environments and is related closely to the disturbed area [31]. The approach of seed dispersal could indirectly reflect the effect of habitat fragmentation and human disturbance, thus it was included in this study [9]. The data of plant traits were acquired from the field measurements and available published data (see Supplementary B for further details). Considering that the trait values retrieved from the database may be inaccurate, qualitative values instead of quantitative values were adopted to minimize the deviations attributed to the use of trait databases.

Table 2. Ten trait groups and trait states used in the trait matrix. The sources of literature were listed in Supplementary B.

Trait	Trait State
Life form	Annual forb; Perennial forb; Shrub; Fern
Height (cm)	1–50; 51–100; 101–150; 151–200; More than 200
Reproduction	Vegetative; Vegetative and seed; Seed
Shade tolerance	Intolerant; Mid-tolerant; Tolerant
Wetness level	Upland; Facultative upland; Facultative; Facultative riparian; Riparian
Growth rate	Rapid; Moderate; Slow
Seed bank	Transient; Persistent
Seed abundance	High; Medium; Low
Fertility requirement	High; Medium; Low
Seed dispersal	Wind; Water/gravity; animal, multiple

2.5. Land-Use (Land Cover) and Habitat Data

Given the differences in LULC distribution and combination activities existing among three groups of degradation levels [15], the proportions of various land-use types in the surroundings of the sampling plots were extracted to assess the effect of the anthropogenic factors on floodplain floras. To be specific, three predominant land-use types in the studied floodplain landscape were identified, which consisted of (1) impervious surface (rigid pavement area, i.e., buildings, pavement, and roads), (2) forest, and (3) farmland. Different land-use types were delineated in a 500 m radius circular buffer zone around each sampling plot, with Google Earth imagery (2019) as a base layer. To interpret the surrounding land-use type of each sampling plot, we used feature-extraction techniques with ArcGIS 10.2 software (ESRI, 2013, Redlands, CA, USA). In this classification processing step, aerial photograph interpretation and ground features are crucial in providing reference information for each land-use class [57]. Moreover, the management method of floodplains and soil texture was used. Artificial construction was considered as a predictor of degradation of the riparian area, as the construction altered the sediment regimes and hydrological conditions, and added intense

human recreational activities [58]. Soil texture was used as an environmental factor related to local environmental conditions [59]. Coarse-textured floodplain soil displayed a constant link to intensive flush flooding. Soil texture was identified as silt (<0.05 mm), sand (0.05–2 mm), and gravel (>2 mm) using a Malvern Mastersizer 3000 (Malvern Panalytical Ltd., Malvern, UK).

2.6. Statistical Analysis

2.6.1. α - and β -Diversity

The species α diversity was quantified by species richness. Species richness was determined by counting the number of species in plant communities at the plot scale. Furthermore, one-way analysis of variance (ANOVA) was conducted by the least significant difference (LSD) test.

To investigate the variation of species and plant traits in plant assemblages, the taxonomic and functional β -diversity across the river basin were calculated. The β -diversity here denoted the total β -diversity (dissimilarity among all the sampling plots), which was assessed by the Bray–Curtis dissimilarity [60]. The Bray–Curtis dissimilarity ranged from 0 to 1, where 0 meant that the two plots had the same composition, and 1 meant that the two plots did not share any species or functional groups.

To delve into the effect of anthropogenic disturbance on floristic homogenization, taxonomic and functional facets were calculated following three steps. First, a functional matrix was built by multiplying the species-by-trait matrix with the plot-by-species matrix. For the plot-by-species matrix, we used species relative abundance data to measure the dominance of a species on each sampling plot.

Second, for an in-depth analysis, the species matrix and the functional matrix should be transformed into a plot-by-plot distance matrix. For taxonomic β -diversity, the Bray–Curtis distance on the plot-by-species matrix was employed to generate the plot-by-plot distance matrix. For functional β -diversity, the plot-by-plot distance matrix was computed on the plot-by-trait using the Gower distance.

Third, we tested whether anthropogenic disturbance was responsible for floristic homogenization by the approach of Test for Homogeneity of Multivariate Dispersions [61]. This test could analyze the β -diversity (the distance of each site to their group centroid) based on the plot-by-plot distance matrix and subject the acquired values to permutation tests to verify whether these distances differed among groups. Then, we tested the site distances to centroid using ANOVA with 9999 permutations to determine whether the dispersion of three groups of degradation levels differed. Furthermore, the differences in the variations in taxonomic and functional compositions (location differences between centroids) were tested using PERMANOVA [62], and the significance was assessed using 9999 permutations with pseudo-F ratios. The differences in taxonomic and functional multivariate dispersion and composition among three groups of degradation levels were visualized by Principal Coordinate Analysis (PCoA).

2.6.2. Effect of Increase of Non-Native Species

The effect of non-native species on floristic homogenization could be measured by the variations of β -diversity. Thus, the β -diversity (site distance to the centroid) for all plant species was compared to that for natives only. This approach could simulate the invasion of non-natives in a plant community by comparing the changes of β -diversity after “adding” them; on that basis, whether they lead to homogenization can be evaluated. The native β -diversity was compared to that of all species by paired sample *t*-tests, and *p*-values were adjusted by the multiple test Holm correction.

