

主論文

The effects of anthropogenic disturbance on riparian vegetation of two rivers  
with different urbanization in central Japan

(日本中部の都市化影響の異なる 2 河川の河畔植生に対する人為攪乱の影響)

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## Abstract

Ongoing urbanization profoundly impacts ecosystems worldwide by changing environmental conditions and reducing biodiversity. Despite the great significance of riparian habitat as an essential component of urban ecosystems, the effects of urban development on the biodiversity of riparian ecosystems remain poorly understood. In this dissertation, this issue was addressed by investigating the effects of anthropogenic disturbance on riparian plant assemblages in central Japan. To achieve this, I applied an urbanization gradient approach, comparing the species diversity and composition of sites in different levels of anthropogenic disturbance. This dissertation consists of three studies.

**The first study (chapter 2)** aimed to disentangle the roles of urbanization on vegetation communities in riparian areas. To do this, I starting from a new perspective, comparing plant communities in the same riparian habitat type whereas at different levels of urbanization, instead of using the traditional urban-rural gradient. Plant diversity and abundance were recorded in 96 plots along the Shonai River and Miya River. Various urbanization and local environmental characteristics of each sampling plot were assessed to describe the urbanization level. In this study, we compared species richness, types of vegetation, and composition patterns of the plants in our study. From the species diversity aspect, I found the response of species richness to urbanization varied according to the habitat types. In artificial habitats, the sites with relatively high levels of urbanization had the highest species richness, while the opposite trend was observed in semi-natural habitats. From the plant community composition aspect, I found that a high level of urbanization was always associated with a large abundance of alien and ruderal species in both artificial and in semi-natural habitats. Furthermore, every component of urbanization that contributed to the variation of species richness was examined in this study. The results showed the dominant factors that determine the species diversity pattern differed from habitat types. In artificial habitats, the proportion of impervious surface was the strongest predictor of the variation in species richness and was associated with the richness of alien, native, and riparian species. In semi-natural habitats, most of the richness of alien and native species were associated with the distance to the city center. These results clarified the response of plant assemblages

to urbanization was varied with habitat types, and recommend the methods of pair comparison of multiple rivers to analyze the impact of urbanization on plant species in riparian areas.

As a crucial component of species diversity,  $\beta$ -diversity of plant assemblages was investigated in **the second study (chapter 3)**. The aim of this study is to investigate the effects of anthropogenic disturbance on the  $\beta$ -diversity pattern of plant communities in riparian areas (the Miya River, Mie Prefecture, Japan). I first compared the taxonomic and functional  $\beta$ -diversity among different degradation levels by using the tests for homogeneity in multivariate dispersions. As revealed from the results, anthropogenic disturbance led to taxonomic homogenization at a regional scale while the homogenization was absent in the functional aspect. I then examined the effects of non-native species and environmental factors on  $\beta$ -diversity. I found the increase in non-native invasions tended to improve homogenization both in taxonomic and functional aspects. However, at a low degradation level, the occurrence of non-natives species was related to taxonomic differentiation. Finally, I assessed the relationship between environmental factors and the  $\beta$ -diversity pattern of plant assemblages. The taxonomic  $\beta$ -diversity was significantly affected by the proportion of impervious surface and NDVI, while the functional  $\beta$ -diversity was associated with the artificial management of riverbank and the proportion of forest. According to these results, this study highlighted the significance of looking at riparian areas in the different levels of degradation, and both invasions of non-native species and environmental factors should be considered to gain insights into the response of ecosystems to anthropogenic disturbance. Furthermore, this study suggested that conservation programs in riparian areas should place more emphasis on the preservation of natural processes and forest resources.

The reduction of specialist species might be a symptom of biodiversity loss driven by humans. In **the third study (chapter 4)**, I use the *phragmites australis* as a target species, exploring the variation of specialist species under the pressure of urbanization at individual and community levels. In this study, 40 sampling plots were established on a suburb-urban gradient along the Shonai River. The results demonstrated that urban areas were associated with degraded dominance of *P. australis* and elevated soil chemical attributes. With decreasing coverage of *P.*

*australis*, the height, stem diameter, and leaf area of *P. australis* showed a decreasing trend. Among all of the environmental factors, soil water content (SWC) and imperviousness were the major factors affecting the characteristics of *P. australis* (40.9% and 22.9% relative explanation, respectively). Compared with land cover factors, soil properties had a greater impact on the characteristics of *P. australis* (75.5% relative explanation in total). Concerning the environmental variables, the soil water content, total nitrogen, pH, and electrical conductivity exerted significant effects. The above results contribute to further confirming the link between urban areas, soil physicochemical properties, and native plant colonization. Moreover, this study provided a reference for the conservation of native aquatic plants in urban areas.

This dissertation provides insight into the effects of anthropogenic disturbance on the riparian habitat in central Japan, which may have important impacts on ecosystem services and biodiversity. According to the results, appropriate management actions are suggested to prevent further degradation of riparian ecosystems. It is expected that this dissertation may help to better consider all aspects of nature and human well-being in the future planning process of central Japan.

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# **Chapter 1: General introduction**

## **1.1 Research background**

More than half of global populations now lives in urban areas, and this proportion is still rising (Seto et al. 2011). The growing human population associated with a rising of anthropogenic pressure is considered the most important driver leading to ecosystem degradation (Evans et al. 2014). Environmental factors of anthropogenic origins, such as pollution, land-use conversion, habitat loss and fragmentation, disruption of hydrological systems, alteration of temperature regime (or the urban heat island effect) and rainfall patterns, and the introduction of alien species, are usually followed by loss of both ecological services and biodiversity (Pickett et al. 2011; Fornal-Pieniak et al. 2019).

Given the urgent need for more ecological information in urban and exurban environments to create more sustainable cities, ecologists and natural resource managers have emphasized the relationship between human disturbance and species diversity. Besides, the intensity of anthropogenic disturbance can be defined by the levels of urbanization (Kolbe et al. 2016; Taglioretti et al. 2018) considering that urban areas are the aggregation of the human population and drastic anthropogenic modifications (McKinney 2002). To date, urbanization-biodiversity-associated studies can be divided into temporal and spatial aspects (McDonnell and Hahs 2008). Temporal studies have employed herbarium records and other historical accounts of species occurrences to identify changes in species composition in cities over time (Stehlik et al. 2007; Hahs et al. 2009; Duncan et al. 2011). However, there are few such temporal studies in urban areas ascribed to the lack of accurate and detailed historical records of pre-urbanization (Trentanovi et al. 2013). Therefore, spatial measures have become a common approach to examine the ecological response of species diversity to urbanization (Burton et al. 2009). In the early 1990s, McDonnell and Pickett proposed the urban-rural gradient method to investigate the ecology of urban and exurban areas (McDonnell and Pickett 1990). The urban-rural gradients can be measured by comparing sites at different levels of urbanization. Examples of measures of urban-rural gradient include the distances to the city center (McDonnell et al. 1997; Song et al. 2019), various measures of the



amount of urban development surrounding sites (e.g., impervious surface cover and population density) (Zhang et al. 2017), and some indices reflecting the variety of different urbanization level (e.g., NDVI and NDBI) (Zha et al. 2003; Brice et al. 2017; Blouin et al. 2019). Regarding species diversity patterns along the urban-rural gradient, the existing studies have yielded mixed results. According to several reports, plant species can adapt to urban environments while there was no significant loss of plant diversity (Croci et al. 2008; Soanes and Lentini 2019). Conversely, a decline in plant species diversity has been observed in urban cores (McKinney 2002; Zerbe et al. 2003). Possible explanations for these different results can be concluded by the patterns of urbanization process, spatial heterogeneity, and intermediate disturbance (McKinney 2008). Except for the distinct findings, these studies have collectively exhibited several general trends on the urban-rural gradient. One is an increase in alien species in many urban areas, contributing to a global homogenization of species composition on various scales (Groffman et al. 2014). The other trend is that different species respond to urbanization differently; some species act as “urban avoiders” while others tend to be “urban exploiters” (Blair 1996). Moreover, the natural communities within and around the urban areas could be influenced by the changes in the local environment, the structure of habitats, and the introduction of new species (Williams et al. 2009).

However, the relationship between anthropogenic disturbance and biodiversity still needs to be further explored. Although riparian areas are one of the most threatened ecosystems in the world, there is surprisingly little research on the impacts of human disturbance on riparian plant assemblages compared to other ecosystems (Loiselle et al. 2020). Studies involving riparian plant assemblages may be significant for linking the response of the plant community to the urbanization-related changes (Price et al. 2020). Riparian areas are environmentally and ecologically essential systems sensitive to human-driven environmental changes (Meek et al. 2010). Urban expansion engulfs riparian habitat and fills it with urban infrastructure, causing habitat fragmentation and loss (Pennington et al. 2010). From another perspective, human disturbance (e.g., construction of dams, channelization programs, removal of riparian vegetation and wood, sand/gravel extraction, and trampling) alters sediment structure and hydrological conditions, resulting in significant changes in riparian ecosystems (White and Greer 2006). The combination of the previously mentioned factors leads to riparian habitat degradation and triggers an alteration in the structure of riparian species communities, opening up a new niche for alien species invasion

(Holmes et al. 2008; O'Toole et al. 2009). Hence, from a conservation standpoint, it is necessary and urgent to comprehensively and systematically investigate the response of species diversity to different intensities of anthropogenic disturbance in riparian areas to better support their ecological services.

## **1.2 Description of the study area and research scope**

Vegetation and environmental data were collected for my research along the Shonai River and Miya River. The Shonai and Miya Rivers belong to the Class A river in Japan. These two rivers originate from Mt. Yudachi and Mt. Ōdaigahara, respectively, and both of them flow into the Ise Bay. The basin areas of the Shonai and Miya Rivers are in the same climatic region and characterized by the same regional species pool. The Shonai River is regarded as one of the most urbanized rivers in Japan. In the basin area of the Shonai River, the urbanization process has been remarkably developed since the 1950s because the metropolitan city, Nagoya, and its satellite cities are located in the lower and middle reaches. At present, the population of the basin exceeds 2.4 million. In the Moriyama ward of Nagoya City, urbanization development is still underway. Contrary to the Shonai River, the Miya River harbor only one small city (Ise) in the lower reach and 140 thousand people live in the basin area. Moreover, the Shonai and Miya Rivers varied in land-use status. The Shonai River basin area is composed of 44% forest, 16% farmland, and 40% urban area (e.g., homestead). Meanwhile, the Miya River basin is nearly 84% mountainous areas, about 8% farmland, about 4% urban area, and approximately 4% other areas (Ministry of Land, Infrastructure, Transport and Tourism, 2016). The differences in human population and land-use suggest that Shonai and Miya rivers are exposed to different levels of urbanization. Moreover, several studies on urban ecology have been conducted in major cities of Japan (e.g., Tokyo, Osaka) and involved many rivers (e.g., the Ashida River, the Miyako River, the Tama River, and Yamato River) (Inoue and Nakagoshi 2001; Nakamura et al. 2006; Lee and Kwon 2015). However, there is little research on central Japan, despite ongoing urban sprawl in this region.

The riparian area provides vital ecosystem services and yet, is highly vulnerable and easily degraded. Considering the importance and particularity of the riparian zone, it is taken as the research area of my dissertation. Furthermore, the distinct urbanization level of these two rivers and the obvious urban-rural gradient of the Miya Rivers make it an ideal study system for assessing the influence of human disturbance and urbanization on the plant assemblages in

riparian areas. In this research, I conducted a comparative study at two hierarchical levels: (1) within river: in each river, I explored the differences of plant communities at different urbanization or disturbance level to obtain a comprehensive understanding of the response of biodiversity to human disturbance; (2) between rivers: I also compared the plant diversity and composition of two rivers and investigate the differences of plant communities between the rivers.

### 1.3 Summary of the chapters

In this dissertation, three studies were conducted based on one dataset of plant communities spanning an urban-to-rural gradient to answer the question: how is urban development influencing the riparian plant species? I emphasized the use of informative measures of ecological drivers influenced by urbanization (e.g., land use and land cover, environmental conditions) and plant community responses. In these three studies (Chapters 2-4), I use different analytical methods and different response variables to describe measures of community structure: alpha diversity, trait composition, and beta diversity (species turnover or changes in species composition across sites). Here, I briefly summarize each of these chapters and highlight their contributions to understanding the mechanisms underlying the community changes with anthropogenic disturbance.

Specific urban conditions (e.g., human population and the density of the developed area) are usually highly associated with urbanization. Previous studies revealed the changes in species diversity and species composition along the urban-rural gradient. Nevertheless, disentangling the effects of urbanization on riparian systems in the urban-rural gradient is difficult because this gradient is a complex mosaic of patches in reality, especially when considering riparian areas. Except for the urbanization effect, the driving factors such as land-use type and landscape structure are broadly recognized for the difference between urban and rural areas while they influence mutually. Few studies have explicitly examined the variation of plant species in some particular land-use categories in riparian areas. So far, how and to what extent urbanization influences the vegetation of riparian areas remain unclear. In **Chapter 2**, I conducted urban ecological research from a novel perspective, and compared the plant diversity and composition in artificial and semi-natural habitats located in two rivers with different levels of urbanization. Precisely, I compared  $\alpha$ -diversity of total flora and alien,

native, riparian, and ruderal plant species in artificial and semi-natural habitats. The species richness was positively associated with urbanization in the artificial habitat. Nevertheless, the opposite result was observed in the semi-natural habitat, suggesting that the response of species  $\alpha$ -diversity to urbanization was observed to vary with the types of habitat. Moreover, I used the generalized linear model (GLMs) and canonical correspondence analysis (CCA) to examine the effects of local environmental variables (annual precipitation, forest cover, altitude, slope, soil pH) and variables related to urbanization (population density, traffic density, distance to the city center, and the proportion of impervious surface) on plant  $\alpha$ -diversity and species composition. Differences in species richness and composition were observed between different urbanization levels regardless of habitat types, suggesting that urbanization variables affected plant assemblages. In these urbanization variables, distance to the city center and the proportion of impervious surfaces significantly influenced the plant  $\alpha$ -diversity and species composition. Overall, these findings indicate that urbanization could affect the riparian plant assemblages by promoting the spread of alien or common species while reducing the number of specialist species.

Despite the relationship between species  $\alpha$ -diversity and the urbanization process was well examined in previous studies, another important component of species diversity,  $\beta$ -diversity, has not been widely studied in riparian areas. Habitat heterogeneity and fragmentation are considered the main consequences of urbanization and human disturbance. Moreover, anthropogenic disturbance could induce habitat degradation by changing soil, hydrological condition, biogeochemical cycles, and temperature regime, resulting in the replacement of diverse plant assemblages by more tolerant species. The combination of the aforementioned factors can cause floristic dissimilarity to be overall reduced in disturbed environments. Therefore, the effect of anthropogenic disturbance on  $\beta$ -diversity (floristic homogenization is generally evaluated by the variation of  $\beta$ -diversity) has become an emerging hotspot in the science of ecology, recently. In **Chapter 3**, I analyzed the floristic homogenization in the floodplain landscape to explore the effects of urbanization on the similarity of plant assemblages. I used two facets of floristic homogenization to assess the effects of urbanization: taxonomic (the composition of plant species) and functional (the composition of species' traits related to environmental tolerances, habitat preferences, and dispersal abilities) homogenization. In that chapter, I tested: (1) Whether human disturbance induces floristic homogenization? (2) Whether the increase of non-native species that generate

these processes? (3) How does the effects of the environmental matrix (land-use and land cover parameters and human disturbance) affect floristic homogenization? The finding indicates that human disturbance can cause floristic homogenization at a regional scale. The ecological processes associated with anthropogenic disturbances, such as land-use transformation, local environmental condition change, and alien species invasion is of great significance to the formation of the  $\beta$ -diversity pattern of riparian plant assemblages.

Given the loss of biodiversity generated by urbanization and human disturbance, it is urgent to investigate riparian specialist species for their significance in the restoration and conservation of riparian habitats. Yet, the studies linking riparian species to anthropogenic disturbance remain limited. In **Chapter 4**, I assessed the effects of urbanization and human disturbance on traits of a native riparian species, *Phragmites australis*. In that chapter, I answered two questions: (1) How do the ecological characteristics of *P.australis* vary among urban and suburban areas? (2) Whether the anthropogenic disturbance affects the ecological characteristics of *P.australis* or not. Precisely, I selected height, stem diameter, leaf area, coverage, and Shannon-Winner diversity index as individual and community level traits of *P. australis*. Moreover, land-use and land cover parameters, soil properties, and moisture were selected as environmental factors. I created multiple models to determine how environmental factors influence *P. australis*' traits and whether urbanization-related factors induce the variation of *P. australis*' traits. The results revealed the differences in the structure of *P. australis* communities and a significant explanation of the variation of urbanization-related factors, indicating the importance of anthropogenic disturbance in structuring riparian plant species at the individual and community levels. Furthermore, this chapter highlights the use of species' traits to identify mechanisms underlying species composition patterns.

**Chapter 5** serves as a conclusion to this dissertation, summarizing the results of Chapters 2-4. In that chapter, I provided the implications of these results for the conservation and restoration of the riparian area in central Japan and point out some remaining knowledge gaps and areas for future research.

## 1.4 Figures

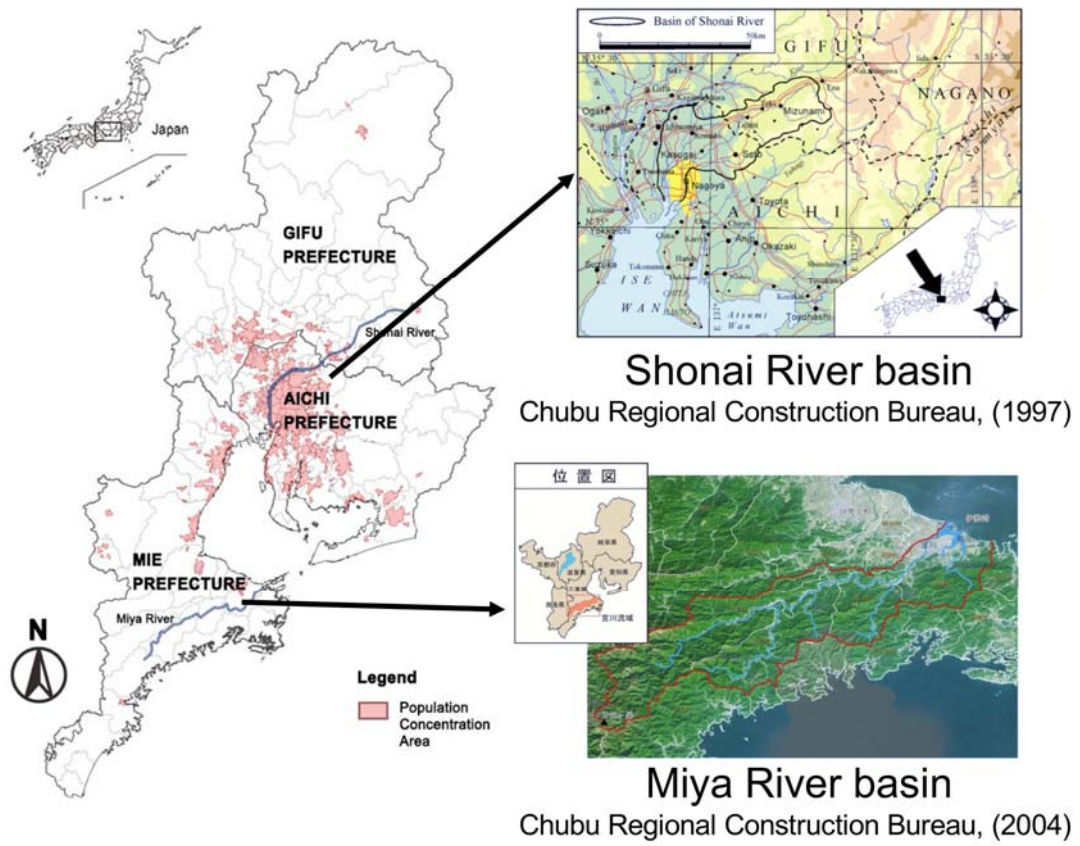


Fig. 1-1 Study areas

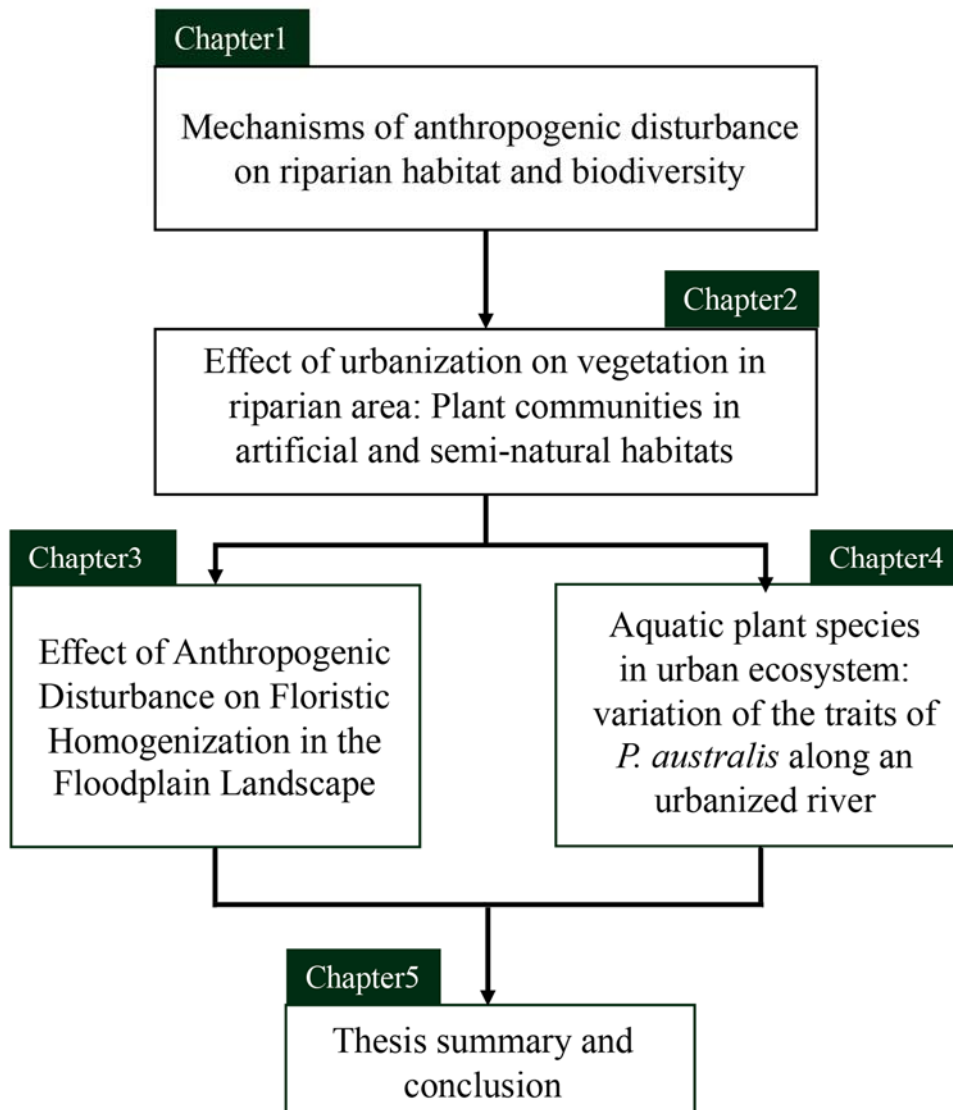


Fig. 1-2 workflows

## **Chapter 2: Effect of urbanization on vegetation in riparian area: plant communities in artificial and semi-natural Habitats**