2.6.3. Effect of Environmental Matrix on β -Diversity

The entire set of predictor variables consisted of the proportion of impervious surface, the proportion of forest, proportion of farmland, management method of floodplains, soil texture, as well as the dominance of non-native species (the sum of relative abundance of the non-native species in each plot). First, these predictors were subjected to one-way ANOVA to determine the differences among degradation groups. Correlation analysis (Pearson *r*) was first performed among the predictors

to determine the multicollinearity in our models. We found the dominance of non-native species was correlated with the proportion of impervious surface ($r = 0.48$). Since the joint effects of non-natives and environmental factors on β -diversity should be determined and the r value was less than 0.7, all the predictors were kept. With the total β -diversity of sample plots as the response, we performed boosted regression tree analysis (BRT) [63] to analyze the effect of environmental variables on taxonomic and functional β -diversity. BRT was used for its good interpretability and its flexibility in handling different types of predictors and less sensitivity to multicollinearity [64]. BRT ranks the relative significance and displays the individual effects of each variable in a partial dependence plot. The proportion of forest was included since forest is a crucial component in the floodplain area and forest could be used as a predictor responsible for floristic homogenization, where plots with a large cover of forest, in general, also have high diversity. The BRT model was performed using a tree complexity of five, a learning rate of 0.001, and a bag fraction of 0.5.

All statistical analyses that we applied here were implemented in R version 3.2.2. The k-means cluster analyses, Pearson correlation analysis, and LSD tests in ANOVA were performed with the stats package. The functional trait matrix was implemented in the “fd” package with the “functcomp” function [65]. The multivariate dispersion analyses were performed in the “vegan” package with the “betadisper” function [66]. The comparisons of the distance of each plot to the centroid were drawn with the “permutest.betadisper”, and the comparisons of location using “rda” and “anova.cca” (vegan) were conducted. The BRTs were adopted using the code from the ‘gbm’ incorporated in the “dismo” package [67].

3. Results

3.1. Species Richness and Composition of Plant Assemblages

A total of 124 species were found across all study sites, 37 of which were non-native species. Significant differences were identified between different degradation levels for total, native, and non-native species richness (Figure 3). The total species richness was significantly higher at the low degradation level than moderate and high degradation levels; the species richness of non-natives was significantly higher in highly disturbed areas and reached its lowest value at the low degradation level. The species richness of natives was significantly higher at the low degradation level than that in the moderate and high degradation levels.

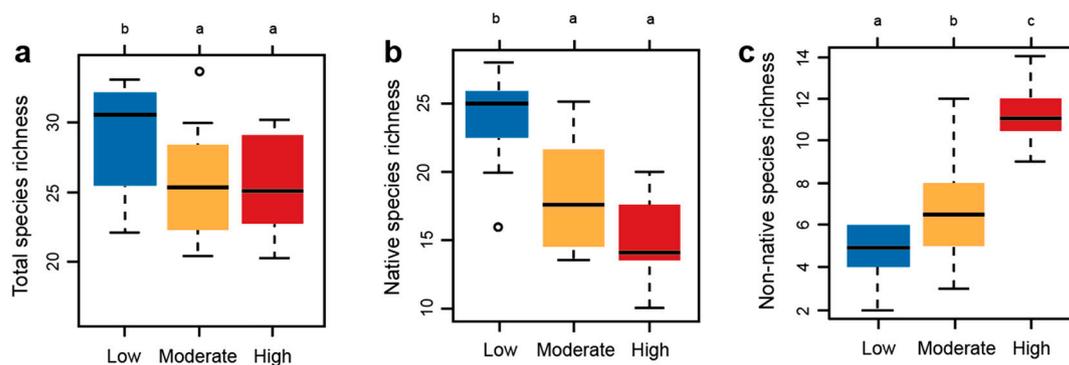


Figure 3. Total species richness (a), native species richness (b), and non-native species richness (c) in different levels of degradation. Data provided show the median (bold line), 25%–75% quartiles (boxes), ranges (whiskers), and outliers (white dot). Significant differences are presented by different letters ($p < 0.05$).

Regarding the most frequent species found in the floodplain area, six native species represent the widespread common species that were observed in most plots throughout the study area. Besides, four non-native species were included in the top ten most frequent plant species (Table 3). These non-native species were recorded at high frequency (more than 41.7%) at high and moderate degradation

levels, whereas there was a relatively low frequency (less than 20.8%) of non-natives observed in areas at the low degradation level. Riparian plant species, such as *Miscanthus sacchariflorus* (Maxim.) Franch. and *Phragmites japonica*, were recorded with a higher frequency in areas at the low degradation level than those in highly disturbed areas.

Table 3. The top 10 most frequent plant species found in floodplain area. Plant species were ranked by frequency of occurrence in all sampling plots ($n = 72$ plots). Notes: species in bold indicate non-native species.

Family	Species	High (%)	Moderate (%)	Low (%)
Polygonaceae	<i>Rumex acetosa</i> (L.)	66.7	54.2	58.3
Asteraceae	<i>Artemisia indica</i> Willd. var. <i>maximowiczii</i> (Nakai) H. Hara	75	70.8	25.0
Asteraceae	<i>Solidago altissima</i> (L.)	79.2	70.8	4.2
Asteraceae	<i>Erigeron annuus</i> (L.) Pers.	83.3	41.7	8.3
Poaceae	<i>Lolium multiflorum</i> Lam.	50.0	58.3	20.8
Rosaceae	<i>Rosa multiflora</i> Thunb.	58.3	33.3	37.5
Poaceae	<i>Miscanthus sacchariflorus</i>	37.5	41.7	45.8
Fabaceae	<i>Trifolium repens</i> (L.)	54.2	50	20.8
Poaceae	<i>Phragmites japonica</i>	25	37.5	41.7
Poaceae	<i>Festuca arundinacea</i> Scherb.	50	37.5	8.3

3.2. Taxonomic and Functional β -Diversity

For the taxonomic aspect, the β -diversity differed significantly with different degradation levels (significant multivariate dispersion tests; Table 4). The dissimilarity was lower at high degradation levels than that at low levels (see polygon size on Figure 4a; and average sites-to-centroid distance illustrated in Figure 4c), indicating that a relatively high degradation level caused taxonomic homogenization. For the functional aspect, however, homogenization phenomenon was absent in degradation levels. Though the β -diversity was lower in highly disturbed areas compared with the areas at moderate and low degradation levels (Figure 4b,d), the differences were not significant by significant multivariate dispersion tests (Table 4).

β -diversity changes were associated with the species and trait composition among degradation levels. The PERMANOVA revealed significant shifts in taxonomic and functional compositions (centroid location) for both taxonomic and functional β -diversity (Table 4), as represented by the isolated location of the centroid at a low degradation level relative to that at high and moderate degradation levels (Figure 4). As revealed from the differences in the location of the centroid, species and traits diverged between the low degradation level and the other two types of degradation levels. However, the relatively short distance between centroids at high and moderate degradation levels showed that the shifts in species and traits composition were similar in these two types of degradation levels.

Table 4. Differences in β -diversity and composition in the floodplain landscape, according to three groups of degradation levels. Note: difference in β -diversity was tested with ANOVA by permutations on site-centroids distances and difference in location of centroid was tested with PERMANOVA.

	Taxonomic Aspect		Functional Aspect	
	F Ratio	<i>p</i> -Value	F Ratio	<i>p</i> -Value
β -diversity	16.92	<0.001	4.09	0.064
Shift in composition	3.34	0.009	2.15	0.037