### **2.1 Introduction**

Riparian areas represent one of the most important habitats in the urban ecosystem. Riparian areas provide various essential ecosystem services including flood regulation, riverbank stabilization, nutrient cycling, and providing habitats for plants and animals (Naiman and Décamps 1997; Ewel et al. 2001). With the possible exception of ecosystem services, rivers enhance the aesthetic value of urban and suburban regions and improve people's willingness to do outdoor activities. These services are particularly valuable in riparian areas worldwide, where humans rely on these services for well-being (Higgins et al. 2019).

Facing the ongoing urban development, an understanding of the ecosystem response to urbanization is urgently needed in order to ensure that urban areas are managed to meet the needs of the citizens and the sustainability of nature (Niemelä 2011). With the development of urbanization, urban areas and the human population are increasing rapidly; human-driven alteration including climate change, habitat loss and fragmentation, land-use conversion, pollution and invasion of alien species are confirmed to impact the biodiversity in urban areas (Hanski 2005; Cai et al. 2019). As an attraction for human development, riparian areas are severely affected by urbanization. Firstly, urbanization within riparian areas increases the area of impervious surface, which decreases the infiltration of rainfall and leads to loss of original riparian habitat (White and Greer 2006). Secondly, urbanization increases the load of human activities on riparian areas (Barnosky et al. 2012; Yuan et al. 2016). Some of the most apparent types of disturbance consists of soil pollution, trampling of vegetation, and soil compaction (Lundholm and Marlin 2006; Cameron et al. 2015). These disturbances can facilitate the establishment of alien and ruderal species that can become common due to additional nutrient availability and because of the high input of propagules from habitat degradation and fragmentation (Washitani 2001). Although managing urbanization impacts has become a conservation priority worldwide, the maintenance of riparian areas is often ignored.

Flora is closely related to habitat conditions and is directly or indirectly affected by



urbanization and anthropogenic disturbance (Aronson et al. 2014; Beninde et al. 2015). In recent decades, studies involving the effects of urbanization on plant assemblages have been conducted at multiple spatial scales (Porter et al. 2001; Duguay et al. 2007). The urban–rural gradient is the most commonly used methodology, and it is considered to be a linear transect that radiates from the city core to the undisturbed area (McDonnell and Pickett 1990). Nevertheless, disentangling the effects of urbanization on riparian systems in an urban–rural gradient is difficult because this gradient is surrounded by heterogeneous patches, especially when considering riparian areas (Naiman R.J. 2005). Besides the urbanization effect, driving factors such as land-use type and landscape structure are widely recognized for their difference between urban and rural areas, and they influence one another mutually (Gerstner et al. 2014; Amici et al. 2015). Few studies have explicitly examined the variation of plant species in some particular land-use categories in riparian areas. To date, how and to what extent urbanization may influence the riparian plant assemblages is not well appreciated. For this study, I focused on the effect of urbanization on vegetation in central Japan, a region where most of the cities are developed in the lower reach of rivers. In Japan, the basins of rivers distinctly differ in urbanization level and in the intensity of anthropogenic disturbance (Inoue and Nakagoshi 2001). These rivers can flow through metropolises and their satellite cities; thus, the riparian areas have been intensively transformed for the needs of irrigation, drinking water, and recreation of people, and are associated with a large number of residents and immigrant population (Wang et al. 2001; Guzy et al. 2018). Several river basins have not been changed by urban sprawl, and just a few small cities and villages are distributed along these rivers. The response of species richness to urbanization among different rivers is still poorly understood, which could hinder the implementation of effective management practices.

Understanding how urbanization influences vegetation in riparian areas is essential because plant communities play an important role in providing a variety of ecosystem services and maintaining a high level of biodiversity (Naiman and Décamps 1997). Valuable information for the management of these areas can be obtained by comparing the plant species diversity and composition in sites at different levels of urbanization. For this study, I examined the effects of urbanization on riparian vegetation from a novel perspective. This study aimed to analyze plant species within the same land-use type but under different degrees of urbanization. Specifically, I conducted comparisons of artificial (located inside urban area) and semi-natural (located outside urban areas) habitats of two rivers with different

degrees of urbanization and development. The objectives of the current study were to:

(1) Study the changes in plant species richness and composition in artificial and semi-natural habitats along an urbanization gradient. I expected that the species richness and abundance of alien and ruderal species might benefit from the urbanization.

(2) Analyze which urbanization and environmental variables influence plant diversity and species composition in artificial and semi-natural habitats along an urbanization gradient. I hypothesized that the effects of urbanization factors on vegetation might vary with habitat type and that the dominant factor of plant species would also vary in habitat type.

## **2.2 Materials and methods**

### **2.2.1 Study area**

The study was conducted in the central Japan. I selected the riparian areas of Shonai River and Miya River for this study (Fig. 2-1). The Shonai and Miya River originate from Mt. Yudachi and Mt. Odaigahara, respectively, and both of them flow into the Ise Bay. These two rivers belong to the same climatic region and are characterized by the same regional species pool. The geographical and environmental characteristics of the two rivers are listed in Table 2-1.

The Shonai River is regarded as one of the most urbanized rivers in Japan. In the basin area of the Shonai River, since the metropolitan city, Nagoya, and its satellite cities are located in the lower and middle reaches, the urbanization process has been remarkably developed since the 1950s. At present, the population of the basin exceeds 2.4 million. In the Moriyama ward of Nagoya City, urbanization development is still underway. In contrast to the Shonai River, the Miya River harbors only one small city (Ise) in its lower reaches, and 140,000 people live in the basin area. The populations in the basins and different land-use types reveal that Shonai and Miya River differ in levels of urbanization.

To explore the effect of urbanization on plant diversity and floristic composition, I selected riparian parks and wastelands as artificial and semi-natural habitats, in order to conduct a comparison of riparian areas of the two rivers.

Riparian parks were located in the city areas of Nagoya and Ise. These parks are close to residential areas and provide open recreational space for people living in the city areas. In

order to access easily to the river flow and enjoy river scenery, all of the parks are riparian areas modified by a series of squares, playgrounds, hydrophilic platforms, and trails.

Wastelands were located outside the cities and surrounded by farmland, forest, and other unmanaged lands. They are abandoned and without vegetation management. Most of the wastelands kept their semi-natural appearance and provided habitats for wildlife. Due to the effect of urban sprawl, the wastelands along the Shonai River are fragmented by cities, while the wastelands along the Miya River present a relatively continuous area (Fig. 2-1).

### **2.2.2 Vegetation sampling**

I selected three artificial habitats and three semi-natural habitats in each river (Table 2-2). Field surveys were conducted from 2018 to 2019, between April and July. The waterside lowland and major bed of riparian area were selected as the primary sampling area.

In each sampling site, four transects were established with 200 m intervals vertically to the river (Fig. 2-2). To weaken the marginal effect, I excluded the area within two meters of the rivers. Two  $20 \times 10$  m plots were established systematically, separated by 5 m distance along each transect. I recorded all the tree species in the  $20 \times 10$  m plot, and two subplots of size  $5 \times 2$  m were set for the sampling of shrubs and nested in the  $20 \times 10$  m plot. The herbs were sampled in five small plots of  $1 \times 1$  m and nested randomly in the  $20 \times 10$  m plot.

### **2.2.3 Data collection**

In each plot, I measured several variables describing the characteristics of plant communities: the name, density, and coverage of all present plant species. The coverage of each species was measured by visual estimation (Damgaard 2014), and the density of each shrub and herb species was measured by recording the number of plants in a  $1 \times 1$  m range. Plant specimens were identified to the species level in the field, and the crop plants were excluded from the record. For the plant species that were not easily identifiable, specimens were collected and brought back to the laboratory, where they were identified by matching with an illustrated handbook of vegetation and preserved herbarium specimens.

According to the literature and field observations, each plant was classified using the following life-history attributes: (1) origins: alien (species introduced after the 19th century, when Japan abandoned its policy of national isolation) or native species (Muranaka 2008); (2)

naturalness: riparian (riverside-endemic and hygrophilous species) or ruderal (synanthropic species and weeds, usually appearing with human activity) (Miyawaki 2004); species richness (SR), as the total number of different species represented in an ecological community or habitat (Lawton 1994) was used to account for the diversity of vegetation in this study.

I used several predictors to analyze the correlations between urbanization components and plant assemblages. I used imperviousness (defined as rigid pavement area, i.e., roads, pavement, and ground, calculated in a buffer with a radius of 100 meters within the riparian area), human population density (number of residents per km<sup>2</sup> of the district where the sample plot was located), nearest distance to the city center, and traffic density (daily vehicle flow of the nearest road beside the riparian area). I also used other environmental factors known to affect plant diversity, such as climatic and topographic features and proportion of forest in a buffer with a radius of 100 meters. The data were collected as field measurements, downloaded from the government website, and calculated by ArcGIS 9.3 (ESRI, Redlands, CA, USA). A detailed description of urbanization and other environmental variables is shown in Table 2-3.

#### **2.2.4 Statistical analysis**

The statistical analyses included three aspects; the statistical analyses mentioned in this study were conducted by using the R 3.0.2 (R Core Team 2014, Vienna, Austria).

For the first aspect, the number of species and components of urbanization in different habitat types was compared between two river basins. The differences were tested using the least significant difference (LSD) test in a one-way analysis of variance (ANOVA). The *P* values were corrected by a multiple-test Holm's correction procedure. The package "agricolae" was used for LSD test with multiple-test Holm's correction.

For the second aspect, to explore the relationships between urbanization and species richness, I used generalized linear model (GLM) to analyze the species richness of the different types of plant with Poisson error distribution for count data. Both urbanization variables and other environmental variables were considered in the models. To avoid possible bias caused by multicollinearity, I conducted a multicollinearity test among all the variables. The results showed that there was no apparent multicollinearity between variables (Kappa value = 36.12). The best-fitting models were selected base on the corrected Akaike's information criterion (AICc). I also calculated the variable importance for each urbanization variable so that the effect of each variable on species richness could be compared. Variable importance is the sum

of the weights of AICc, which indicates the overall likelihood of interesting parameters appearing in the selected model. The values of variable importance are bounded between 0 (variables excluded from all selected models) to 1 (variables included in all selected models). I calculated the variable importance according to the sum of the Akaike weights base on the criteria ( $\Delta AICc \leq 4$ ). The packages “glm2” and “MASS” were used for GLM, and “MuMIn” was used for model averaging.

For the third aspect, canonical correspondence analysis (CCA) was conducted to find the effect of urbanization and other environmental predictors on plant community composition. I used the abundance in each plot as species data, and for the environmental matrix, the urbanization (population density, traffic density, distance to the city center, and proportion of impervious surface) and other environmental factors (annual precipitation, mean annual temperature, the proportion of forest, altitude, and slope) were used. The package “vegan” was used for CCA. Data from artificial and semi-natural habitats were analyzed separately.

## **2.3 Results**

### **2.3.1 Plant species richness in artificial and semi-natural habitats**

In the current study, the response of species richness to urbanization was observed to vary according to the types of habitat (Fig. 2-3). In artificial habitat, the sites located within the Shonai River basin showed a higher species richness than those within the Miya River basin. Nevertheless, in semi-natural habitat, the sites located within the Miya River basin showed a higher degree of total species richness than the Shonai River.

The results of species origins analysis indicated that both alien and native species richness of the Shonai River was higher than those located along the Miya River in artificial habitat (Fig. 2-4). In particular, alien species of the Shonai River showed a significantly higher richness than of the Miya River (ANOVA,  $P \leq 0.05$ ). Concerning semi-natural habitat, the number of alien and native species differed significantly between two rivers (ANOVA,  $P \leq 0.05$ ). The number of alien species was higher in the wastelands of the Shonai River. However, comparing the richness of native species of two rivers indicated a significantly high richness of the Miya River.

Considering the naturalness of species in the artificial habitat, I found very little

difference in riparian species between two rivers (Fig. 2-4). High richness of ruderal species was found in the sites along Shonai River. In semi-natural habitat, both riparian and ruderal species differed between Shonai and Miya rivers. The number of riparian species showed a significantly high value in the sites of the Miya River (ANOVA,  $P \leq 0.05$ ).

### **2.3.2 Components of urbanization**

In the different riverside environments, the degree of population and traffic density significantly differed both in artificial and semi-natural habitat (Table 2-4). However, in the semi-natural habitat, a significant difference was observed on the variable of the distance to the city center between two rivers, although there was not a similar trend in artificial habitat. Considering the proportion of impervious surface, artificial and semi-natural habitats did not differ significantly, but the mean value of the proportion of impervious surface was slightly higher in artificial habitats compared to semi-natural habitats.

### **2.3.3 Effects of urbanization on species richness**

Results of GLM analyses revealed that in artificial habitats, the alien species richness was mainly affected by precipitation and proportion of impervious surface (Table 2-5, Fig. 2-5). The best explanation model for the variation of native species richness included the proportion of impervious surface and traffic density; however, no significant effects were shown within the variables. The richness of riparian species tended to decrease with the increasing impervious surface. Considering the ruderal species richness, the proportion of forest area was shown to be the best predictor.

In semi-natural habitats, the number of alien species was influenced by both the distance to the city center and the proportion of impervious surface (Table 2-5, Fig. 2-5). The richness of native species was positively affected by distance to the city center; the richness of riparian species tended to decrease with the impervious surface; ruderal species richness was positively influenced by the proportion of impervious surface. Furthermore, the number of ruderal species was impacted by the distance to the city center and tended to increase with decreased distance.

The results of variable importance showed that the dominant component of urbanization contributed to the variation of species richness with habitat and vegetation types (Fig. 2-6). In artificial habitats, among the urbanization factors, the proportion of impervious surface was the

best predictor for the variation of the species richness, accounting for about 1.2 variable importance in total. It adequately explained the variation of alien, native, and riparian species richness. However, in semi-natural habitats, distance to the city center was the best predictor for the variation of the species richness and was strongly associated with the variation of the number of alien, native, and ruderal species.

#### **2.3.4 Effects of urbanization on plant community composition**

Patterns of plant composition and the correlation between plant species and environmental constraints was shown in CCA diagrams (Fig. 2-7). The total ordination constraint in the CCA of artificial habitats was 6.065, which was the sum of all eigenvalues; 2.517 was constrained and 3.548 remained unconstrained. With regard to the CCA for semi-natural habitats, the total ordination constraint was 9.411; constrained and unconstrained were 4.530 and 4.881, respectively. Results of the correlations between CCA community scores and environmental constraints are summarized in Table 2-7. In both artificial and semi-natural habitats, Axis 1 was positively associated with distance to the city center and negatively associated with the proportion of impervious surface, population, and traffic density, and represented a gradient of high to low urbanization level (Fig. 2-7; Table 2-7).

The result of CCA in the artificial habitats showed that the sites of two rivers were not a distinct dispersion along the first axis (Fig. 2-7 A). The eigenvalue for the first axis was highly significant according to the Monte Carlo permutation test (Axis 1 = 0.46,  $P = 0.002$ ), indicating that the plant data were well explained by selected environmental variables. The species-environment correlations represent the ability of environmental parameters to explain the species composition, were 0.85 for Axis 1, and 0.73 for Axis 2 (Table 2-6). Furthermore, all canonical axes combined were assessed by the Monte Carlo tests, suggesting that the relationship between environmental factors and community composition was significant ( $P = 0.002$ ). Artificial sites along the Shonai River were positively associated with population density, proportion of impervious surface, traffic density, pH, and mean annual temperature. The plant communities which occurred in the artificial habitat of Miya River always positively related to the distance to the city center, the proportion of impervious surface, mean annual precipitation, and proportion of forest. The urbanization variables were strongly linked by part of environmental factors, further explaining the patterns of plant composition along the Shonai and Miya Rivers. The soil pH and temperature were strongly correlated with impervious surface

and traffic density, suggesting that urbanization might affect soil properties and microclimates.

The species composition pattern was obvious with most alien (e.g., *Festuca arundinacea*, *Lolium multiflorum*, *Erigeron annuus*, *Avena fatua*, *Ambrosia artemisiifolia*, *Plantago major*, *Conyza canadensis*, *Conyza bonariensis*, *Solidago altissima*, *Briza maxima*, *Trifolium repens*, and *Taraxacum officinale*) and ruderal species (e.g., *Imperata cylindrica*, *Poa annua*), being associated with the negative, “urbanized” end of Axis 1 and correlated to the impervious surface and traffic density. Native species (e.g., *Artemisia indica* var. *maximowiczii*, *Phragmites australis* and *Miscanthus sacchariflorus*, and *Gynostemma pentaphyllum*) were located at the positive end. Species composition on Axis 2 did not exhibit an obvious trend, with alien and native species distributed at two ends (Fig. 2-7 A).

In contrast to the artificial habitats, the result of CCA in the semi-natural habitats showed that the sites of two rivers were distinctive along the first axis (Fig. 2-7 B). The first axis was significant according to the results of the Monte Carlo permutation test (Axis 1 = 0.66,  $P = 0.001$ ); the results of species-environment correlations were 0.95 for Axis 1, and 0.82 for Axis 2 (Table 6). Monte Carlo test for all canonical axes combined indicated that the relationship between plant composition and selected environmental factors was significant ( $P = 0.001$ ). Similar to the CCA results for the artificial habitats, the soil pH was correlated with the impervious surface; the temperature was highly related to the traffic density and population density. In semi-natural habitats, the alien species (e.g., *F. arundinacea*, *L. multiflorum*, *E. annuus*, *C. canadensis*, *S. altissima*, *T. repens*, and *T. officinale*) also dominated in the more urbanized areas and correlated to the impervious surface, pH, and traffic density; however, in the less urbanized plots, there are almost native species (e.g., *Iris japonica*, *Farfugium japonicum*, *Geranium wilfordii*, *Typha orientalis*, *Vicia sativa*, and *Phyllostachys bambusoides*). The species categorized as both ruderal and native species (e.g., *Cayratia japonica*, *Rubus parvifolius*, and *Equisetum arvense*) also dominated in these less urbanized areas (Fig. 2-7 B).