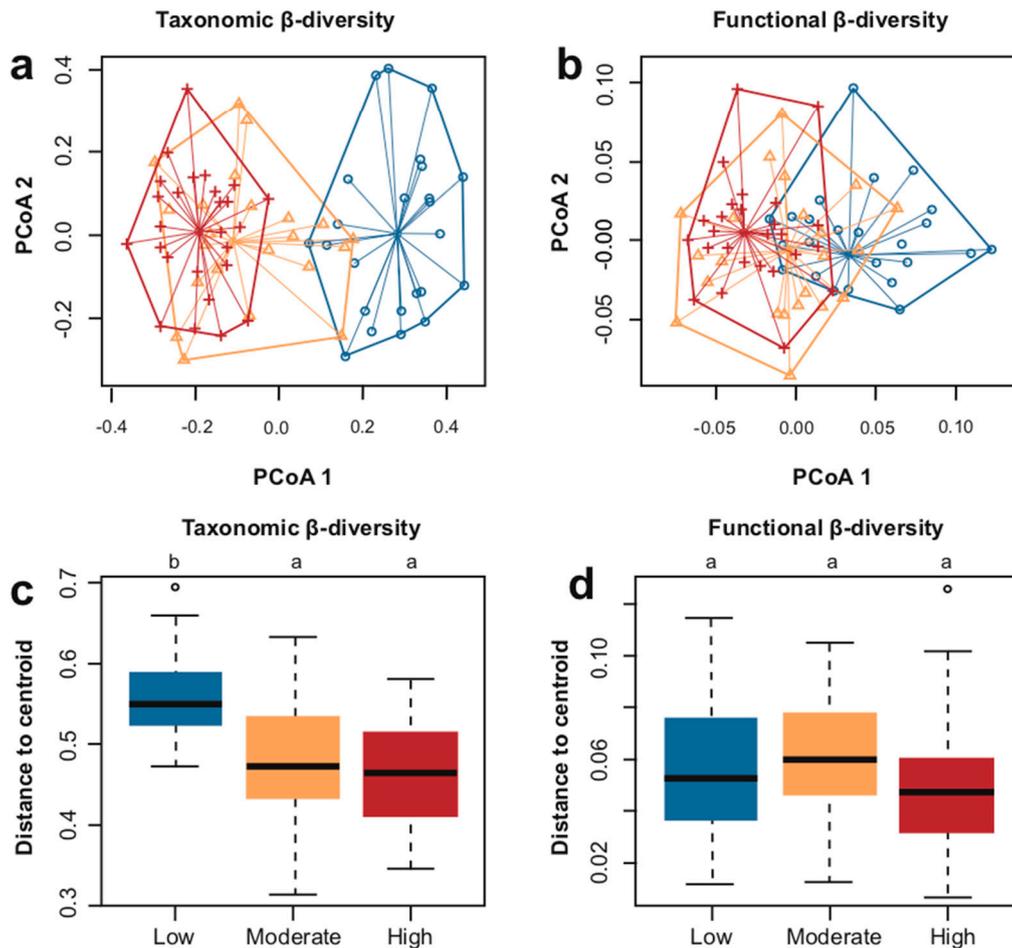


Figure 4. Effect of different degradation levels on the multivariate dispersion of species (a,c) and trait (b,d) composition in floodplain landscape. Taxonomic and functional β -diversity is measured as the distance of sites to their group centroid (using Bray–Curtis and Gower distances, respectively), here represented on the first two axes of a PCoA and using a boxplot (median and quartiles) of the sites-to-centroid distance. On the PCoA, a change in site dispersion around the centroid represents a change in β -diversity, while a change in the centroid location represents a species/trait turnover. Symbols represent each plot in different degradation levels: + = high, Δ = moderate, and \circ = low. Values share same letter are not significantly different at 0.05 significance level.

3.3. The Role of Non-Native Species in β -Diversity

In the taxonomic and functional aspects of the flora, the results of this study showed that the invasion of non-native species in native plant assemblages drives different variation patterns of β -diversity (Figure 5, Supplementary C). The homogenization effect was significant at a high degradation level both in taxonomic and functional aspects after the Holm correction. The increase in non-native species at the moderate degradation level improved homogenization only in functional aspects, while the change of β -diversity in taxonomic aspects was slight. At the low degradation level, the increase in non-native species indeed caused a slight taxonomic differentiation, while it did cause a slight homogenization in functional aspect.

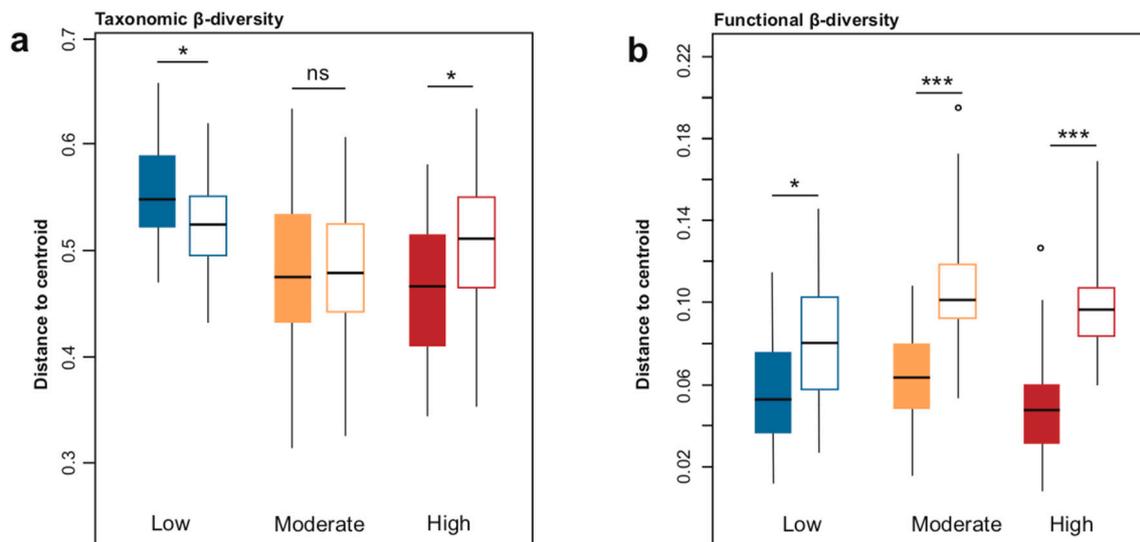


Figure 5. Differences in taxonomic (a) and functional (b) β -diversity induced by non-native species in three groups of degradation level. Variations in β -diversity were assessed by comparing the distances of sites to centroids of native species (native plant species that recorded in all sampling plots) to those of the total flora (complete plant species that are recorded in all sampling plots). Notes: the color-filled boxes represent the β -diversity of total species, and the color-outlined boxes represent the β -diversity of native species. Asterisks indicate a significant change in paired sample t-tests that are adjusted by the multiple test Holm correction. Significance levels: * $p < 0.05$; *** $p < 0.001$; ns, not significant.

3.4. Joint Effects of Non-Native Species and Environmental Matrix

The predictor variables are shown in Table 5. The results of the BRT model reflected the direct or indirect effects of environmental factors on β -diversity. In our study, the BRT model had greater predictive power on functional β -diversity (explained deviance: 0.481) than that on taxonomic β -diversity (explained deviance: 0.429), and the relative contribution of the predictors varied between these two diversity aspects (Figure 6).