## **2.4 Discussion**

### **2.4.1 Plant species richness in artificial and semi-natural habitats**

In artificial habitats, the higher richness of the total species at the sites with a high level



of urbanization indicated that the species richness tends to increase with the increase of urbanization. In accordance with the present results, previous studies have demonstrated that relatively high anthropogenic disturbance promotes the coexistence of various types of plants in urban areas (Stadler et al. 2000; Wania et al. 2006). In this study, the high species richness of parks along the Shonai River was observed owing to a large number of alien and ruderal species. These observations confirmed that high species richness is associated with the development of urbanization, often as a result of the spread of alien species (Pyšek et al. 2010; Gaertner et al. 2017). The increase of ruderal species in the parks located along the Shonai River suggested that colonization of ruderal species depended more on the massive artificial disturbances in a megacity. Consistent with this study, many studies have reported that a large number of ruderal plants are always recognized in urban areas with stronger anthropogenic pressure (Dubois and Cheptou 2017; Guo et al. 2018). Interestingly, the semi-natural habitats showed opposite trends to artificial habitats. The better performance of species richness under low-level of urbanization could be due to the characteristics of semi-natural habitat: the range of habitats suitable for native species conservation was probably broader and more continuous in the less-urbanized sites than in the urbanized sites. Thus the loss of plant species could be induced by anthropogenic pressure and habitat fragmentation (Cousins et al. 2007). This result was also in concordance with earlier research stating that native plant species diversity is relatively high in less disturbed habitats, which might be the result of the existence of multiple dominant species in the less disturbed habitats (Hobbs and Huenneke 1992; McKinney 2002). Additionally, native species diversity can quickly recover after being disturbed, but not if the disturbance was continuous (Selmants and Knight 2003; Zhu et al. 2007). This finding suggested that semi-natural habitats under a low urbanization intensity could be linked to the relatively high richness of native species and should be managed for the conservation and improvement of the diversity of native species.

#### **2.4.2 Driving factors affecting different types of vegetation**

The proportion of impervious surface acted as the best predictor for the variation of species richness in artificial habitats, and this was positively associated with the alien species richness in both artificial and semi-natural habitats. In most of the riparian habitats in Japan, the impervious surfaces are mainly formed by the reinforced riverbed. The surface of the riverbed has been levelled off, promoting the utilization of these riverbeds as recreation spaces,

and footpaths (Inoue and Nakagoshi 2001). Following such construction, riparian areas are strongly linked to riparian degradation, alternation of the hydrological and sediment regimes, and intense human recreational activities (Paul and Meyer 2001; McKinney 2002). Thus, alien species could benefit from disturbances of this nature, especially along the riverbanks, since the river corridor is known to be an effective dispersal mechanism (Nilsson et al. 2002; Aronson et al. 2017). Additionally, it is widely assumed that the propagation of alien plants in public spaces and on trails by humans is an important factor for their invasion (Christen and Matlack 2009). Given the efficient propagation of alien species, native species could be influenced by the alien species in numerous ways, including the induced changes in the physical habitats, via competitive suppression, or via some other trophic interaction (Tilman and Lehman 2001; Salinitro et al. 2018). Surprisingly, the result revealed that the species richness of alien species decreased with the increase in the annual precipitation, and it was contrary to most of the previous studies (Levine et al. 2004; Dinga 2017). This result persuaded us to hypothesize that the native species were better adapted to colonizing high rainfall environments than the alien species, since Japan has a typically humid, temperate marine climate. In high rainfall environments, an increase in the biological resistance of the native plant communities might be a reason for the lower richness of the alien species (Levine 2000). Nevertheless, despite the significant relationship between the alien species and precipitation, these results might not convincingly predict how species would respond to changes in the environment at a local level within a limited species pool. Further studies in the future could take these variables into account.

In semi-natural habitats, I found the distance to the city center was the most effective predictors for both alien and native species, reflecting the substantial impact of urban expansion on suburban areas. This result was in line with previous studies revealing a declining trend of alien species from the city center to the suburban areas (Burton et al. 2005). This result can be explained by the introduction of humans and the ability of alien species to take advantage of the new resources in those urban areas (McKinney 2002). Thus, the sites with a relatively short distance to the urban area could be more likely to withstand propagation from the alien species. Moreover, the urban areas provide numerous dispersal corridors that might enhance the spread of alien plants from urban areas to semi-natural habitats (Tikka et al. 2001). Owing to the high urbanization intensity and rapid urban sprawl, the semi-natural habitats along the Shonai River are surrounded by a number of cities, thus resulting in a relatively short distance to the city and multi-directional exportation from the cities, leading to an increase in the alien species.

Riparian species are recognized as the plants that were endemic to the riparian areas. It was observed that the proportion of impervious surface was an effective predictor for riparian species both in artificial and semi-natural habitats. As several previous studies have revealed, biodiversity and habitat quality are inversely proportional to the amount of adjacent impervious surface (Yan et al. 2019). In recent decades, moist grasslands and gravelly floodplains in Japan have been largely lost to construction activities, which has been linked to urban living and flood control measures (Inoue and Nakagoshi 2001). Hence, the loss of habitat could be a major factor contributing to the decrease of riparian plant species. The construction of flood protection measures and recreational spaces also leads to trampling and habitat degradation, while fostering the establishment of undesirable, alien plants, which establish more quickly than other vegetation in these areas (Miyawaki 2004). In the current study, some of the riparian species included in the IUCN Red List as “endangered” were only observed in unchanged riparian areas, such as *Veronica undulata*, *Lespedeza tomentosa*, and *Epelobium hirsutum*.

The ruderal species reportedly tended to occur in intensively altered habitats and were maintained at early successional stages by persistent urban disturbance (McKinney 2006). In artificial habitats, the richness of ruderal species was only significantly influenced by the proportion of forest. A large forest cover was usually considered to be more resistant to the colonization of ruderal species than a thin forest cover (Charbonneau and Fahrig 2004). Although the distance to the city center was included in the GLM model, the effect was more robust in the semi-natural habitat. This negative relationship has been aptly explained by the increased habitat diversity and human disturbance at the urban centers (Dubois and Cheptou 2017; Guo et al. 2018). Hence, a short distance to the city increases the possibility of the propagation of ruderal plants. The richness of ruderal species richness was also impacted by the proportion of impervious surface in the semi-natural habitats. This result could be explained by the intensity of the habitats modified, in which the ruderal species could occupy the disturbed habitats more quickly owing to their high tolerance for anthropogenic stress situations (Lososová et al. 2006). Moreover, agricultural activities were significantly related to the occurrence of weeds. Most weeds in agricultural systems are competitively adapted to take over disturbed habitats (Grime 1977). Consequently, environments favoring ruderal species include the riparian meadows that are subject to the disturbances like anthropogenic pressure, as well as agricultural buildings and fields.

### 2.4.3 Effects on plant community composition

The result of this study revealed that urbanization has had distinct effects on the flora of the studied artificial and semi-natural habitats. Alien species *F. arundinacea*, *L. multiflorum*, *E. annuus*, *C. canadensis*, *S. altissima*, and *T. officinale* were found at the urbanized sites in both the artificial and semi-natural habitats. *F. arundinacea* and *L. multiflorum* have been reported as being highly invasive to disturbed riparian areas in Japan. These alien species escaped from construction sites in urbanized riversides, where they were seeded to prevent soil erosion (Miyawaki 2004). *E. annuus*, *C. canadensis*, *S. altissima*, and *T. officinale* were widespread and abundant in the disturbed habitats in Japan. These species have a high ability to tolerate competition and strong seed production, and anthropogenic disturbance has promoted the expansion of these species (Yura 1997; Turner et al. 2005; Stewart et al. 2009; Djurdjević et al. 2011; Patamsytè et al. 2013). Ruderal species such as *P. annua* and *I. cylindrical* were also found to be dominant at the urbanized sites in both the artificial and semi-natural habitats. These species are highly resistant to urban growing conditions and appear to be able to take advantage of anthropogenic disturbances. Additionally, the results of similar dominant species in the urbanized areas revealed that urbanization could pose a severe risk to biodiversity (McKinney 2006). The propagation and introduction of a large number of non-native and ruderal plants by human activities in urbanized areas is a well-known consequence of urbanization, and results in floristic homogenization (Pino et al. 2009). Many studies documented that the anthropogenic disturbance is one of the major drivers of floristic homogenization (Smart et al. 2006; Martínez-Ramos et al. 2016). Thus, appropriate suggestions for the management of artificial habitats, such as controlling the construction and expansion of impervious space, are indispensable. However, it is also necessary to take urban riparian areas into consideration when planning urban expansion.

In the semi-natural habitats, distance to the city center had a significant effect on the distribution of plant communities along the Miya River, and these plant communities were dominated by native species. In this research, the places far from the city center were always linked to landscape mosaics like natural floodplains, forests, and villages. This indicated that, compared with the urban residential area, the rural area had a relatively low output of alien species to the surrounding riparian areas (Štajerová et al. 2017). On the other hand, a relatively long distance from the city center could reduce human disturbance and the inhibit propagation

of alien and ruderal species (Alston and Richardson 2006). Although semi-natural habitats are the critical areas to maintaining local plant and biodiversity, plant structure is changed under high human pressure. It is crucial to mention that in semi-natural habitats under high-intensity of urbanization, a considerable number of alien and ruderal species were shown, implying the colonization of these species may still be going on. Thus, conservation management should be adopted to avoid the propagation of ruderal and non-native plants, as it is widely known that the cost of taking preventive measures is far lower than that of trying to control these plants when they have become well established. Therefore, the management of the semi-natural habitats should include a designation of selected plots as nature reserves.

## 2.5 Tables

**Table 2-1.** The geographical and environmental characteristics of the Shonai River and Miya River (information source: Ministry of Land, Infrastructure, Transport and Tourism, Japan).

	Shonai River	Miya River
Latitude	35°04'–35°24'N	34°10'–34°20'N
Longitude	136°49'–137°20' E	136°14'–136°45' E
Climate zone	Warm temperate climate	Warm temperate climate
Basin area	1010km <sup>2</sup>	920km <sup>2</sup>
Length	96km	91km
topography	Inclined from the northeast to the southwest	Inclined from the southwest to the northeast
Temperature	27.8°C (August)and 4.5 °C (January)	25.3°C(August) and 5.1 °C (January)
Population	2461000	140000
Altitude	0-843m	0-1695m
Precipitation	1400mm-2000mm	1700-2500mm
Major Cities	Nagoya, Tajimi, Tasugai	Ise
Land use	Forest 44%, agriculture field 16% urban area 40%	Forest 84%, agriculture field 12% urban area 4%

**Table 2-2.** The number of study areas, the number of plots in each study area, the total number of plots, and information about the characteristics of the studied area types.

Characteristic	Artificial habitats	Semi-natural habitats
Number of sampling sites	Shonai River:3; Miya River:3	Shonai River:3; Miya River:3
Location of sampling sites	Shonai River: Shonai Greenspace Park, Biwajima Park, Araizeki Park. Miya River: Miyagawatutumi Park, Love River Park, Miyagawashinsui Park.	Shonai River: Sakurasa Cho area, Kanori Cho area, Shimohadagawa Cho area. Miya River: Souchi Cho area, Watarai Cho area, Taiki Cho area.
Number of plots in each sampling site	8	8
Total number of plots	48	48

**Table 2-3.** Data sources and definitions of predictors, including urbanization and other environmental variables for the plots.

Predictor	Definition	Data source
Population density	Number of human inhabitants (residents) per km <sup>2</sup>	Statistics Bureau of Japan, <a href="https://www.stat.go.jp/data/jinsui/new.html">https://www.stat.go.jp/data/jinsui/new.html</a> (2015)
Traffic density	Daily vehicle flow of the nearest road beside the riparian area (cars/day)	Ministry of Land, Infrastructure, Transport and Tourism, <a href="http://www.mlit.go.jp/road/census/h27/index.html">http://www.mlit.go.jp/road/census/h27/index.html</a> (2015)
Mean annual temperature	Average value of monthly mean temperatures (°C)	Japan Meteorological Agency, <a href="https://www.data.jma.go.jp/obd/stats/etrn/index.php">https://www.data.jma.go.jp/obd/stats/etrn/index.php</a> (2018)
Annual precipitation	Sum of monthly precipitation (mm)	Japan Meteorological Agency, <a href="https://www.data.jma.go.jp/obd/stats/etrn/index.php">https://www.data.jma.go.jp/obd/stats/etrn/index.php</a> (2018)
Imperviousness	The rigid pavement area in a 100 m radius from plot center within the riparian area (%)	Geospatial Information Authority of Japan, <a href="https://www.gsi.go.jp/tizu-kutyu.html">https://www.gsi.go.jp/tizu-kutyu.html</a>
Distance to the city center	Distance from plots to the nearest neighbor city center (m)	Geospatial Information Authority of Japan, <a href="https://www.gsi.go.jp/tizu-kutyu.html">https://www.gsi.go.jp/tizu-kutyu.html</a>
Forest	The proportion of the plot area occupied by trees (%)	Geospatial Information Authority of Japan, <a href="https://www.gsi.go.jp/tizu-kutyu.html">https://www.gsi.go.jp/tizu-kutyu.html</a>
Altitude and slope	The elevation and degree of inclination in each plot	Measured using GPS and clinometer, respectively
pH	The pH of the soil with the depth of 20 cm in each plot	Measured using an electric pH meter

**Table 2-4.** The characteristics of urbanization factors in artificial and semi-natural habitats of two rivers. Significant results are in bold ( $P < 0.05$ , the  $P$ -values were corrected by the multiple testing Holm's correction).

Urbanization factors		SHONAI RIVER (Mean ± SD)	MIYA RIVER (Mean ± SD)	Difference between rivers
Artificial habitats	Population density	6707.33±391.40	610	$P < 0.001$
	Impervious surface (%)	22.22±2.14	20.88±1.62	$P = 0.34$
	Distance to the city center	3.33±0.08	3.72±0.07	$P = 0.53$
	Traffic density	6810.66±337.71	4865.83±444.98	$P = 0.002$
Semi-natural habitats	Population density	2222.67±246.85	160±32.48	$P < 0.001$
	Impervious surface (%)	7.7±0.63	5.86±0.96	$P = 0.23$
	Distance to the city center	4.32±0.19	15.49±1.44	$P < 0.001$
	Traffic density	3334.54±307.80	2083.79±380.27	$P = 0.041$

**Table 2-5.** Summary of GLMs testing the effects of urbanization factors on the richness of alien, native, riparian and ruderal species in the artificial, and semi-natural habitats.

	AIC	Pop.	Imp.	Dis.	Tra.	Temp.	Precip.	Alt.	Slo.	Forest	pH
<b>Alien species</b>											
Artificial	182.24		0.364				0.315				
Semi-natural	144.65		0.466	0.432				0.225			
<b>Native species</b>											
Artificial	205.29		0.327		0.156						
Semi-natural	216.17			0.464							
<b>Riparian species</b>											
rArtificial	141.90		0.397								
Semi-natural	164.36		0.423			0.250	0.260				
<b>Ruderal species</b>											
Artificial	185.78			0.201						0.305	
Semi-natural	175.81		0.381	0.419				0.197	0.256		0.328

Models were run for each type of habitat separately. If an explanatory factor was excluded from the best model, the cell is shown as blank spaces. Otherwise, the relative importance of the variable is reported. For the significant explanatory variables, a cell shaded-blue is a positive relationship, and red is a negative relationship between the explanatory factors and plant species richness. Notes: Pop: human population density, Imp: the proportion of impervious surface, Dis: distance to the city center, Tra: traffic density, Temp: mean annual temperature, Precip: annual rainfall, Alt: altitude, Slo: slope, Forest: the proportion of forest area.



**Table 2-6.** Summary statistics for CCA ordinations.

	Artificial habitats		Semi-natural habitats	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.462	0.374	0.659	0.423
Constrained proportion	0.261	0.212	0.281	0.177
Cumulative Proportion	0.261	0.473	0.281	0.459
Species-environment correlations	0.859	0.737	0.946	0.828

**Table 2-7.** Correlations between the environmental variables and the first two axes of the CCA plant species ordination scores in the artificial and semi-natural habitats.

Variable	Artificial habitats		Semi-natural habitats	
	Axis 1	Axis 2	Axis 1	Axis2
Pop	-0.444	0.182	-0.638	-0.245
Imp	-0.426	-0.575	-0.369	0.575
Dis	0.171	-0.795	0.744	0.210
Tra	-0.227	-0.126	-0.324	0.060
Temp	-0.569	0.213	-0.332	-0.318
Precip	0.365	-0.351	0.901	0.139
Alt	0.360	0.042	-0.278	0.261
Slo	-0.183	-0.098	-0.168	0.002
Forest	0.300	-0.295	0.040	-0.087
pH	-0.598	0.368	-0.029	0.287

**Table 2-8.** Family, species, abbreviation, distribution pattern, and type of all plant species recorded in this study. Notes: AS, artificial habitats along the Shonai River; AM, artificial habitats along the Miya River; SS, semi-natural habitats along the Shonai River; SM, semi-natural habitats along the Miya River; NA, native species; AL, alien species; RU, ruderal species; RA, riparian species.

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Amaranthaceae	<i>Achyranthes bidentata</i> Blume var. <i>japonica</i> Miq.	Achbid				√	NA
Amaranthaceae	<i>Chenopodium album</i> (L.)	Chealb			√	√	NA RU
Amaryllidaceae	<i>Allium macrostemon</i> Bunge	Allmac		√		√	NA
Amaryllidaceae	<i>Zephyranthes candida</i> (Lindl.) Herb.	Zepcan				√	NA
Apiaceae	<i>Torilis scabra</i> (Thunb.) DC.	Torsca		√		√	NA
Araliaceae	<i>Eleutherococcus sciadophylloides</i> (Franch. et Sav.) H.Ohashi	Elesci				√	NA
Araliaceae	<i>Hydrocotyle sibthorpioides</i> Lam.	Hydsib				√	NA
Asteraceae	<i>Erigeron annuus</i> (L.)	Eriann	√	√	√	√	AL RU
Asteraceae	<i>Taraxacum japonicum</i> Koidz	Tarjap		√	√	√	NA
Asteraceae	<i>Taraxacum officinale</i> (L.)	Taroff	√	√	√		AL RU
Asteraceae	<i>Artemisia indica</i> var. <i>maximowiczii</i>	Artind	√	√	√	√	NA
Asteraceae	<i>Ambrosia artemisiifolia</i> (L.)	Ambart	√				AL RU

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Asteraceae	<i>Ambrosia trifida</i> (L.)	Ambtri	√		√		AL RU
Asteraceae	<i>Solidago altissima</i> (L.)	Solalt	√	√	√		AL RU
Asteraceae	<i>Cirsium japonicum</i> Fisch. ex DC.	Cirjap	√	√			NA
Asteraceae	<i>Bidens pilosa</i> (L.)	Bidpil	√	√			AL RU
Asteraceae	<i>Conyza bonariensis</i> (L.)	Conbon	√				AL RU
Asteraceae	<i>Coreopsis lanceolata</i> (L.)	Corlan	√	√			AL
Asteraceae	<i>Helianthus tuberosus</i>	Heltub			√		AL
Asteraceae	<i>Lactuca indica</i> (L.)	Lacind			√		NA
Asteraceae	<i>Cosmos bipinnatus</i> Cav.	Cosbip			√		AL
Asteraceae	<i>Gamochaeta pensylvanica</i> (Willd.) A.L.Cabrera	Gampen	√	√			AL
Asteraceae	<i>Aster tataricus</i> L.f.	Astatt		√			NA
Asteraceae	<i>Kalimeris indica</i> (L.) Sch. Bip.	Kalind		√		√	NA
Asteraceae	<i>Petasites japonicus</i> (Siebold et Zucc.) Maxim.	Petjap				√	NA RA
Asteraceae	<i>Farfugium japonicum</i> (L.) Kitamura	Farjap				√	NA RA

Table 2-8. (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Asteraceae	<i>Picris hieracioides</i> L. subsp. <i>japonica</i> (Thunb.) Krylov	Pichie	√		√	√	NA
Asteraceae	<i>Ixeris tamagawaensis</i> (Makino) Kitam.	Ixetam	√		√	√	NA RA
Asteraceae	<i>Conyza canadensis</i> (L.) Cronquist	Concan	√	√	√		AL RU
Asteraceae	<i>Xanthium strumarium</i> (L.)	Xanstr			√	√	NA
Asteraceae	<i>Erigeron philadelphicus</i> (L.)	Eriphi	√	√	√	√	AL RU
Asteraceae	<i>Artemisia capillaris</i> Thunb.	Artcap	√		√	√	NA RA
Asteraceae	<i>Solidago canadensis</i> var. <i>scabra</i> (L.)	Solcan	√	√	√		AL RU
Brassicaceae	<i>Brassica rapa</i> (L.)	Brarap	√		√		NA
Brassicaceae	<i>Orychophragmus violaceus</i> (L.)	Oryvio			√	√	NA
Brassicaceae	<i>Cardamine hirsuta</i> (L.)	Carhir	√		√	√	AL RA
Brassicaceae	<i>Brassica juncea</i> var. <i>cernua</i> Jorb. et Hem.	Brajun	√			√	NA
Brassicaceae	<i>Cardamine scutata</i> Thunb.	Carscu				√	NA RA
Brassicaceae	<i>Nasturtium officinale</i> R. Br.	Nasoff				√	AL RA
Calycanthaceae	<i>Chimonanthus praecox</i> (L.) Link	Chipra	√				NA
Cannabaceae	<i>Humulus japonicus</i> (L.)	Humjap			√	√	NA RU

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Cannabaceae	<i>Celtis sinensis</i> Pers.	Celsin		√			NA
Caprifoliaceae	<i>Abelia serrata</i> Siebold et Zucc.	Abeser	√				NA
Caryophyllaceae	<i>Cerastium glomeratum</i> Thuill.	Cerglo	√	√	√	√	AL RU
Caryophyllaceae	<i>Sagina japonica</i> (Sw.) Ohwi	Sagjap				√	NA
Caryophyllaceae	<i>Stellaria aquatica</i> (L.) Scop.	Steaqu				√	NA
Caryophyllaceae	<i>Silene armeria</i> (L.)	Silarm				√	NA
Commelinaceae	<i>Tradescantia fluminensis</i> (L.)	Traflu		√			AL RA
Commelinaceae	<i>Commelina communis</i> (L.)	Comcom				√	NA
Convolvulaceae	<i>Calystegia japonica</i> (L.)	Caljap	√				NA
Convolvulaceae	<i>Calystegia soldanella</i> (L.) Roem. et Schult.	Calsol				√	NA RA
Cucurbitaceae	<i>Gynostemma pentaphyllum</i>	Gynpen		√		√	NA
Cucurbitaceae	<i>Sicyos angulatus</i> (L.)	Sicang	√		√		AL RU
Cupressaceae	<i>Cryptomeria japonica</i> (Thunb. ex L.f.) D.Don	Cryjap				√	NA
Cupressaceae	<i>Chamaecyparis pisifera</i> (Sieb. & Zucc.) Endl.	Chapis				√	NA
Cyperaceae	<i>Carex curvicolis</i> Franch. et Savat.	Carcur				√	NA RA
Cyperaceae	<i>Cyperus rotundus</i> (L.)	Cyprot	√				NA RU

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Equisetaceae	<i>Equisetum arvense</i> (L.)	Equarv	√		√	√	NA RU
Ericaceae	<i>Rhododendron</i> (L.)	Rhodod		√			NA
Euphorbiaceae	<i>Mallotus japonicus</i> (Thunb.) Müll.Arg.	Maljap		√			NA
Fabaceae	<i>Trifolium repens</i> (L.)	Trirep	√	√	√	√	AL
Fabaceae	<i>Trifolium pretense</i> (L.)	Tripre	√		√		AL
Fabaceae	<i>Amorpha fruticosa</i> (L.)	Amofru	√		√		AL
Fabaceae	<i>Vicia sativa</i> (L.)	Vicsat			√	√	NA
Fabaceae	<i>Pueraria montana var. lobata</i>	Puemon	√	√	√	√	NA
Fabaceae	<i>Robinia pseudoacacia</i>	Robpse	√		√		AL
Fabaceae	<i>Wisteria brachybotrys</i> Siebold et Zucc.	Wisbra			√	√	NA
Fabaceae	<i>Indigofera tinctoria</i> (L.)	Indtin		√		√	NA
Fabaceae	<i>Vicia cracca</i> (L.)	Viccra				√	NA
Fabaceae	<i>Lespedeza tomentosa</i> (Thunb.) Siebold ex Maxim.	Lestom				√	NA RA
Fagaceae	<i>Quercus serrata</i> (L.)	Queser	√			√	NA
Geraniaceae	<i>Geranium wilfordii</i> Maxim.	Gerwil	√	√	√	√	NA
Hydrangeaceae	<i>Deutzia scabra</i> Thunb.	Deusca				√	NA

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Iridaceae	<i>Iris pseudacorus</i> (L.)	Iripse	√		√	√	AL RA
Iridaceae	<i>Sisyrinchium rosulatum</i>	Sisros	√	√			NA
Iridaceae	<i>Iris japonica</i> Thunb.	Irijap				√	NA RA
Juncaceae	<i>Juncus effusus</i> var. <i>decipens</i>	Juneff	√	√	√	√	NA RA
Lamiaceae	<i>Glechoma hederacea</i> subsp. <i>grandis</i>	Glehed			√		NA
Lamiaceae	<i>Perilla frutescens</i> (L.) Britton var. <i>crispa</i> (Thunb.) H.Deane	Perfru				√	NA
Lamiaceae	<i>Ajuga ciliata</i> Bunge var. <i>villosior</i> A.Gray ex Nakai	Ajucil				√	NA
Lamiaceae	<i>Lamium amplexicaule</i> (L.)	Lamamp	√				NA RU
Lamiaceae	<i>Lamium album</i> (L.) var. <i>barbatum</i> (Siebold et Zucc.) Franch. et Sav.	Lamalb	√				NA RU
Lauraceae	<i>Cinnamomum camphora</i> (L.) J.Presl	Cincam				√	NA
Lythraceae	<i>Lythrum anceps</i> Makino	Lytanc				√	NA RA
Meliaceae	<i>Melia azedarach</i> (L.)	Melaze		√			NA
Moraceae	<i>Morus alba</i> (L.)	Moralb	√				NA

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Oleaceae	<i>Forsythia viridissima</i> Lindl.	Forvir	√				NA
Onagraceae	<i>Oenothera drummondii</i> Hook.	Oendru		√			AL RA
Onagraceae	<i>Epelobium hirsutum</i> (L.)	Epehir			√	√	NA RA
Onagraceae	<i>Oenothera speciosa</i> Nutt.	Oenspe	√				AL
Orobanchaceae	<i>Pedicularis resupinata</i> (L.) subsp	Pedres	√	√			NA
Osmundaceae	<i>Osmunda japonica</i> Thunb.	Osmjap				√	NA RA
Oxalidaceae	<i>Oxalis debilis</i> Kunth subsp. <i>corymbosa</i> (DC.)	Oxadeb	√				AL RU
Papaveraceae	<i>Macleaya cordata</i> (Willd.) R.Br.	Maccor				√	NA
Pentaphragaceae	<i>Eurya japonica</i> Thunb.	Eurjap				√	NA
Pinaceae	<i>Pinus densiflora</i> Sieb. & Zucc.	Pinden				√	NA
Plantaginaceae	<i>Plantago depressa</i> (L.)	Pladep	√		√	√	AL RU
Plantaginaceae	<i>Veronica persica</i> (L.)	Verper	√		√		AL
Plantaginaceae	<i>Veronica polita</i> var. <i>lilacina</i>	Verpol				√	NA
Plantaginaceae	<i>Veronica undulata</i> Wall.	Verund				√	NA RA
Plantaginaceae	<i>Veronica anagallis-aquatica</i> (L.)	Verana	√		√		AL RA
Poaceae	<i>Poa annua</i> (L.)	Poaann	√	√	√	√	NA RU



**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Poaceae	<i>Miscanthus sinensis</i> Anderss.	Missin	√	√	√	√	NA
Poaceae	<i>Lolium perenne</i> (L.)	Lolper	√	√	√	√	AL RU
Poaceae	<i>Lolium multiflorum</i> Lam.	Lolmul	√	√	√	√	AL RU
Poaceae	<i>Alopecurus aequalis</i> Sobol.	Aloaeq	√		√	√	NA RU
Poaceae	<i>Avena fatua</i> (L.)	Avefat	√		√		AL
Poaceae	<i>Echinochloa crus-galli</i> (L.) P.Beauv.	Echcru	√				NA RU
Poaceae	<i>Phragmites australis</i> (Cav.) Trin. ex Steud	Phraus	√	√	√	√	NA RA
Poaceae	<i>Miscanthus sacchariflorus</i> (L.)	Missac	√	√	√	√	NA RA
Poaceae	<i>Imperata cylindrica</i> (L.) P.Beauv.	Impcyl	√	√			NA RU
Poaceae	<i>Arundo donax</i>	Arudon	√				NA RA
Poaceae	<i>Arundinella hirta</i> Thunb.	Aruhir	√	√		√	NA
Poaceae	<i>Phalaris arundinacea</i> (L.)	Phaaru			√	√	NA RA
Poaceae	<i>Phyllostachys bambusoides</i>	Phybam			√	√	NA
Poaceae	<i>Coix lacryma-jobi</i>	Coilac			√	√	NA RA
Poaceae	<i>Festuca arundinacea</i> Sherb.	Fesaru	√	√	√	√	AL RU
Poaceae	<i>Festuca parvigluma</i> (L.)	Fespar	√	√	√	√	AL

**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Poaceae	<i>Phragmites japonica</i> (L.)	Phrjap	√	√	√	√	NA RA
Poaceae	<i>Briza maxima</i> (L.)	Brimax	√	√			AL RU
Poaceae	<i>Briza minor</i> (L.)	Brimin	√	√			NA
Poaceae	<i>Cynodon dactylon</i> (L.)	Cyndac	√	√	√		NA RU
Poaceae	<i>Eleusine indica</i> (L.) Gaertn.	Eleind	√	√	√		NA RU
Poaceae	<i>Digitaria ciliaris</i> (Retz.) Koel	Digcil		√			NA RU
Polygonaceae	<i>Rumex acetosa</i> (L.)	Rumace	√	√	√	√	NA
Polygonaceae	<i>Reynoutria japonica</i> Houtt.	Reyjap	√	√	√	√	NA
Polygonaceae	<i>Fagopyrum esculentum</i> (L.)	Fagesc			√		NA
Polygonaceae	<i>Rumex japonicus</i> Houtt.	Rumjap	√	√	√	√	NA
Polygonaceae	<i>Rumex acetosella</i> (L.)	Rumace	√		√	√	NA RU
Polygonaceae	<i>Persicaria senticosa</i> (Meisn.) H.Gross	Persen				√	NA
Polygonaceae	<i>Persicaria hydropiper</i> (L.) Delarbre	Perhyd	√	√		√	NA RA
Portulacaceae	<i>Talinum paniculatum</i> (Jacq.) Gaertn.	Talpan	√				NA
Primulaceae	<i>Primula japonica</i> A.Gray	Prijap				√	
Ranunculaceae	<i>Ranunculus japonicus</i> Thunb.	Ranjap				√	NA

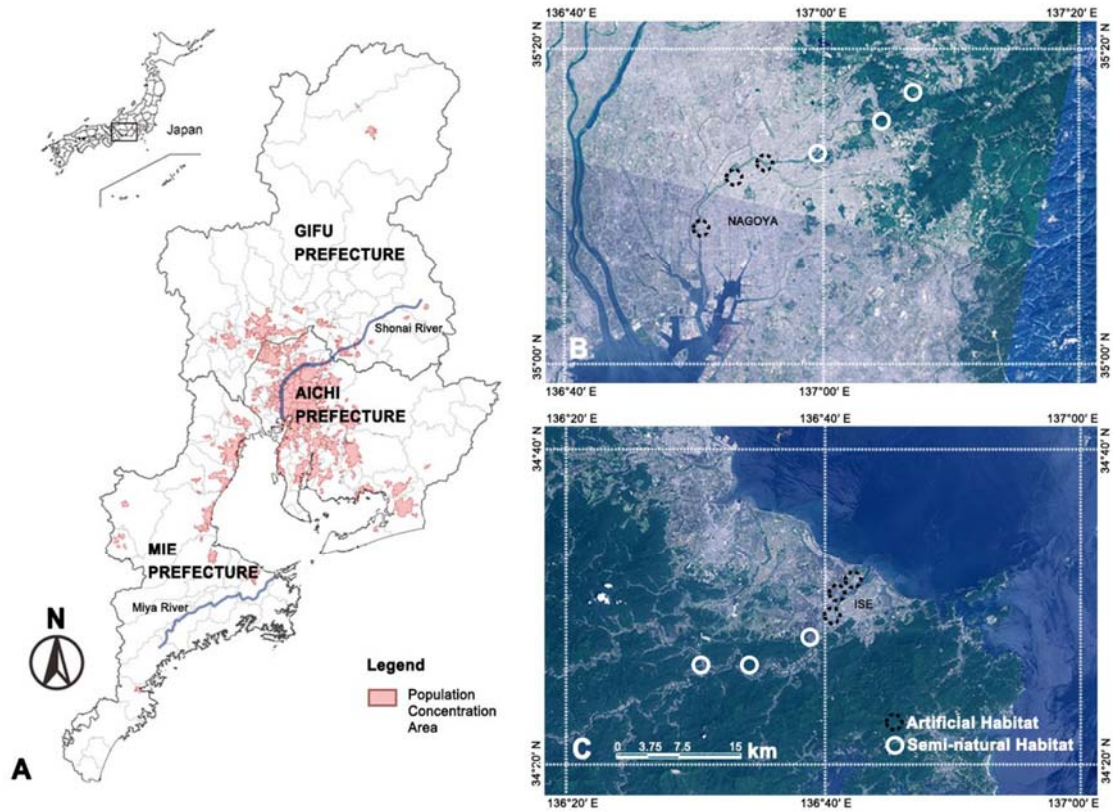
**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Rosaceae	<i>Cerasus jamasakura</i> (Sieb. ex Koidz.)	Cerjam	√	√			NA
Rosaceae	<i>Rosa multiflora</i> Thunb.	Rosmul	√	√	√	√	NA
Rosaceae	<i>Aria alnifolia</i> (Siebold et Zucc.) Decne.	Arialn				√	NA
Rosaceae	<i>Rubus parvifolius</i> (L.)	Rubpar			√	√	NA RU
Rosaceae	<i>Spiraea japonica</i> (L.)	Spijap				√	NA
Rosaceae	<i>Potentilla indica</i> (Andrews) Th.Wolf	Potind				√	NA RU
Rosaceae	<i>Potentilla chinensis</i> Ser.	Potchi	√			√	NA RA
Rosaceae	<i>Rubus buergeri</i> Miq.	Rubbue				√	NA
Rubiaceae	<i>Galium spurium</i> (L.) var. echinospermon	Galspu	√	√	√	√	NA RU
Rubiaceae	<i>Paederia scandens</i> (Lour.) Merr.	Paesca	√	√	√	√	NA RU
Salicaceae	<i>Salix gracilistyla</i> Miq.	Salgra				√	NA RA
Salicaceae	<i>Salix gilgiana</i> Seemen.	Salgil	√		√		NA RA
Saururaceae	<i>Houttuynia cordata</i> (L.)	Houcor			√		NA RU
Saxifragaceae	<i>Saxifraga fortunei</i> Hook.f. var. alpina (Matsum. et Nakai) Nakai	Saxfor		√		√	NA RA
Schisandraceae	<i>Schisandra chinensis</i> (L.)	Schchi				√	NA

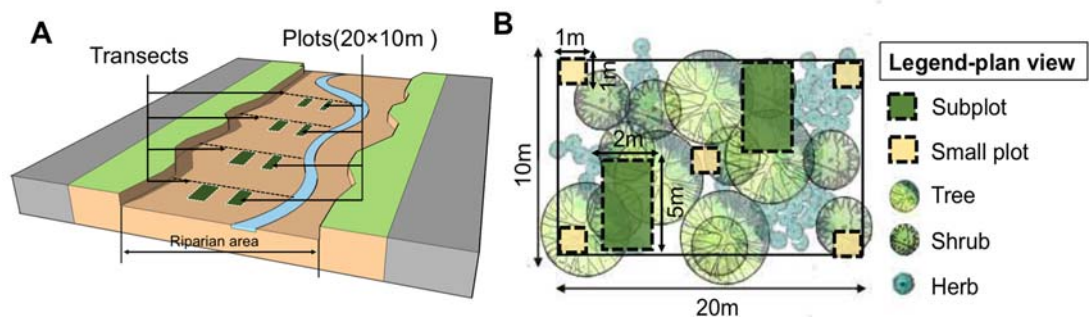
**Table 2-8.** (Continued)

Family	Species	Abbreviation	AS	AM	SS	SM	Type
Sciadopityaceae	<i>Sciadopitys verticillata</i> (Thunb.) Sieb. et Zucc.	Sciver				√	NA
Solanaceae	<i>Solanum nigrum</i> (L.)	Solnig		√		√	NA
Solanaceae	<i>Lycium chinense</i> Mill.	Lycchi				√	NA RA
Theaceae	<i>Camellia japonica</i> (L.)	Camjap				√	NA
Typhaceae	<i>Typha orientalis</i> C.Presl	Typori				√	NA RA
Ulmaceae	<i>Ulmus pumila</i> (L.)	Ulpum	√				NA
Ulmaceae	<i>Zelkova serrata</i> (Thunb.) Makino	Zelser				√	NA
Urticaceae	<i>Boehmeria nivea</i> var. <i>nippononivea</i>	Boeniv		√		√	NA
Verbenaceae	<i>Verbena officinalis</i> (L.)	Veroff	√	√	√	√	AL
Vitaceae	<i>Cayratia japonica</i> (L.)	Cayjap			√	√	NA
Zingiberaceae	<i>Alpinia japonica</i> (Thunb.) Miq.	Alpjap				√	NA

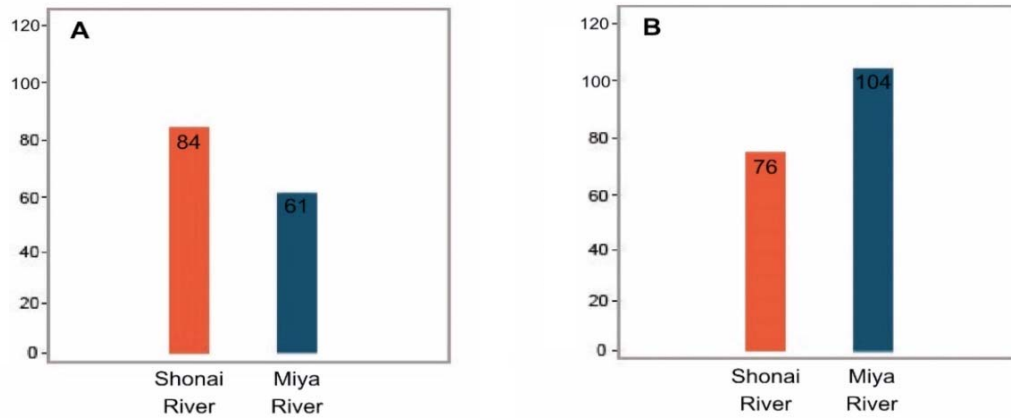
## 2.6 Figures



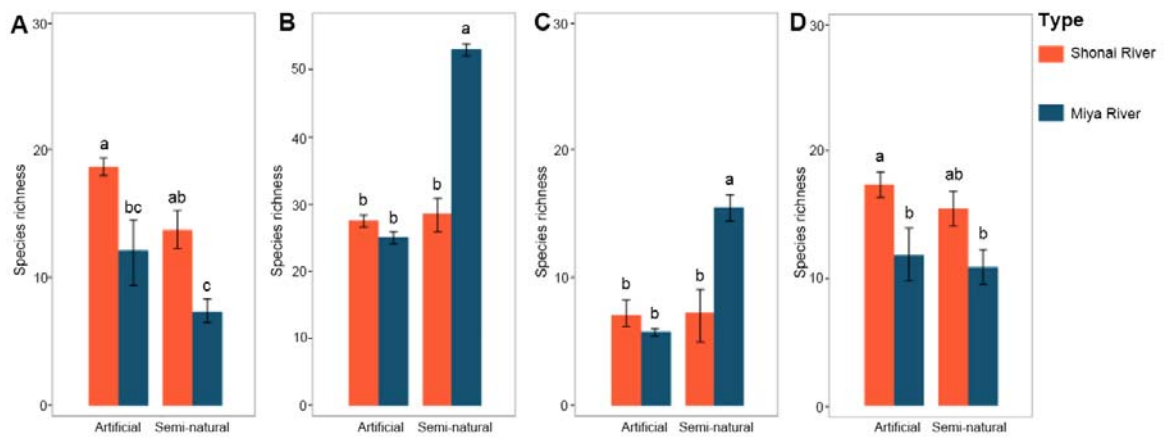
**Fig. 2-1.** An overview of the Shonai River and Miya River system in Japan(A) and the location of research sites along the Shonai River (B) and the Miya River(C). Notes: the information of the population concentration area was derived from the Geospatial Information Authority of Japan.