The proportion of impervious surfaces had the strongest influence on the taxonomic β -diversity in sampling plots (explaining 34.6% of the variability in taxonomic β -diversity patterns). Taxonomic β -diversity strongly decreased between 10% and 20% of impervious surfaces, implied a relative small proportion of impervious surface sustains higher taxonomic β -diversity. The NDVI also had a significant effect on taxonomic β -diversity and explained 25.9% of the variation of taxonomic β -diversity. The percentage of forest also critically impacted the shaping of taxonomic β -diversity (explaining 17.7% of the variability in taxonomic β -diversity patterns), and taxonomic β -diversity significantly increased beyond approximately 20% of forest cover. The dominance of non-native species was also an important predictor of taxonomic β -diversity and explained 11.4% of the variability in taxonomic β -diversity. For functional β -diversity, artificial management was the top predictor (explaining 26.1% of the variability in functional β -diversity patterns). Partial dependency plots showed that the functional β -diversity was higher in natural floodplains than in floodplains that have been artificially transformed. Besides, functional β -diversity was also strongly explained by the percentage of forest and significantly increased between 20% and 30% of the percentage of forest. In addition, soil texture and the proportion of impervious surface showed strong explanatory effects on functional β -diversity and explained 19.7% and 17.4% of the variability, respectively. For both taxonomic and functional β -diversity, the effect of the percentage of farmland was negligible.

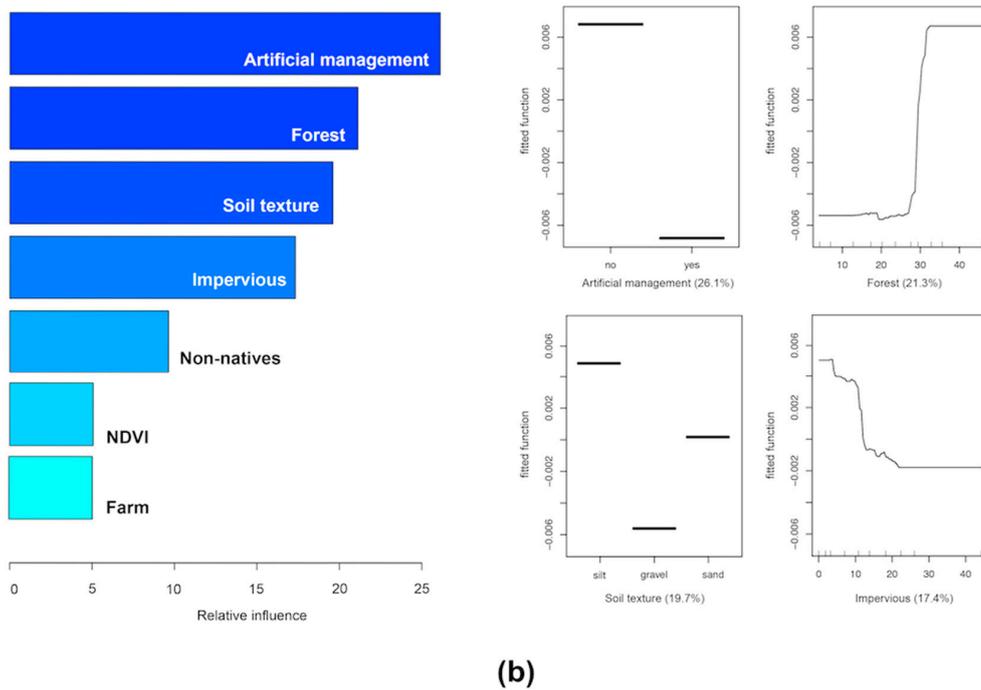
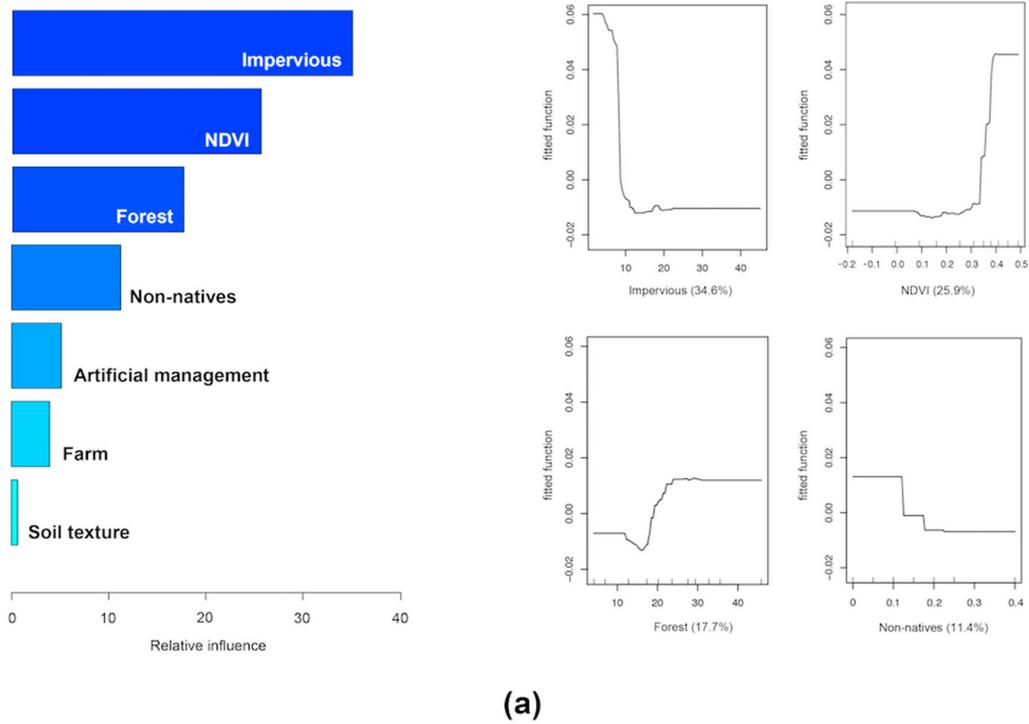