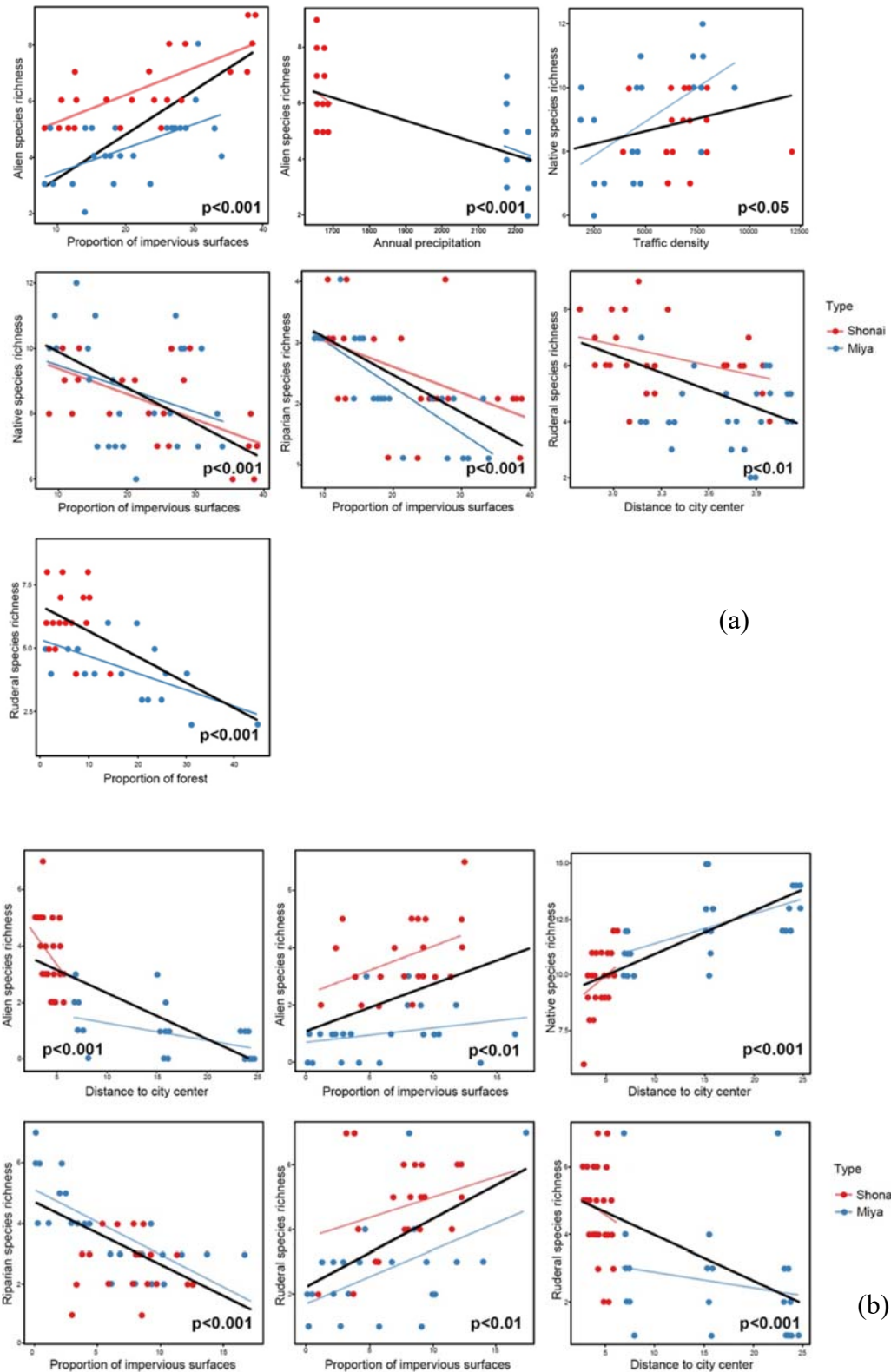
**Fig. 2-2.** Schematic of vegetation survey method (A) and plan view of a vegetation plot (B).



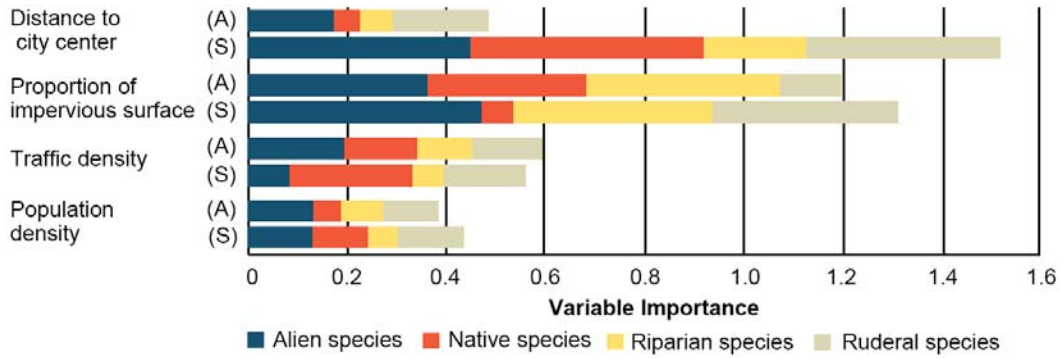
**Fig. 2-3.** Total species richness for the artificial (A) and semi-natural habitats (B). Notes: The red boxes represent the species richness in the habitats with a high level of urbanization (Shonai River), while the blue boxes represent the species richness in the relatively less urbanized habitats (Miya River).



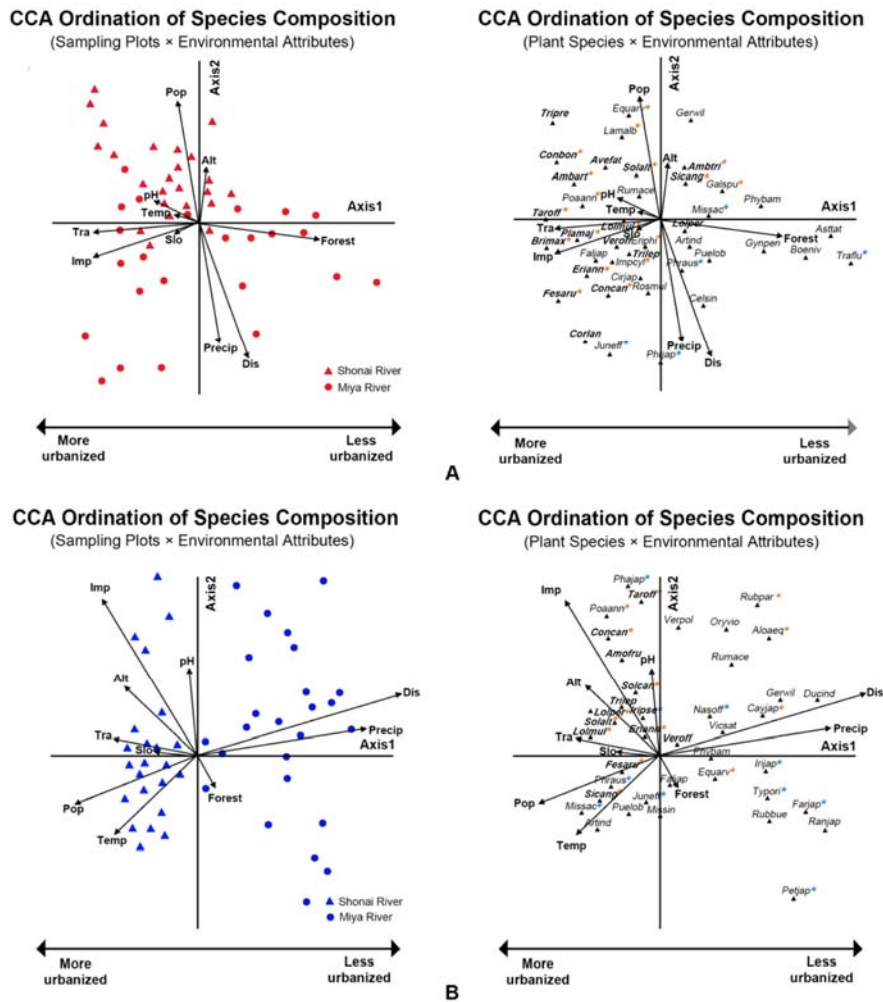
**Fig. 2-4.** Average species richness / site for the artificial (A) and semi-natural habitats (B). Notes: The red boxes represent the species richness in the habitats with a high level of urbanization (Shonai River), while the blue boxes represent the species richness in the relatively less urbanized habitats (Miya River).



**Fig. 2-5.** The number of alien, native, riparian and ruderal species in relation to urbanization and environmental factors of artificial (a) and semi-natural habitats (b) in central Japan. A regression line is only shown for significant relationships. Black thick lines are the relationships across all the riversides, and thinner red and blue lines are the relationships within the Shonai and Miya River.



**Fig. 2-6.** Variable importance. Shown are variable importance of population density, traffic density, the proportion of impervious surface, and distance to the city center for alien, native, riparian, and ruderal species in artificial (A) and semi-natural (S) habitats



**Fig. 2-7** Canonical correspondence analysis diagram showing the ordination of species composition in the artificial (A) and semi-natural (B) habitats. Notes: shapes correspond to individual study plots; codes of individual species (Table 2-8) show their scores as a function of the first two axes. The direction and length of arrows shows the degree of correlation between plant community types and the variables; species in bold represent alien species; species with yellow and blue "\*" represent ruderal and riparian species, respectively.



## **Chapter 3: Effect of anthropogenic disturbance on the floristic homogenization in the floodplain landscape: insights from the taxonomic and functional perspectives**

### **3.1 Introduction**

Floristic homogenization has been defined as the rise in the spatial and temporal similarity of floras (McKinney and Lockwood 1999). Overall, such loss of plant  $\beta$ -diversity in ecological processes is generally attributed to the extinction of native species and widespread of non-natives (Pino et al. 2009; Zeeman et al. 2017). Since floristic homogenization can destroy the biodiversity in ecology and evolution processes and even affect human well-being (Olden et al. 2004; Olden and Rooney 2006), how  $\beta$ -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 (Socolar et al. 2016; Price et al. 2020).

Humans have an adverse effect on natural habitats due to various activities, including urbanization, deforestation, roads, farming, and change of environmental conditions (Scanes 2018). Therefore, anthropogenic disturbance was considered one of the most important and rapid human-driven factors that lead to habitat degradation and biodiversity loss (Kowarik 2011). Habitat heterogeneity and fragmentation are considered to be the main consequences of human disturbance (Fischer and Lindenmayer 2007). 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 (Knapp 2010). 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 (Kowarik and Säumel 2007). 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 (McKinney 2006; La Sorte et al. 2007; Trentanovi et al. 2013; Blouin et al. 2019). Thus far, studies on floristic homogenization have been primarily conducted by comparing the plant assemblages at different urbanization and habitat disturbance levels (Lougheed et al. 2008;

Gong et al. 2013; Trentanovi et al. 2013; Aronson et al. 2015; Mayor et al. 2015; Brice et al. 2017). However, existing studies have achieved divergent results. Some of the studies reported a decrease in  $\beta$ -diversity with the increase in anthropogenic disturbance, while others detected an increase or even no change at all (Aronson et al. 2015; Mayor et al. 2015; Brice et al. 2017). In any case, extinction of native or specialist species and invasions of non-native species are the primary triggers 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 (Brice et al. 2016; Yang et al. 2017). However, a comparison of floristic similarity among sites at different disturbance levels has been commonly performed after removing the effect of environmental factors (Wang et al. 2014; Brice et al. 2017; Blouin et al. 2019). 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 also be manifested in increased similarity in the trait composition, a process known as functional homogenization, which is arousing gradual attention (Tobias and Monika 2012; Villéger et al. 2014; White et al. 2018). Traits are crucial indicators to determine biodiversity as impacted by their roles of shaping species distribution patterns (Pollock et al. 2012), promoting ecosystem stability and functioning (Olden et al. 2004), as well as determining responses to environmental changes (Newbold et al. 2013). 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) (Williams et al. 2009; Williams et al. 2015). Since functional traits often reflect the requirements of vegetation for the environment and show close relationships with human disturbance (Violle et al. 2007), 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 (Entwistle et al. 2019); research involving riparian plant

assemblages may be highly conducive to connecting local floras' responses to degradation level with  $\beta$ -diversity. However, it is noteworthy that limited studies assessing the impacts of anthropogenic disturbance on the  $\beta$ -diversity of plant communities have been conducted in riparian areas (Brice et al. 2017; Loiselle et al. 2020; Price et al. 2020). 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 (Catford and Jansson 2014). However, as an attraction of urbanization and human activities, riparian areas and plant assemblages come under the pressure of artificial disturbances (Richardson et al. 2007; Johnson et al. 2014). 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 (White and Greer 2006; Cao and Natuhara 2020). On the other hand, humans impose intensive pressures on floodplain areas. These human-driven pressures consist of soil compaction, trampling of vegetation, water and soil pollution, and introduction of non-native species (O'Toole et al. 2009; Grella et al. 2018). 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 (Junk et al. 2006; Monk et al. 2019). It has been increasingly evidenced that anthropogenic disturbance affects biodiversity, whereas most of the relevant studies have focused on residential areas or parks (Wang et al. 2007; Gong et al. 2013; Blouin et al. 2019). 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) (Opperman et al. 2010).

Thus, this study analyzed floristic homogenization in the floodplain landscape to explore the responses of  $\beta$ -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 (Lyon and Sagers 1998; Gilliam 2007). The current study aimed to assess the effects of anthropogenic disturbance on 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 might affect the pattern of  $\beta$ -diversity of plant assemblages.

## 3.2 Materials and methods

### 3.2.1 Study location

The study area was located in the Mie Prefecture (Central Japan). The floodplain area of the Miya River was selected for this study (Fig. 3-1). The Miya River originates from Mt. Odaigahara and flows into the Ise Bay, and is one of the Class A rivers that flow solely through Mie Prefecture. This river exhibits a 91 km length and a basin area of approximately 920 km<sup>2</sup>. 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, Odai 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.

### 3.2.2 Field sampling

Ideally, the 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 1 km<sup>2</sup> (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 obtained from the government website (Japan Integrated Biodiversity Information System, 2013) were used as Supplementary Materials. Then, a total of 49 floodplain areas was selected according to previously mentioned criteria. Meanwhile, to eliminate the influence of inaccessibility and significant differences in environmental conditions, a field reconnaissance survey was conducted 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 I selected major beds and waterside lowlands of the floodplain areas as the sampling area (Fig. 3-2).

A vegetation survey was conducted in 2019, from April to August. In each of the selected sampling sites, transects were established perpendicular to the river at intervals of 50–100 m, and several 10 × 10 m sampling plots were established along each transect. 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% (Damgaard 2014). 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 mean stem number 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 in situ. For those species that cannot be identified immediately, 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 labelled plastic bags immediately afterwards.

### 3.2.3 Delineation of sampling sites into different level of habitat degradation

The level of habitat degradation was delineated according to the Normalized Difference Vegetation Index (NDVI) (Tucker 1979) (Fig. 3-3). I set 500-m buffer zones around sampling sites to calculate the NDVI. This index could be calculated by measuring the difference in reflectance between the red band and near-infrared band of the satellite images. The range of NDVI is 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 (Zhang et al. 2009). The NDVI was calculated by:

$$\text{NDVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED}}$$

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). k-means clustering based on mean NDVI values of each sampling plot was used to classify floodplains into different habitat degradation levels—high, moderate, and low (Table 3-1). 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 (Wang et al. 2012). Furthermore, the NDVI was reported to be a powerful proxy and screening tool for monitoring and assessment of riparian habitats (Griffith et al. 2002).

### 3.2.4 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 3-2) were select for their representativeness as responses to natural and anthropogenic disturbances (Williams et al. 2015). 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 (Violle et al. 2007). 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) (Valladares and Niinemets 2008). 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 (Van Doren et al. 2017). Fertility requirement was considered for high nutrition environments and is related closely to the disturbed area (Williams et al. 2015). The approach of seed dispersal could indirectly reflect the effect of habitat fragmentation and human disturbance; thus it was included in this study (Kowarik 2011). The data of plant traits were acquired from the field measurements and available published data. 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.

### **3.2.5 Land-use (land cover) and habitat data**

Given the differences in LULC distribution and combination activities existing among three groups of degradation levels, 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 circle around each sampling plot with a radius of 500-m, with Google Earth imagery (2019) as a base layer. To interpret the surrounding land-use type of each sampling plot, I 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 (Lockaby et al. 2005). 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 (Pennington et al. 2010). Soil texture was used as an



environmental factor related to local environmental conditions (Roncucci et al. 2015). 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.).

### 3.2.6 Statistical analysis

**$\alpha$ - and  $\beta$ -diversity:** The species  $\alpha$  diversity was quantified by species richness. Species richness was measured by counting the total number of plant species at the plot scale. Furthermore, the 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  $\beta$ -diversity across the river basin were calculated. The  $\beta$ -diversity here denoted the total  $\beta$ -diversity (dissimilarity among all the sampling plots), which was assessed by the Bray-Curtis dissimilarity (Baselga 2013). This index 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 traits.

To delve into the effect of anthropogenic disturbance on floristic homogenization, taxonomic and functional facets were calculated following three steps. First, I built a functional matrix by multiplying the species-by-trait matrix with the plot-by-species matrix. For the plot-by-species matrix, the species relative abundance data were used to determine the dominance of a species in 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 aspect, the Bray-Curtis distance on the plot-by-species matrix was employed to generate the plot-by-plot distance matrix. For the functional aspect, the plot-by-plot matrix was calculated based on the plot-by-trait matrix using the Gower distance.

Third, I tested whether anthropogenic disturbance was responsible for floristic homogenization by the approach of Test for Homogeneity of Multivariate Dispersions (Anderson et al. 2006). This test could analyze the  $\beta$ -diversity 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, I tested the mean  $\beta$ -diversity using ANOVA with 9999 permutations to assess whether the dispersion of three groups of degradation levels was

different. Furthermore, the differences in the variations in taxonomic and functional compositions (the differences of centroid locations among groups) were tested using PERMANOVA (Anderson 2001), and the significance was determined by 9999 permutations. The differences in composition and multivariate dispersion among three groups of degradation levels were visualized by Principal Coordinate Analysis (PCoA).

**Effect of Increase of non-natives:** The roles of non-native species on floristic homogenization could be measured by the variations of  $\beta$ -diversity. Thus, the  $\beta$ -diversity for total flora was compared to that for natives only. The previously mentioned approach could simulate the invasion of non-natives in a plant community by comparing the changes of  $\beta$ -diversity after “adding” them; on that basis, whether they lead to homogenization can be evaluated. The native  $\beta$ -diversity was compared to that of all species by paired sample t-tests, and *p*-values were adjusted using the multiple test Holm correction.

**Effect of the environmental matrix on  $\beta$ -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 these models. I 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 predictors on  $\beta$ -diversity should be determined and the *r* value was less than 0.7, all the predictors were kept. With the total  $\beta$ -diversity of sample plots as the response, the boosted regression tree analysis (BRT) was performed to analyze the effect of environmental variables on taxonomic and functional  $\beta$ -diversity. BRT was used for its good interpretability and its flexibility in handling different types of predictors and less sensitivity to multicollinearity (Dormann et al. 2013). 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 bag fraction of 0.5, and a learning rate of 0.001.

All statistical analyses that 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. I conducted the multivariate dispersion analyses in the “vegan” package with the “betadisper” function. The comparisons of the distance of each plot to the centroid were drawn with the “permutest. betadisper”. Moreover, I performed the comparisons of location by “rda” and “anova.cca” (vegan). The BRTs were adopted using the code from the ‘gbm’ incorporated in the “dismo” package.

### **3.3 Results**

#### **3.3.1 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 (Fig. 3-4). 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.

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 3-3). 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.

#### **3.3.2 Taxonomic and functional $\beta$ -diversity**

For the taxonomic aspect, the  $\beta$ -diversity differed significantly with different degradation levels (ANOVA test with permutations; Table 3-4). The dissimilarity was

relatively low at high degradation levels (see polygon size on Fig. 3-5 a; and average sites-to-centroid distance illustrated in Fig. 3-5 c), indicating that a relatively high degradation level caused taxonomic homogenization. For the functional aspect, however, the homogenization phenomenon was absent in degradation levels. Though the  $\beta$ -diversity was lower in highly disturbed areas compared with the areas at moderate and low degradation levels (Fig. 3-5 b, d), the differences were not significant by significant multivariate dispersion tests (Table 3-4).

$\beta$ -diversity changes were related to the species and trait composition among degradation groups. The results of PERMANOVA showed significant shifts in taxonomic and functional compositions (centroid location) for both taxonomic and functional  $\beta$ -diversity (Table 3-4), as reflected by the isolated location of the centroid at a low degradation level relative to that at high and moderate degradation levels (Fig. 3-5). 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.