Figure 6. Relative influence of predictors and partial dependency plots for boosted regression tree analyses on taxonomic (a) and functional (b) β -diversity. For taxonomic β -diversity, explained deviance: 0.429; For functional β -diversity, explained deviance: 0.481. Numbers enclosed inside parenthesis indicated the relative importance of predictors. Notes: forest, proportion of forest cover in a 500-m buffer zone; impervious, proportion of impervious surface in a 500-m buffer zone, farm, proportion of farmland in a 500-m buffer zone; non-natives, the dominance of non-native species; NDVI; mean NDVI value in a 500-m buffer zone.

Table 5. Environmental variables in three groups of degradation level. Values represent means \pm SE. Values that share the same letter are not significantly different at 0.05 significance level. Notes: forest, proportion of forest cover in a 500-m buffer zone; impervious, proportion of impervious surface in a 500-m buffer zone, farm, proportion of farmland in a 500-m buffer zone; gravel, percentage of gravel content; sand, percentage of sand content; silt, percentage of silt content; non-natives, the dominance of non-native species (range from 0 to 1); artificial management, presence of reinforced riverbank in the vicinity. NDVI value, mean NDVI value in a 500-m buffer zone (range from -1 to 1).

Predictors	Degradation Level		
	High	Moderate	Low
Land-use and land cover			
Impervious (%)	25.47 \pm 3.17 ^a	12.97 \pm 1.13 ^b	5.31 \pm 0.52 ^c
Forest (%)	16.07 \pm 1.76 ^c	23.27 \pm 2.07 ^b	30.32 \pm 1.68 ^a
Farm (%)	10.61 \pm 2.93 ^b	9.94 \pm 1.67 ^b	16.34 \pm 1.06 ^a
Soil texture			
Gravel (%)	19.81 \pm 4.30 ^a	21.69 \pm 5.97 ^a	22.58 \pm 5.71 ^a
Sand (%)	37.62 \pm 5.45 ^a	36.87 \pm 6.29 ^a	39.82 \pm 1.66 ^a
Silt (%)	42.57 \pm 5.45 ^a	41.44 \pm 7.01 ^a	37.59 \pm 5.41 ^a
Invasion			
Non-natives	0.32 \pm 0.05 ^a	0.25 \pm 0.03 ^b	0.07 \pm 0.01 ^c
Human disturbance			
Artificial management (%)	69.23	36.36	25
NDVI value	0.06 \pm 0.02 ^c	0.27 \pm 0.02 ^b	0.49 \pm 0.01 ^a

4. Discussion

4.1. Floristic Homogenization with Degradation Levels

Most of the studies at a local scale reported that anthropogenic disturbance caused floristic differentiation or absence of the variation of β -diversity [18,19,21], while this study suggested that human disturbance could induce taxonomic homogenization in floodplain landscapes. As revealed by the results of this study, non-native species invasion was responsible for the homogenization in urbanized floodplains. Usually, highly disturbed areas are relatively rich in non-native species [9,14], which has been observed in the current study (Figure 3). It was hypothesized previously that the increase in non-native species might induce taxonomic differentiation in highly disturbed areas [18,68]. However, if some non-native species propagate in most of the sites within the highly disturbed area, they may also enhance homogenization [17]. In the study region, non-native species, including *Erigeron annuus* L., *Solidago altissima* L., and *Lolium multiflorum*, were abundant in nearly all study sites (Table 3). When compared with highly disturbed areas, interestingly, this study reported that the addition of non-native species had a significant impact on taxonomic differentiation at the low degradation level (Figure 5). This can be explained by a lower non-native species number compared to native species at a low degradation level (Figure 3); the plant assemblages likely shared little non-natives. Therefore, the presence of non-native species may have a disproportionately significant impact on β -diversity variations, since the homogenization effect of a non-native species will depend on its high frequency in all the communities. The introduction of a non-native species will lead to differentiation when this species exists as a rare species, while when a non-native species exists extensively, it will induce homogenization [69,70].