### **3.3.3 The role of non-native species in $\beta$ -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  $\beta$ -diversity (Fig. 3-6, Table 3-5). 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  $\beta$ -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.

### **3.3.4 Joint effects of non-native species and environmental matrix**

The predictor variables are shown in Table 3-6. The results of the BRT model reflected the direct or indirect effects of environmental factors on  $\beta$ -diversity. In this study, the BRT model had greater predictive power on functional  $\beta$ -diversity (explained deviance: 0.481) than that on taxonomic  $\beta$ -diversity (explained deviance: 0.429), and the relative contribution of the

predictors varied between these two diversity aspects (Fig. 3-7).

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

### **3.4 Discussion**

#### **3.4.1 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  $\beta$ -diversity (Aronson et al. 2015; Mayor et al. 2015; Brice et al. 2017), 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 (Kowarik 2011; Blouin et al. 2019), which has been observed in the current study (Fig. 3-4). It was hypothesized previously that the increase in non-native species might induce taxonomic differentiation in

highly disturbed areas (Rooney et al. 2007; Brice et al. 2017). However, if some non-native species propagate in most of the sites within the highly disturbed area, they may also enhance homogenization (Gong et al. 2013). 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 3-3). When compared with highly disturbed areas, interestingly, this study reported that the addition of non-native species exhibited a significant impact on taxonomic differentiation at the low degradation level (Fig. 3-6). This can be explained by a lower non-native species number compared to natives at a low degradation level (Fig. 3-4); the plant assemblages likely shared little non-natives. Therefore, the presence of non-native species may have a disproportionately significant impact on  $\beta$ -diversity variations, since the homogenization effect of a non-native species depend on its high frequency in all the assemblages. 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 (McKinney 2004; Rosenblad and Sax 2017).

For the functional aspect, there were no significant differences in  $\beta$ -diversity at different levels of degradation. However, this study reported that anthropogenic disturbance could indirectly induce functional homogenization for the introduction of non-natives in 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* (Miyawaki 2004). 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 (Miyawaki 2004; Okimura and Mori 2018). 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 (Petsch 2016). The species adapted to that natural or specific habitat are more likely affected because they cannot access alternative resources that non-native species can (Richardson et al. 2007). Overall, non-native species significantly impacted the functional  $\beta$ -diversity, which demonstrated that their traits were dissimilar to that of natives, and some functional traits of non-native species have been preserved after being environmentally filtered (Díaz and Cabido 2001; Mayfield et al. 2010).

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 this study area reflected more recent urban development than the metropolis (Kuussaari et al. 2009), 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 (Pennington et al. 2010). Each of these changes could potentially act as an environmental stressor that differentially shapes plant species distribution depending on their environmental niches and traits (Knapp 2010). Thus the distinction of species composition might be explained by the regeneration time, or lifespan, or the dominant species in floodplains at different degradation levels (Loiselle et al. 2020). 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 revealed in a certain delay in less disturbed floodplains to urban development and the distinct plant communities identified in this study.

#### **3.4.2 Driving factors of the different pattern of $\beta$ -diversity**

Although environmental filtering that was driven indirectly by human disturbance was predominant in the formation of plant assemblages, responses of taxonomic and functional  $\beta$ -diversity to environmental predictors were different within the floodplain areas. The taxonomic dissimilarity indicates that a proportion of impervious surface exhibits a relatively low  $\beta$ -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 (McKinney 2002). 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 (Hill et al. 2002), are partially responsible for the homogenization. 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 (Walsh et al. 2005). Following the construction of impervious surfaces, floodplain areas might be subjected to a shift in plant community composition towards non-native and tolerant species (White and Greer 2006). In addition, it was found that there was a positive association between taxonomic  $\beta$ -diversity and NDVI, which was similar to previous studies (Chase and Ryberg 2004; Harrison et al. 2006). The NDVI is closely correlated to variables of ecological interest such as urbanization level and habitat degradation (Wang et al. 2012). In this 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 3-1). 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 (Rapport et al. 1985). 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 large size of species pool, thus reducing the risk of species extinction (Rowhani et al. 2008).

It is noteworthy that functional  $\beta$ -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 (Johnson et al. 2014). The current study suggested that human disturbances could reduce the functional  $\beta$ -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 alteration, riparian degradation, and intense human recreational activities. Hydrological alteration leads to floodplains a habitat with low inundation frequency and short duration time, thus facilitating the colonization of numerous terrestrial species (Groffman et al. 2003; Pennington et al. 2010), 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  $\beta$ -diversity. Coarse-textured floodplain soil is usually associated with frequent scouring flows, which washed away much smaller soil particles (Campbell et al. 2002). Plant functional traits



were affected by the roles of nutrient scarcity, water balance, and competition, which were mediated by soil texture (Roncucci et al. 2015). 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 (Huang et al. 2013). This 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  $\beta$ -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  $\beta$ -diversity of herbaceous and shrubs, leading to the interactive effects of forest type, forest structure, and forest size. (Erdős et al. 2018) concluded that species diversity and composition were significantly different in edge-like forests and forests with core areas. (Chávez and Macdonald 2012) 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  $\beta$ -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 the current study, however, the environmental factors more significantly impacted the  $\beta$ -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 forming 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 (Díaz et al. 1999; Levine 2016).

### 3.4.3 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 (Pennington et al. 2010; Gong et al. 2013), the aggravation of anthropogenic disturbances and consequent habitat homogenization pose a great challenge for conservation in floodplain landscapes (Richardson et al. 2007; Grella et al. 2018). Hence, there is an urgent need to maintain habitat heterogeneity within floodplain landscapes. In concordance with the findings of (Erdős et al. 2018), 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 the 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 (Watanabe 2012), 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.

### 3.5 Tables

**Table 3-1.** 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

**Table 3-2.** Ten trait groups and trait states use in the trait matrix.

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

**Table 3-3.** The top 10 most frequent plant species found in floodplain areas with different degradation level. 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

**Table 3-4.** Differences in  $\beta$ -diversity and composition in the floodplain landscape, according to three groups of degradation levels. Note: difference in  $\beta$ -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	p-Value	F Ratio	p-Value
$\beta$ -diversity	16.92	<0.001	4.09	0.064
Shift in composition	3.34	0.009	2.15	0.037

**Table 3-5.** The results of paired sample t-test. Permutational t and P-values of paired sample t-test associated with Fig. 3-6 in main text. Differences in taxonomic and functional  $\beta$ -diversity caused by non-native species among different degradation levels were shown..

	Degradation levels	
	t	P
Taxonomic $\beta$ -diversity		
Low	2.1779	0.0279
Moderate	0.3226	0.4652
High	-0.7124	0.0371
Functional $\beta$ -diversity		
Low	-3.0391	0.0162
Moderate	-6.7526	<0.001
High	-7.2790	<0.001

**Table 3-6.** 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 <sup>a</sup>	12.97 $\pm$ 1.13 <sup>b</sup>	5.31 $\pm$ 0.52 <sup>c</sup>
Forest (%)	16.07 $\pm$ 1.76 <sup>c</sup>	23.27 $\pm$ 2.07 <sup>b</sup>	30.32 $\pm$ 1.68 <sup>a</sup>
Farm (%)	10.61 $\pm$ 2.93 <sup>b</sup>	9.94 $\pm$ 1.67 <sup>b</sup>	16.34 $\pm$ 1.06 <sup>a</sup>
Soil texture			
Gravel (%)	19.81 $\pm$ 4.30 <sup>a</sup>	21.69 $\pm$ 5.97 <sup>a</sup>	22.58 $\pm$ 5.71 <sup>a</sup>
Sand (%)	37.62 $\pm$ 5.45 <sup>a</sup>	36.87 $\pm$ 6.29 <sup>a</sup>	39.82 $\pm$ 1.66 <sup>a</sup>
Silt (%)	42.57 $\pm$ 5.45 <sup>a</sup>	41.44 $\pm$ 7.01 <sup>a</sup>	37.59 $\pm$ 5.41 <sup>a</sup>
Invasion			
Non-natives	0.32 $\pm$ 0.05 <sup>a</sup>	0.25 $\pm$ 0.03 <sup>b</sup>	0.07 $\pm$ 0.01 <sup>c</sup>
Human disturbance			
Artificial management (%)	69.23	36.36	25
NDVI value	0.06 $\pm$ 0.02 <sup>c</sup>	0.27 $\pm$ 0.02 <sup>b</sup>	0.49 $\pm$ 0.01 <sup>a</sup>

**Table 3-7.** The species names and traits of all plant species found in 72 sampling plots. Life form is indicated as 1= annual forb, 2= perennial forb, 3= shrub and 4= fern; height is indicated as 1= 1-50 cm, 2=51-100 cm, 3=101-150 cm, 4=151-200 cm and 5= more than 200 cm; Reproduction is indicated as 1= vegetative, 2=vegetative and seed and 3= seed; Shade tolerance is indicated as 1= intolerant, 2= mid-tolerant and 3= tolerant; Wetness is indicated as 1= upland, 2= facultative upland, 3=facultative, 4= facultative riparian and 5= riparian.

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Achyranthes bidentata</i> Blume	2	3	3	2	3	moderate	transient	high	medium	wind
<i>var. japonica</i> Miq.										
<i>Allium macrostemon</i> Bunge	2	2	3	1	3	moderate	transient	medium	medium	multiple
<i>Alopecurus aequalis</i> Sobol.	1	2	3	2	4	moderate	persistent	medium	high	wind
<i>Alpinia japonica</i> Miq.	2	2	3	3	4	slow	transient	medium	medium	wind
<i>Ambrosia artemisiifolia</i> (L.)	1	5	3	1	2	rapid	persistent	high	low	multiple
<i>Ambrosia trifida</i> (L.)	1	5	3	1	4	rapid	persistent	high	low	multiple
<i>Artemisia capillaris</i> Thunb.	2	2	3	1	4	moderate	transient	low	low	multiple
<i>Artemisia indica</i> var.										
<i>maximowiczii</i>	2	3	2	2	3	rapid	transient	high	low	multiple
<i>Arundinella hirta</i> Thunb.	3	3	2	2	2	rapid	persistent	medium	medium	multiple
<i>Aster tataricus</i> L.f.	2	2	2	2	4	rapid	transient	medium	medium	multiple
<i>Avena fatua</i> (L.)	3	3	3	1	3	rapid	persistent	high	low	water or gravity
<i>Bidens pilosa</i> (L.)	1	3	3	2	3	rapid	persistent	high	medium	multiple

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Boehmeria nivea</i> var. <i>nipononivea</i>	2	4	1	2	3	rapid	persistent	medium	high	multiple
<i>Botrychium japonicum</i> (Prantl)Underw.	4	2	1	3	4	moderate	transient	high	medium	wind
<i>Brassica juncea</i> var. <i>cernua</i> <i>Jorb. et Hem.</i>	1	3	3	1	3	rapid	transient	medium	medium	multiple
<i>Briza maxima</i> (L.)	1	2	3	1	2	rapid	persistent	medium	low	multiple
<i>Briza minor</i> (L.)	1	2	3	1	2	rapid	transient	medium	low	multiple
<i>Calanthe discolor</i> Lindl.	2	2	1	3	3	moderate	persistent	medium	high	wind
<i>Cardamine hirsuta</i> (L.)	1	2	3	3	4	rapid	persistent	medium	high	multiple
<i>Cardamine scutata</i> <i>Thunb.</i>	1	2	3	2	4	rapid	transient	medium	medium	multiple
<i>Carex dimorpholepis</i> Steud.	3	2	3	2	4	rapid	persistent	high	medium	wind
<i>Cayratia japonica</i> (L.)	2	1	2	2	3	rapid	transient	high	low	multiple
<i>Cerastium glomeratum</i> Thuill.	1	2	3	2	3	rapid	transient	high	medium	multiple

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Chenopodium album</i> (L.)	1	3	3	2	3	rapid	transient	high	medium	wind
<i>Cimicifuga japonica</i> (Thunb.) Spreng.	2	2	2	2	2	moderate	persistent	medium	medium	multiple
<i>Cirsium japonicum</i> Fisch. ex	2	3	3	2	3	moderate	transient	medium	medium	wind
<i>Coix lacryma-jobi</i> (L.)	1	5	3	2	5	moderate	transient	low	high	multiple
<i>Commelina communis</i> (L.)	1	2	3	3	4	rapid	persistent	high	high	multiple
<i>Conyza bonariensis</i> (L.)	1	2	3	2	2	rapid	persistent	high	low	wind
<i>Conyza canadensis</i> (L.) Cronquist	2	2	3	1	2	rapid	persistent	high	medium	wind
<i>Coreopsis lanceolata</i> (L.)	2	2	3	3	4	moderate	persistent	high	medium	multiple
<i>Cyperus rotundus</i> (L.)	2	2	2	1	4	rapid	transient	medium	medium	water or gravity
<i>Deparia japonica</i> (Thunb.) M.Kato	4	2	1	3	4	moderate	transient	high	medium	wind
<i>Digitaria ciliaris</i> (Retz.) Koel)	2	2	3	1	2	rapid	transient	high	medium	multiple



**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Disporum sessile</i> <i>D. Don ex Schult. &amp; Schult.f.</i>	2	2	1	3	3	moderate	transient	low	medium	multiple
<i>Eleusine indica (L.) Gaertn.</i>	1	2	3	1	2	rapid	transient	medium	medium	multiple
<i>Epelobium hirsutum (L.)</i>	2	5	3	2	4	moderate	persistent	medium	medium	multiple
<i>Equisetum arvense (L.)</i>	4	2	1	2	3	slow	transient	medium	low	water or gravity
<i>Erigeron annuus (L.)</i>	1	4	3	1	2	rapid	persistent	high	low	multiple
<i>Erigeron philadelphicus (L.)</i>	1	4	2	1	3	moderate	transient	high	high	wind
<i>Fagopyrum tataricum (L.)</i> <i>Gaertn.</i>	1	3	2	2	3	rapid	transient	high	high	multiple
<i>Fallopia japonica (Houtt.)</i> <i>Ronse Decr. var. japonica</i>	3	5	2	2	3	rapid	transient	high	low	water or gravity
<i>Farfugium japonicum (L.)</i> <i>Kitamura</i>	2	2	2	3	4	slow	persistent	medium	medium	multiple
<i>Festuca arundinacea Sherb.</i>	1	4	2	2	2	rapid	transient	medium	low	multiple

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Festuca parvigluma</i> (L.)	1	2	2	3	3	rapid	transient	medium	low	Multiple
<i>Galium spurium</i> (L.) var. <i>echinospermon</i>	1	2	3	2	2	rapid	persistent	medium	high	multiple
<i>Gamochaeta pensylvanica</i> (Willd.) A.L.Cabrera	2	1	3	2	2	rapid	transient	medium	medium	multiple
<i>Geranium wilfordii</i> Maxim.	2	1	1	2	3	moderate	transient	medium	medium	multiple
<i>Gynostemma pentaphyllum</i> (Thunb.) Makino	2	2	2	3	3	moderate	transient	medium	high	multiple
<i>Humulus japonicus</i> (L.)	2	2	3	2	3	moderate	persistent	high	low	multiple
<i>Hydrocotyle sibthorpioides</i> Lam.	2	1	2	3	4	slow	transient	medium	medium	multiple
<i>Imperata cylindrica</i> (L.) P.Beauv.	3	3	2	2	3	rapid	transient	high	medium	wind
<i>Indigofera tinctoria</i> (L.)	3	4	2	1	3	rapid	transient	high	medium	multiple
<i>Iris japonica</i> Thunb.	2	4	2	1	5	moderate	transient	medium	medium	water or gravity

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Iris pseudacorus</i> (L.)	2	4	2	1	5	moderate	transient	medium	medium	water or gravity
<i>Ixeris tamagawaensis</i> (Makino) Kitam.	1	2	3	2	4	rapid	transient	medium	medium	multiple
<i>Ixeris tamagawaensis</i> (Makino) Kitam.	2	2	2	1	4	rapid	transient	medium	medium	multiple
<i>Juncus effusus</i> var. <i>decipens</i>	3	4	2	2	5	moderate	persistent	medium	medium	multiple
<i>Kalimeris indica</i> (L.) Sch.	2	2	2	2	3	moderate	transient	medium	medium	multiple
<i>Lespedeza juncea</i> (L.fil.) <i>Pers.</i> var. <i>subsessilis</i> Miq.	2	3	2	1	3	moderate	persistent	high	low	multiple
<i>Lespedeza tomentosa</i> (Thunb.) Siebold ex Maxim.	3	4	2	2	4	moderate	transient	medium	medium	multiple
<i>Lolium multiflorum</i> Lam.	1	3	3	2	2	rapid	transient	high	medium	multiple
<i>Lolium perenne</i> (L.)	1	3	3	2	3	moderate	transient	medium	medium	animal
<i>Macleaya cordata</i> (Willd.) R.Br.	2	4	3	2	3	moderate	transient	high	medium	multiple

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Microlepis strigosa</i> (Thunb.) C.Presl	4	3	1	3	4	moderate	transient	high	medium	Wind
<i>Miscanthus sacchariflorus</i> (L.)	3	5	2	2	4	moderate	transient	low	medium	wind
<i>Miscanthus sinensis</i> Anderss.	3	5	2	2	3	rapid	transient	high	medium	multiple
<i>Nasturtium officinale</i> R. Br.	2	2	2	2	5	rapid	persistent	high	medium	multiple
<i>Oenothera speciosa</i> Nutt.	2	2	2	1	4	rapid	transient	medium	low	multiple
<i>Onychium japonicum</i> (Thunb.) Kunze	4	2	1	3	4	rapid	persistent	high	medium	wind
<i>Orychophragmus violaceus</i> (L.)	1	2	3	2	3	rapid	transient	medium	medium	multiple
<i>Osmunda japonica</i> Thunb.	4	3	1	3	4	moderate	transient	medium	medium	water or gravity
<i>Oxalis debilis</i> Kunth subsp. <i>corymbosa</i> (DC.)	2	1	2	2	3	rapid	transient	medium	medium	wind

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Paederia scandens</i> (Lour.) <i>Merr.</i>	2	4	2	2	3	moderate	persistent	medium	low	Multiple
<i>Pedicularis resupinata</i> <i>subsp. Oppositifolia</i>	2	2	2	2	3	moderate	transient	high	medium	multiple
<i>Penthorum chinense</i> Pursh	2	2	3	2	4	rapid	transient	high	medium	wind
<i>Perilla frutescens</i> (L.) <i>Britton var. crispa</i> (Thunb.) <i>H.Deane</i>	2	2	3	2	3	rapid	transient	medium	high	multiple
<i>Petasites japonicus</i> (Siebold <i>et Zucc.) Maxim.</i>	2	4	1	3	4	slow	persistent	medium	medium	multiple
<i>Phalaris arundinacea</i> (L.)	2	5	1	1	4	rapid	persistent	medium	high	multiple
<i>Phragmites australis</i> (Cav.) <i>Trin. ex Steud</i>	3	5	1	1	5	rapid	transient	medium	medium	wind
<i>Phragmites japonica</i> (L.)	3	5	1	1	5	rapid	transient	low	low	water or gravity

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Picris hieracioides L. subsp. japonica</i> (Thunb.) Krylov	2	2	2	2	3	rapid	transient	high	medium	Wind
<i>Plantago depressa</i> (L.)	2	2	2	1	2	rapid	persistent	medium	low	animal
<i>Poa annua</i> (L.)	2	3	3	2	3	rapid	persistent	high	low	multiple
<i>Polygonum orientale</i> Linn.	1	4	2	1	4	rapid	transient	high	medium	multiple
<i>Potentilla chinensis</i> Ser.	2	2	3	2	5	moderate	persistent	medium	high	multiple
<i>Potentilla indica</i> (Andrews) Th.Wolf	2	3	2	2	3	rapid	transient	medium	medium	multiple
<i>Pueraria montana</i> var. <i>lobata</i>	2	3	2	2	3	rapid	transient	medium	medium	animal
<i>Ranunculus japonicus</i>	2	3	3	2	4	rapid	persistent	medium	medium	multiple
<i>Rosa multiflora</i> Thunb.	3	5	2	2	3	rapid	persistent	medium	medium	multiple
<i>Rubus buergeri</i> Miq.	2	1	1	3	3	moderate	transient	low	medium	multiple
<i>Rubus parvifolius</i> (L.)	1	3	2	3	3	rapid	transient	high	medium	multiple
<i>Rumex acetocella</i> (L.)	2	3	2	2	2	rapid	persistent	high	medium	multiple