For the functional aspect, there were no significant differences in β -diversity in different levels of degradation. However, this study reported that anthropogenic disturbance could indirectly induce functional homogenization for the introduction of non-native species in the native flora. Since the 1960s, Japan has experienced remarkable growth in urban expansion and mass construction works. With the development of roads, residential areas, farmlands, and plantations, the reformation of habitat conditions has facilitated the introduction and spread of non-native species such as *Festuca arundinacea*,

L. multiflorum, *E. annuus*, and *S. altissima* [71]. Since approximately 40% of non-native species in Japan belong to the Compositae and Gramineae families, these non-native species usually have similar traits as generalists, as reflected by a lower proportion of perennial species, faster growth rate, and longer dispersal distance than done by native species [71,72]. On the other hand, the convergence of functional traits was likely associated with the extirpation of specialist species. Urbanization may lead to habitat loss and fragmentation, thus potentially resulting in the decline of specialist species [73]. The species adapted to that natural or specific habitat are more likely affected because they cannot access alternative resources that non-native species can [36]. Overall, non-native species significantly influenced the functional β -diversity, which demonstrated that their traits were dissimilar to that of native species, and some functional traits of non-native species have been preserved after being environmentally filtered [74,75]. Although the impact of anthropogenic disturbance on functional homogenization was absent in this study, the results seem to be an indicator of extinction debt of native species, as our study area reflected more recent urban development than is the case in the metropolis [76], so conservation management should be taken into consideration to minimize potential native species extinctions in the future.

In addition, this study reported that plant assemblages at a low degradation level showed a distinct species composition compared with the plant communities at high and moderate degradation levels. In this study, sampling sites at the high degradation level were subjected to urbanization pressure such as paving and dramatic modification of large areas of land, while at the low degradation level, the sites were under the pressure of agricultural practices. Given that differences in human activities existed among rural and urban land-use categories, abiotic conditions, available resources, and disturbance regimes may be altered [58]. Each of these changes could potentially act as an environmental stressor that differentially shapes plant species distribution depending on their environmental niches and traits [11]. Thus the distinction of species composition might be explained by the regeneration time, or lifespan, of the dominant species in floodplains at different degradation levels [34]. On the other hand, Ise City represented small cities in Central Japan. Over the past few decades, urban expansion has begun to accelerate gradually, which may be reflected in a certain delay in less disturbed floodplains to urbanization and the distinct plant communities identified in this study.

4.2. Driving Factors of the Different Pattern of β -Diversity

Although environmental filtering that was driven indirectly by human disturbance was predominant in the formation of plant assemblages, responses of taxonomic and functional β -diversity to environmental factors were different within the floodplain areas. The taxonomic dissimilarity indicates that a proportion of impervious surface exhibits a relatively low β -diversity. Construction and expansion of impervious surfaces exert multiple effects on the variation of plant species composition. First, the vegetated patches surrounded by buildings and pavements commonly contain low dissimilarity as impacted by pollution, erosion, trampling, and many other human disturbances [77]. Moreover, pruning, mowing, logging, and other common landscaping practices further induce the extirpation of different, especially rare species. Meanwhile, the urban specialists, as the species that are frequently colonized in artificial habitats [78], are partially responsible for the homogenization [79]. On the other hand, the construction of impervious surfaces in floodplain areas created a highly stressful environment that receives frequent hydrological disturbance through scouring flows, together with an increase in nutrient inputs [80]. Following the construction of impervious surfaces, floodplain areas might be subjected to a shift in plant community composition towards non-native and tolerant species [38]. In addition, it was found that there was a positive association between taxonomic β -diversity and NDVI, which was similar to previous studies [81,82]. The NDVI is closely correlated to variables of ecological interest such as urbanization level and habitat degradation [52]. In our study area, most of the sampling plots with relatively low NDVI values were located in urban areas with intensive human activities and land cover modification (Table 1). According to the ecosystem stress hypothesis, anthropogenic disturbance and urbanization resulted in the reduction in habitat heterogeneity and

resource availability, thus having a negative impact on the size of the species pool [83]. On the other hand, the species–energy hypothesis states that the sites surrounded by healthy vegetation could hold more plant species because the resource availability allowed for a large size of species pool, thus reducing the risk of species extinction [84].

It is noteworthy that functional β -diversity is closely related to artificial construction and hydrological disturbance. Anthropogenic disturbances can achieve a regional homogenization of floodplain areas, which was hypothesized to enhance the similarity among riparian plant assemblages in the existing studies [37]. The current study suggested that human disturbances could reduce the functional β -diversity of plant assemblages. Many rivers in Japan are exposed to artificial disturbance (e.g., flood protection measures), and approximately 45% of the riverbanks have been reinforced in the study area, the Miya River (Ministry of Land, Infrastructure, Transport, and Tourism, 2016). By following artificial construction, riparian areas are strongly linked to hydrological alternation, riparian degradation, and intense human recreational activities. Hydrological alternation leads to floodplains which are being inundated less frequently and exist for shorter durations, thus facilitating the establishment of numerous terrestrial species [58,85], and promoting the alternation of vegetation composition; as a typical result, plant trait convergence is generated. As an important local environmental factor, soil texture showed significant effects on functional β -diversity. Coarse-textured floodplain soil is always linked to frequent scouring flows, which washed away much smaller soil particles [86]. Plant functional traits were affected by the roles of nutrient scarcity, water balance, and competition, which were mediated by soil texture [59]. More precisely, coarse-textured soil lacks the ability to hold water and nutrients, which shapes plant assemblages by exerting intense selective pressure on functional traits [87]. Our study implied that local environmental conditions might affect assemblages' composition and exhibit a signal of environmental filter towards the resource-use strategies of plant species.

Both taxonomic and functional β -diversity were significantly correlated with the proportion of forests. Forest could positively affect the dissimilarity of plant assemblages in various ways. First, forests constitute a heterogeneous landscape, namely floodplain–grassland–forest mosaics. Forests create a more closed environment for understory species and show lower daily mean temperature and higher soil and air humidity compared with grassland habitats. Given the distinct differences between forest and grassland habitats, the composition and diversity of plant species may be substantially inconsistent. Second, environmental heterogeneity might critically affect the β -diversity of herbaceous and shrubs, leading to the interactive effects of forest type, forest structure, and forest size. Erdős et al. [88] concluded that species diversity and composition were significantly different in edge-like forests and forests with core areas. Chávez and Macdonald [89] reported that canopy gaps contained more specialist species than forest interiors. Such variation of forest structure might potentially change regional habitats and ecological functions, and consequently, modify patterns of understory plant diversity. This study implied the significance of the conservation value of floodplain–grassland–forest habitat. To conserve a considerable diversity of the species pool in the floodplain landscape, it is necessary to preserve both the meadows and some of the forest habitats.

The dominance of non-native species can significantly predict both taxonomic and functional β -diversity of plants, which could be explained by the regional spread of common non-native species. In addition, a high proportion of non-native species may contribute to the homogenization effect in urban areas by competitive suppression of native species. In this study, however, the environmental factors more significantly impacted the β -diversity of plant assemblages than the invasion of non-native species. This study suggested that environmental parameters might be more crucial than biotic interactions in shaping species communities under intense human disturbances, which was consistent with the finding reported that environmental filtering is assumed to be the strongest at the regional scale [90,91].

4.3. Implication for Conservation

This study highlighted that anthropogenic disturbance was the critical predictor for the biotic homogenization of plant assemblages. Therefore, management strategies in urban areas should aim to restore or preserve natural processes, which are of essential importance to maintaining the taxonomic and functional compositions of the vegetation in floodplains. One of the most direct and effective measures is avoiding any modifications or constructions that separate the floodplain habitat from the river (e.g., public open spaces, embankments) along the riverside. In the scenario of bridges or dams, they are a necessary infrastructure, so they cannot be avoided. Therefore, maintaining several continuous strips of vegetation as a corridor along rivers should be considered.

Although urban areas were characterized by heterogeneous landscape compositions and configurations [17,58], the aggravation of anthropogenic disturbances and consequent habitat homogenization pose a great challenge for conservation in floodplain landscapes [36,41]. Hence, there is an urgent need to maintain habitat heterogeneity within floodplain landscapes. In concordance with the findings of Erdős et al. [88], this study suggests that the conservation of heterogeneous patches in the floodplain area should exhibit high priority. Therefore, it is necessary to take the floodplain areas into consideration when planning urban land expansion for the sake of sustainability of the floodplain ecosystem. On the other hand, incomplete legislation might be a possible reason why the significance of floodplain forests has been neglected in protective management in Japan. It has long been considered that floodplain forests adversely affect flood control, as reflected by reducing the cross-sectional area of the river and causing high-speed flows along embankments. The treatment of floodplain forests, therefore, has been performed conventionally based on felling. Though the Rivers Act of 1997 emphasized the significance of riverside forests for biodiversity conservation [92], there are no specific guidelines for riverside forest conservation. This study suggested that an appropriate management plan can be drawn up by considering floodplain forests on a site-by-site basis instead of viewing them from the viewpoint of the entire river and by specifically analyzing and assessing flood control problems and the role of floodplain forests.

5. Conclusions

Given the striking significance of floodplains, it is notable that this study evidenced the variation of β -diversity patterns of plant assemblages at different levels of degradation. It was highlighted that the environmental matrix was the critical predictor for the floristic homogenization of plant assemblages. In general, both the environmental parameters and the increase in non-native species can change homogenization processes of floodplain flora at anthropogenic disturbance gradients, while in this study area, the environmental factors may be more crucial than biotic interactions in shaping species assemblages. The findings of the mechanisms of floristic homogenization of floodplain floras may help reduce the influences of anthropogenic disturbances on biodiversity. Given the scope of our study, we were not able to directly examine the role of forest management and structure on floodplain vegetation, thus more forest-related environmental factors should be considered in the coming research to delve into the thorough relationship that may be critical to sustainable management in floodplain areas.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/10/1036/s1>, Figure S1: Normalized difference vegetation index (NDVI) map of the study area, Table S1: Descriptions of functional traits, Table S2: The results of paired sample t-test, Table S3: Species name and functional traits that recorded in study area.

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