**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Rumex acetosa</i> (L.)	2	4	2	2	3	rapid	persistent	medium	low	Multiple
<i>Rumex hydrolapathum</i> Huds.	2	3	2	2	3	rapid	persistent	high	low	multiple
<i>Rumex japonicus</i> Houtt.	2	3	2	2	3	moderate	transient	high	medium	multiple
<i>Sagina japonica</i> (Sw.) Ohwi	1	1	3	2	3	slow	persistent	medium	medium	wind
<i>Saxifraga cortusifolia</i> Siebold et Zucc.	2	1	2	3	4	moderate	transient	medium	medium	multiple
<i>Scutellaria pekinensis</i> Maxim. var. <i>transitra</i> (Makino) H.Hara	2	2	3	2	3	rapid	transient	medium	medium	wind
<i>Selaginella tamariscina</i> (P. Beauv.) Spring	4	1	1	3	4	moderate	persistent	high	medium	multiple
<i>Selaginella uncinata</i> (Desv.) Spring	4	2	1	3	4	moderate	persistent	high	high	wind

**Table 3-6.** (Continued)

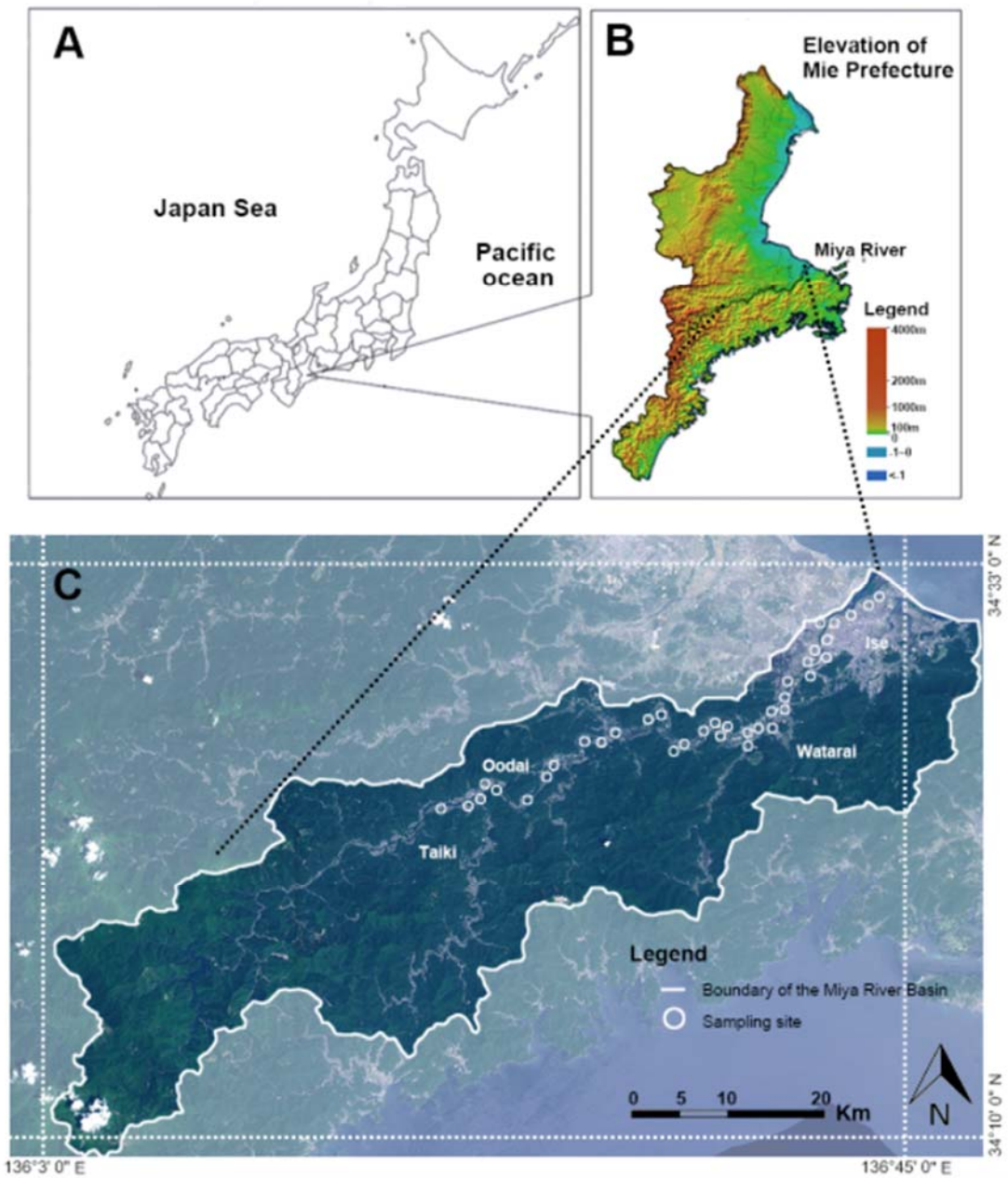
Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Silene armeria (L.)</i>	1	2	3	2	3	rapid	transient	medium	high	Wind
<i>Sisyrinchium rosulatum</i>	1	2	3	2	2	moderate	transient	medium	medium	wind
<i>Solanum nigrum (L.)</i>	1	2	3	2	3	rapid	persistent	high	high	multiple
<i>Solidago altissima (L.)</i>	2	5	2	1	2	rapid	persistent	high	medium	wind
<i>Solidago canadensis var. scabra (L.)</i>	2	5	2	1	2	rapid	persistent	high	medium	wind
<i>Sparganium erectum (L.)</i>	2	3	2	1	5	moderate	persistent	medium	medium	multiple
<i>Spiraea japonica (L.)</i>	3	3	2	2	3	moderate	transient	high	medium	wind
<i>Stellaria aquatica (L.) Scop.</i>	2	2	2	2	3	rapid	transient	high	high	multiple
<i>Suaeda maritima</i>	1	1	2	1	5	rapid	transient	medium	low	multiple
<i>Taraxacum japonicum Koidz</i>	2	2	3	1	2	rapid	persistent	high	low	multiple
<i>Taraxacum officinale (L.)</i>	2	2	3	1	2	rapid	persistent	high	low	multiple
<i>Torilis scabra (Thunb.) DC.</i>	1	2	3	3	3	moderate	transient	low	medium	animal
<i>Tradescantia fluminensis(L.)</i>	2	2	1	3	4	rapid	persistent	low	medium	animal



**Table 3-6.** (Continued)

Species	Life form	Height	Reproduction	Shade tolerance	Wetness	Growth rate	Seed bank	Seed abundance	Fertility requirement	Dispersal method
<i>Trifolium pretense</i> (L.)	2	2	3	1	2	moderate	persistent	high	high	Multiple
<i>Trifolium repens</i> (L.)	2	2	3	1	2	moderate	persistent	high	high	multiple
<i>Typha orientalis</i> <i>C.Presl</i>	3	5	1	1	5	rapid	persistent	high	medium	multiple
<i>Verbena officinalis</i> (L.)	2	4	3	1	3	rapid	transient	low	medium	water or gravity
<i>Veronica persica</i> (L.)	1	1	3	2	3	rapid	transient	medium	medium	multiple
<i>Veronica undulata</i> Wall.	1	3	2	2	5	rapid	transient	medium	medium	multiple
<i>Vicia cracca</i> (L.)	2	1	2	2	2	moderate	transient	medium	low	water or gravity
<i>Vicia sativa</i> subsp. <i>Nigra</i>	2	2	2	1	1	rapid	transient	high	medium	multiple
<i>Xanthium strumarium</i> (L.)	1	3	3	2	3	rapid	transient	medium	medium	animal
<i>Zephyranthes candida</i> <i>(Lindl.) Herb.</i>	2	2	2	2	3	moderate	transient	medium	high	multiple

### 3.6 Figures



**Fig. 3-1.** (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.

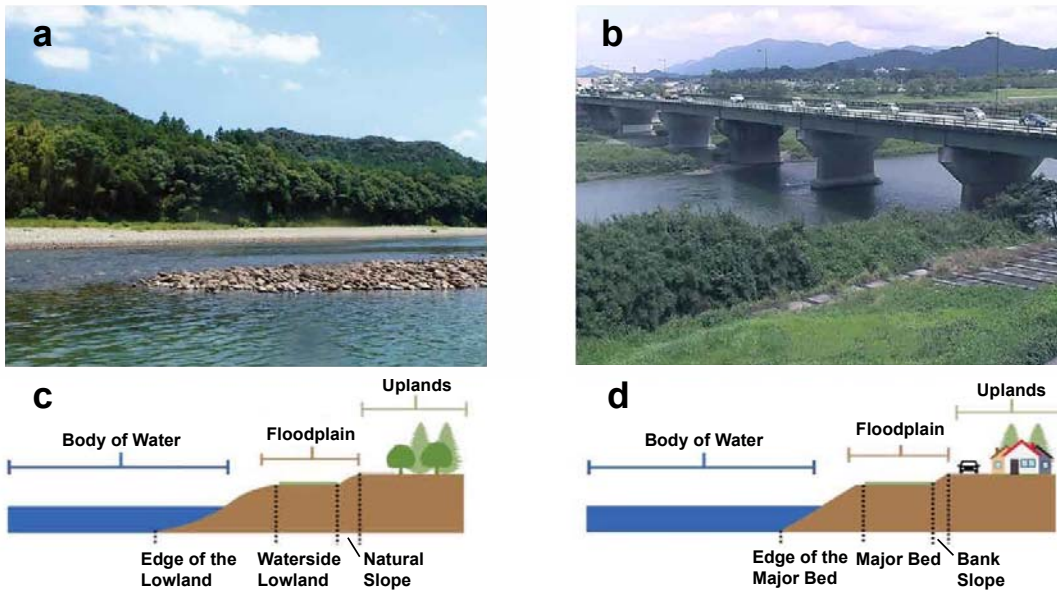


Fig. 3-2. Examples of the sampling area. (a) and (b) example images of waterside lowland and major bed; (c) and (d) example section structure of waterside lowland and major bed.

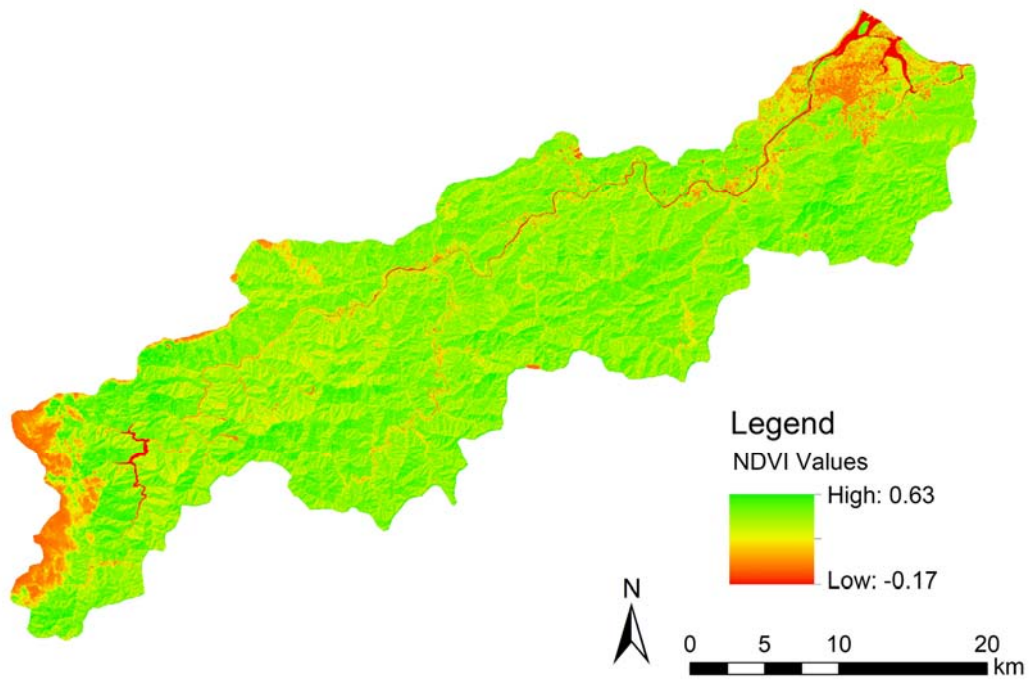
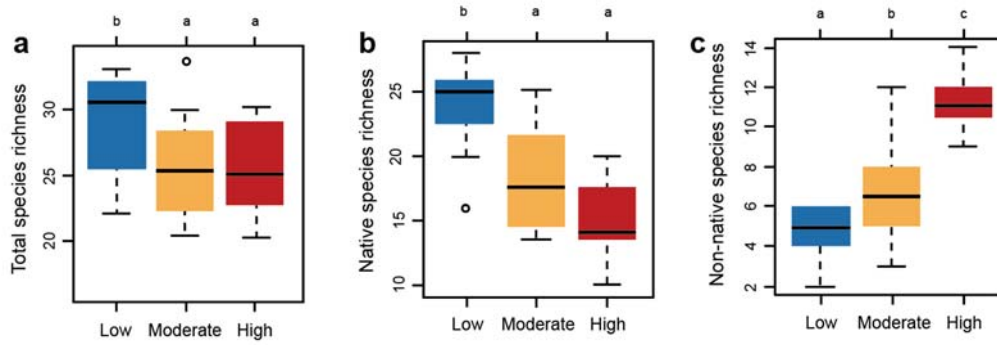
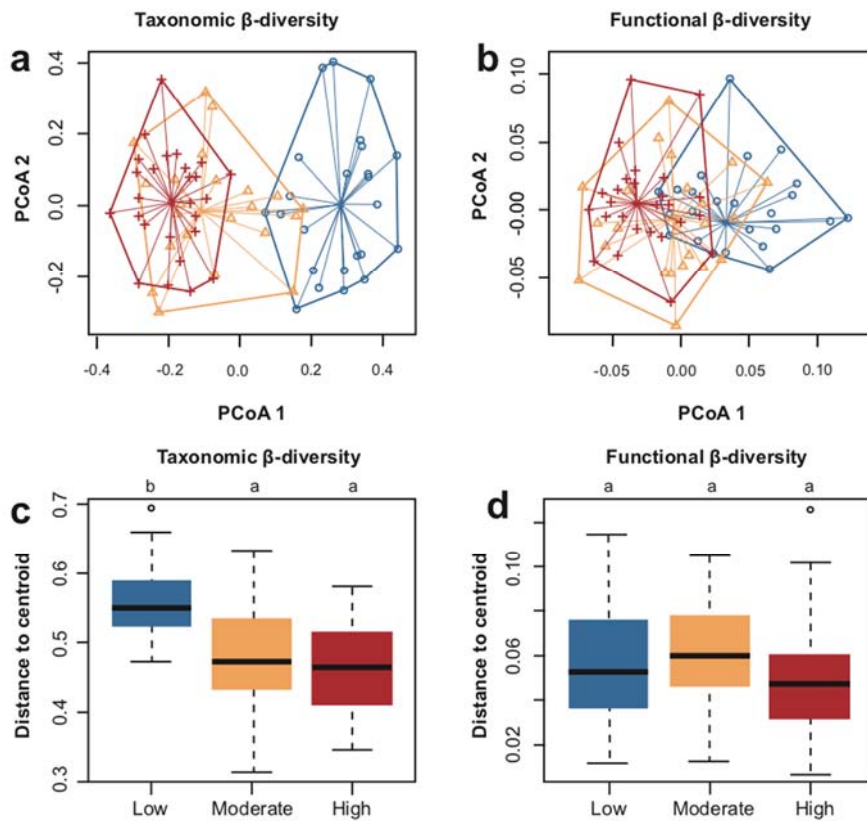


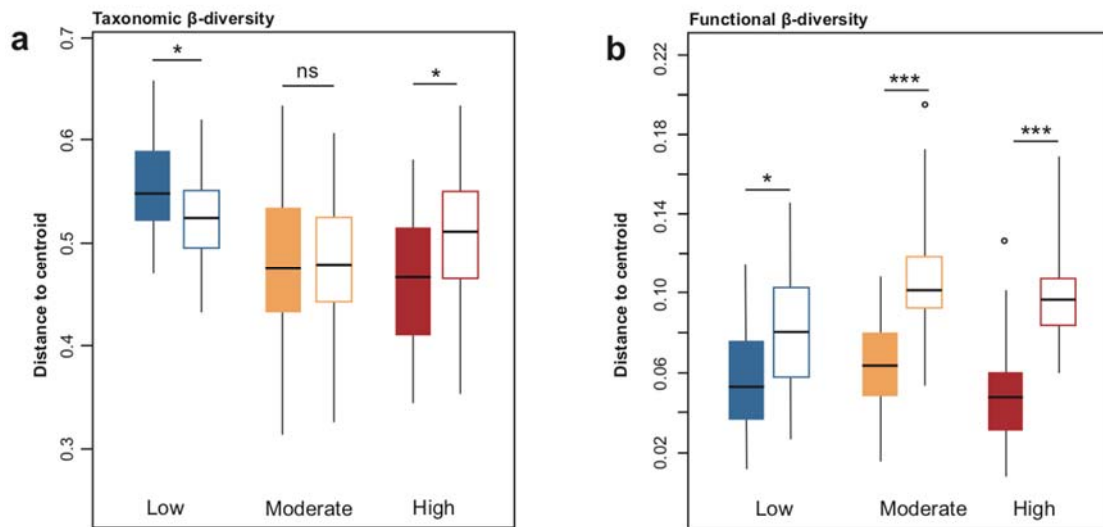
Fig. 3-3. NDVI map of the Miya river basin.



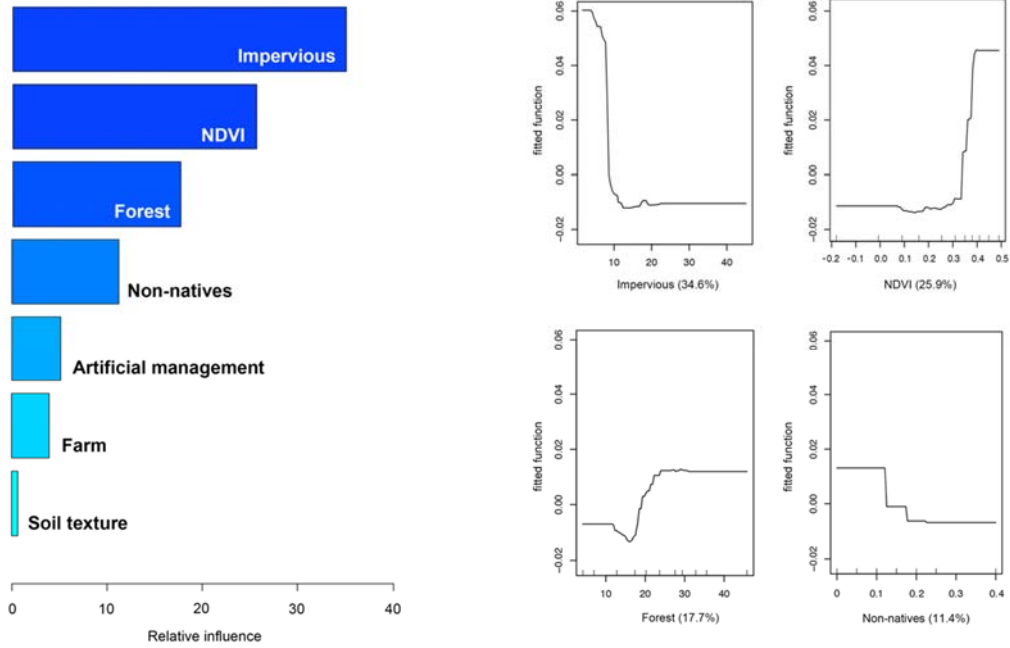
**Fig. 3-4.** Total species richness (a), native species richness (b), and non-native species richness (c) in different levels of degradation. Data provided show the median (bold line), 25%–75% quartiles (boxes), ranges (whiskers), and outliers (white dot). Significant differences are presented by different letters ( $p < 0.05$ ).



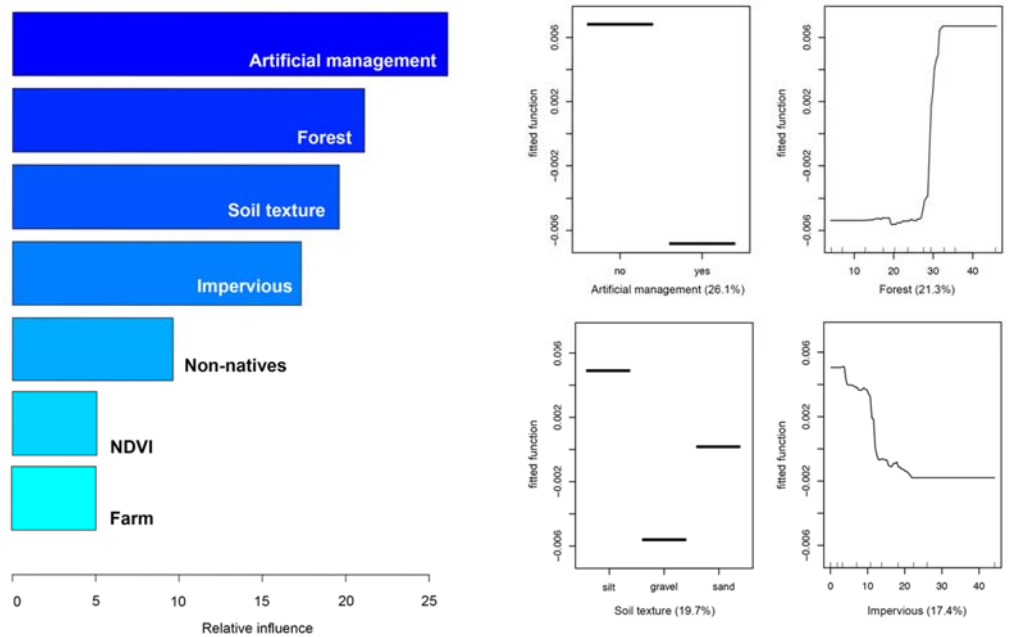
**Fig. 3-5.** Effect of different degradation levels on the multivariate dispersion of species (a, c) and trait (b, d) composition in floodplain landscape. Taxonomic and functional  $\beta$ -diversity is measured as the distance of sites to their group centroid (using Bray-Curtis and Gower distances, 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  $\beta$ -diversity, while a change in the centroid location represents a species/trait turnover. Symbols represent each plot in different degradation levels: + = high,  $\Delta$  = moderate, and  $\circ$  = low. Values share same letter are not significantly different at 0.05 significance level.



**Fig. 3-6.** Differences in taxonomic (a) and functional (b)  $\beta$ -diversity induced by non-native species in three groups of degradation level. Variations in  $\beta$ -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  $\beta$ -diversity of total species, and the color-outlined boxes represent the  $\beta$ -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.



(a)



(b)

**Fig. 3-7.** Relative influence of predictors and partial dependency plots for boosted regression tree analyses on taxonomic (a) and functional (b)  $\beta$ -diversity. For taxonomic  $\beta$ -diversity, explained deviance: 0.429; For functional  $\beta$ -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.

## **Chapter 4: Aquatic Plant Species in Urban Ecosystem: Variation of the Traits of *Phragmites Australis* along an Urbanized River**

### **4.1 Introduction**

Despite accounting for a relatively small proportion of the landscape, riparian ecosystems play a vitally important role in maintaining biodiversity (Sabo et al. 2005). Riparian areas are capable to perform various ecological functions, for example, nutrient cycling, riverbank stabilization, water purification, and regulation of stream temperatures (Décamps et al. 2009). Apart from that, riparian areas could provide shelter for wildlife along the river and act as a corridor to facilitate species movement and vegetative transport (Meek et al. 2010). These ecological functions are closely associated with the critical ecosystem services required by nature and society. Moreover, most of these functions are directly related to urban economic development, including flood control; support for urbanization, industry, and forestry; and provide opportunities for outdoor recreational activities, such as enjoy river scenery, hiking, and fishing (González et al. 2017). Considering the recognized importance of riparian areas for social and ecological reasons, the management of riparian areas has been prioritized globally for biodiversity conservation and environmental preservation.

The conservation of riparian areas is faced with a growing threat from urbanization and human activities. Measurements of flooding protection and the conversion of riparian areas by urban development, industrial, and agriculture are responsible for the degradation and loss of riparian ecosystems worldwide (Nilsson and Berggren 2000; Hughes and Rood 2003). The impact of human disturbance on riparian habitats can manifest itself in different ways. The first one is the change in land cover. Associated with different varieties of land cover, the profound anthropogenic modifications across riparian areas may lead to riparian degradation, which could cause change to the hydrological and sediment regimes (Graf 2006). Due to the inability to get adaptive to this disturbance in their natural riparian habitat, riparian plants and animal communities may face the danger of severe population declines (Dixon et al. 2012). Besides, the changes in land cover associated with the development of infrastructure and urban spaces can result in the fragmentation of riparian vegetation communities (Santos et al. 2016). These changes typically transformed large semi-natural or natural vegetation areas into scattered vegetation patches; these patches are isolated by the surrounding urban areas, and are under the effects of numerous pressures that can influence the growth condition and

performance of perennial plant species (Schwoertzig et al. 2016). In the meantime, due to the accessibility for humans, anthropogenic activity may facilitate the growth and seed dispersal of invasive plant species (Hodkinson and Thompson 1997; Cao and Natuhara 2020), which may paradoxically increase plant diversity in riparian habitats as a temporary stage (Gumiero et al. 2015). Moreover, the pollution associated with human disturbance presents a major threat to the health of riparian areas. Within the urban ecosystem, the runoff and industrial and domestic waste increased loads of pollutants, which is a major contributing factor for the deteriorating quality of soil and water (Hatt et al. 2004). The main pollutants from urban areas primarily involve the increasing nitrogen, phosphorus and inorganic nutrient, all of which have been reported in previous studies (Tromboni and Dodds 2017; Grella et al. 2018).

Considering the increasing disturbance that riparian areas are subject to, it is necessary to gain a better understanding as to the responses of plants to urbanization for sustaining biodiversity and the provision of ecosystem services. Plant traits offer an opportunity to do this. The plants grow in constant-changing environments, as a result of which plant traits can be regarded as the measurable indices that determine how plants interact with the external environment (Lavorel and Garnier 2002). Especially in riparian areas, vegetation is exposed to the impact from various disturbances. Riparian areas include the space between the running water and floodplains, where vegetation is under the pressure of natural disturbance (e.g., inundation, flooding, and sediment) (Catford and Jansson 2014). Meanwhile, as an attraction of urban development and human activities, riparian habitats and plant assemblages are subject to the artificial disturbances as well (Richardson et al. 2007). Despite a number of studies paying attention to the response of riparian vegetation to environmental changes, most of them focus on the changes in plant diversity and community structure, or the impact of a particular environmental variable (Schwoertzig et al. 2016; Song et al. 2019). In riparian areas, changes in the plant traits respond to multiple disturbances that remain largely unexplored.

Aquatic plant species are the species that have adapted to inhabiting in riparian areas, for which their response to the environment could serve as an indicator of the health of riparian habitats. Representing one of the dominant plant species in riparian areas (Washitani 2001), *Phragmites australis* (commonly known as reed) is widely distributed because of its strong adaptability to a range of environmental conditions (Clevering and Lissner 1999). As an endemic riparian species, *P. australis* depends on water resources, or soil moisture to be precise, for maintaining its growth (Ter Heerdt et al. 2017). With a decrease in soil water



content, *P. australis* is unable to sustain its normal growth, which will have an adverse effect on plant size (Mamat et al. 2016). As a well-known stressor of *P. australis*, salinity could inhibit growth and reduce biomass (Liu et al. 2018). Besides, it has been suggested in other studies that increasing the sulfur content in soil can cause the death of *P. australis* (Fogli 2002). With the resources exception of moisture, the growth and distribution of *P. australis* show a close association with the availability of nutrients and the physical properties of soils (Ter Heerdt et al. 2017). Although *P. australis* is not currently threatened in Asia, this species is an important component of riparian ecosystems because it forms dense monospecific communities, and provide habitats for biodiversity conservation (Kiviat 2013; Nakagawa et al. 2013). However, due to the impact of multiple disturbances, the riparian areas are put at the risk of severe degradation and gradual decline of *P. australis* (Washitani 2001). Threats to native *P. australis* include hydrological regulation, unreasonable drainage, conversion to other land uses, and pollution (Packer et al. 2017). With a view to the decline of *P. australis*, declining and contraction ecological condition of reedbeds has been widely discussed in recent decades (Fogli 2002; Li et al. 2013; Saltonstall et al. 2014).

Despite the improved understanding of *P. australis* globally both within its native range and in areas where it is introduced, the studies about traits of *P. australis* concentrate the natural habitats such as wetland, marshland, and grassland (McCormick 2009; Uddin et al. 2017). Moreover, previous studies have primarily focused on the natural disturbance that influence the ecology of *P. australis*, such as hydrology influence, changes in topographical gradient, and variation in substratum condition and salinity level (Isacch et al. 2006; Tang et al. 2013). However, studies considering the effect of anthropogenic factors on the traits of *P. australis* in riparian areas have received only limited attention, which hinders our understanding of the ecological characteristics of *P. australis*, especially in urbanized areas, which are characterized by intense human activities. Therefore, the knowledge and investigations into the ecology of native plants, especially aquatic species, as well as management plans for these plant species are crucial in a sustainable urban riparian ecosystem.

Given the limitations of existing vegetation-environment relationship studies in riparian areas, this study aimed to assess the potential impact of urbanization on the ecological characteristics of *P. australis*. The focus of this study is placed on the main environmental (both regional and local) factors that could have an impact on the characteristics of plant growth at both individual and community levels. In addition, a number

of management strategies are proposed for improving the management of *P.australis* community in the urban ecosystem. I hypothesises:

- (1) The dominance of *P.australis* diminishes with the increase of urbanization level.
- (2) The change of imperviousness and soil property towards the urbanization causes change in the *P.australis* community and individuals.

## **4.2 Materials and methods**

### **4.2.1 Study area**

The study area is located in the riparian areas of the Shonai River (35°04'–35°24' N, 136°49'–137°20' E) in the Aichi and Gifu prefecture in the central Japan (Fig. 4-1). The Shonai River flows through Nagoya City from a 1010 km<sup>2</sup> basin, and with a 96-km-long mainstream. The topography of the Shonai River basin is inclined from northeast to southwest, with an altitude ranging from 0 to 843 m. The region features a typical warm temperate climate, with the maximum and minimum monthly temperatures of 27.8 °C (August) and 4.5 °C (January), respectively. With a 1500 mm mean annual precipitation in the area of research, the plant communities on both sides of the Shonai River were dominated by *P. australis*, *Miscanthus sacchariflorus*, and *Rosa multiflora* in the shrub layer, as well as *Artemisia indica*, *Solidago altissima*, *Lolium perenne* and *Trifolium repens* in the herb layer. The use comprises urban zones (52.9%), agricultural fields (11.1%), and forest (36.0%) in the riparian area of the river (Ministry of Land, Infrastructure, Transport and Tourism, 2018).

The Shonai River is considered to be one of the rivers with the highest level of urbanization across Japan. Since the Meiji Era which dates backs 150 years, the basin of Shonai River had grown into the center of Nagoya Urban Area. At present, it has experienced a rapid process of urbanization and the acceleration of urbanization has resulted in the destruction of riparian vegetation. Currently, the density of the population is approximately 2400 persons/km<sup>2</sup> (Ministry of Land, Infrastructure, Transport and Tourism, 2018).

### **4.2.2 Sampling design**

As the level of urbanization is the major environmental gradient, I selected four sampling

sites from the lower to upper reaches of the Shonai River along an urbanization gradient to cover the whole river basin (Fig. 4-1). Two urban sites, sites A and D, located in Nagoya city and Tajimi city, were selected for their representativeness of a complex urban ecosystem and intense artificial disturbance. Sites B and C were considered as semi-natural habitat with relatively less disturbance (Table 4-1).

The field research was conducted from April to July, 2018. In each sampling site, a total of 5 transects with 500 m-1000 m intervals were established perpendicularly to the river. Two 10 m × 10 m quadrats were established with an interval at each transect and were used for the sampling of trees and shrubs. In each quadrat, five 1 m × 1 m small plots located in the center and at the four corners of each quadrat, were established for the sampling of herbs. Quadrats were separated from each other with a distance ranging from 100 m to 150 m. As this study focused on the traits of *P. australis*, the transects and quadrats were established in the presence of *P. australis*. A total of 40 quadrats were sampled during the process of field research.

#### **4.2.3 Data collection**

In each quadrat, I measured a set of variables describing the traits of *P. australis* communities: 1) the species name, coverage, and density of all plant species in each quadrat; 2) the height, stem diameter, and leaf area of *P. australis*. The density of each species was determined by counting the number of plant individuals in a 1 m × 1 m range; the coverage of each species was measured visually; the height and stem diameter were determined from the mean values of 10 random *P. australis* plants; and the leaf area was measured from the mean values of 10 randomly selected *P. australis* leaves. After collecting the leaves, they were transported to the laboratory and WinSEEDLE image analysis software was applied to calculate the leaf area.

Soil samples were collected from the five small quadrats at depths of 20–40 cm in each quadrat to identify the soil physical and chemical properties. Leaf litter was cleared before the soil samples were taken. All samples were removed with a corer and were immediately stored in labelled plastic ziplock bags. Soil texture was identified as silt (<0.05 mm), sand (0.05-2 mm), and gravel (>2 mm) by using a Malvern Mastersizer 3000. The soil organic matter (SOM), total nitrogen (TN), and total sulfur (TS) were measured using CHNS analysis with an organic elemental analyzer (Flash 2000; Thermo scientific). For this, each sample was weighed in the range of 10–40 mg, and the induction furnace was maintained at 950°C (Bhattacharyya, 2015).

Electrical conductivity (EC) and pH were measured using a conductivity meter and an electric pH meter, respectively. Water content of soil (SWC) was measured by oven-drying the fresh soil samples at 105°C for 48 h to a constant mass.

In addition, to explore the varying level of urbanization along Shonai River, I used classified land cover data that derived from satellite imagery for central Japan area. Land cover data were previously classified into categories, including impervious surfaces, open green spaces, farmlands and water bodies and other land cover types. Impervious surfaces including roads, pavement and rooftops, and other land cover types are characterized by the permeable ground such as bared ground, footpaths and baseball field. The percentage of land cover was calculated in a buffer zone with 100-m radius by ArcGIS 9.3.

#### 4.2.4 Statistical analysis

In this research, ecological data from the 40 quadrats were calculated. Cluster analysis was performed to classify the riparian plant community types. The importance value (calculated by the sum of the relative coverage, relative dominance, and relative density) of each species present in the 40 quadrats was used as the basis of cluster analysis (Álvarez Ruiz and Lugo 2012; Ross et al. 2016).

Species diversity index were determined using Shannon-Wiener index (Magurran 2004) (Eq. 1):

$$H = -\sum_{i=1}^S (P_i \ln P_i)$$

Where  $P_i$  represented relative importance value of species  $i$ , and  $S$  was the total number of plant species in the  $i$ th site. Shannon-Wiener index was determined according to the above equations by R with package “vegan” (version 3.5.1).

The Euclidean distance and Ward’s method were applied to ascertain an optimum pruning point for the result of cluster analysis. The cluster analysis was performed with R (version 3.5.1). In addition, detrended correspondence analysis (DCA) was conducted to test and verify the results of the cluster analysis.

Urbanization process can affect plant characteristics by changing soil environment. To explore this indirect effect, the Kruskal–Wallis was conducted among the site and community group to test differences in soil variables on suburb-urban gradient.

To explore the relationship between the characteristics of *P.australis* and environmental factors, the least significant difference (LSD) test in one-way analysis of variance (ANOVA)

was performed to examine the differences in the traits of *P. australis* among the classified communities. Stepwise multiple linear regression analysis was used between environmental factors and the characteristics of *P. australis* to determine the significance of each environmental variable for the plant indices.

The Monte Carlo forward selection was used to assess which factors affect the characteristics of plant communities and *P. australis*. To further explore the dominant influencing factors, explanations of various predictors were calculated by using Monte Carlo forward selection in redundancy analysis (in CANOCO version 4.5). In redundancy analysis, marginal effects reveal the effects of environmental factors on the traits of *P. australis*, whereas conditional effects reveal the effects of environmental factors on traits of *P. australis* after the anterior factors had been removed. This approach can determine the key predictors by eliminating redundant variables and selecting a set of key environmental factors. In addition, Pearson correlation analysis (in SPSS version 20) was used to determine the possibility of relationships among environmental variables.

## 4.3 Results

### 4.3.1 Classification of *P. australis* communities

In riparian areas along the Shonai River, six types of *P. australis* community were classified based on the cluster analysis and DCA ordination (Fig. 4-2). These six groups of communities were differed mainly in their coverage of *P. australis* and species composition. The characteristics of each community are listed below:

Community 1 was high coverage of *P. australis*. The structure of Community 1 was dominated by *P. australis* with a high coverage (60–75%). *Equisetum arvense*, *Trigonotis pedunculari* were also present as associated species; however, the abundance and coverage of these species were extremely low (average coverage < 4%).

Community 2 was medium coverage of *P. australis* + *Miscanthus sacchariflorus*. This type of community was dominated by *P. australis* and *M. sacchariflorus* (average coverage > 45%) in the shrub layer (average coverage > 40%).

Community 3 was medium coverage of *P. australis* + *Artemisia indica*. Community 3 was dominated by *P. australis* (average coverage > 44%) and *M. sacchariflorus* (average

coverage > 36%). The herb species *Solidago altissima* and *Miscanthus sinensis* were also present in this type of community; however, the importance values were low (0.12–0.19).

Community 4 was medium coverage of *P. australis* + *Miscanthus sinensis* communities. This type of community was dominated by *P. australis* (average coverage >35%) and *M. sinensis* (average coverage > 41%).

Community 5 was low coverage of *P. australis* + *S. altissima* communities. Community 5 was dominated by *S. altissima*, *P. australis* was sparsely distributed in these communities, with low coverage (5–15%).

Community 6 was low coverage of *P. australis* + *M. sacchariflorus* communities. This type of community was dominated by *M. sacchariflorus*, with an average coverage of 62%. *P. australis* was distributed in associated with *M. sacchariflorus* in the shrub layer with average coverage of 7%.

#### **4.3.2 Variation in the traits of *P. australis* in urban and suburban areas**

Coverage presented significantly ( $P < 0.01$ ) higher values in community 1 than in other groups, and reached its lowest value in community 6 ( $P < 0.01$ ).

The height and stem diameter of *P. australis* exhibited a similar variation pattern among communities 1– 6, with higher values in communities 1 and 3 compared with other communities ( $P < 0.05$ ).

The leaf area presented significantly ( $P < 0.05$ ) higher values in communities 1 and 3 than in other communities.

Shannon-Wiener diversity index was presented low values in community 1. (Fig. 4-3).

#### **4.3.3 Variation of environmental variables in *P. australis*'s habitats**

The presence of six types of *P. australis* community was differed from urban-suburb gradient. The communities with relatively high coverage of *P. australis* (community 1) were frequently found in suburb region (sites B and C). By contrary, communities 5 and 6 that with low coverage of *P. australis* all presented to urban areas (Fig. 4-4).

Major land cover composition differed among six types of *P. australis* community. Cover of impervious surface was least surrounding community 1 than all other *P. australis* community types, and greatest surrounding community 5. Cover of farmland was greatest

surrounding community 1, and almost absent from other community types (Fig. 4-4).

Unlike suburb or semi-nature areas, urban areas are recognized as a complex mosaic of land use/cover patches and associated with intensive human activity in this study; Thus may indirectly affect the *P. australis*'s habitat by fragmentation and degradation.

Among the 10 local factors, the value of pH and EC varied significantly among sites A-D (Table 4-2). The pH and EC of soil samples collected from urban area are generally higher than those from suburban areas. Both pH and EC reached the highest and lowest values in sites D and A, respectively. The other local factors did not show significant differences among sampling sites.

Due to the different land use/cover and human activity within the habitats of *P. australis*, the significant difference of the local variables among communities 1–6 are shown (Table 4-3). Similar to the result that found in sites A-D, there were significant differences of pH and EC values in communities 1-6. The soil samples collected from urban area (communities 5 and 6) had the highest pH and EC.

Mean salinity of the soil (as measured by EC in  $\mu\text{S}/\text{cm}$ ), the levels rose more than 2 times from community 1 (37.36  $\mu\text{S}/\text{cm}$  in average; most of the *P. australis* community distributed in suburb areas) to community 5 (88.80  $\mu\text{S}/\text{cm}$ ; all of the *P. australis* community distributed in urban areas). In addition, soil from community 1 were acidic with pH ranging from 5.08 to 6.22 (mean 5.72) while the soils in communities 5 and 6 were generally higher (mean 6.50 and 6.37 in communities 5 and 6, respectively). The significant difference was absent in other soil variables among communities.

#### **4.3.4 Relationship between the traits of *P. australis* and environmental factors**

To determine the effects of environmental variables on the characteristics of *P. australis*, nine environmental indices, including the local factors (i.e., the percentage of gravel, sand and silt, soil water content, total nitrogen, soil organic carbon, total sulfur, electrical conductivity, and pH), and land cover (i.e., the percentage of green space, imperviousness, farmland and water body) were selected in 40 sampling sites from the field research. The result of the Pearson correlation analysis between environmental variables and the characteristics of *P. australis* is shown in (Fig. 4-5). Local factors displayed a strong correlation with the plant structure; the percentage of silt was positively correlated with the height and diameter of *P. australis*, while the percentage of sand showed a negative correlation with those characteristics; the soil water

content was positively correlated with the height, stem diameter, and coverage of *P. australis*. The soil water content was positively correlated with the height and stem diameter of *P. australis*. TN showed a positively correlation with the leaf area and height of *P. australis*; SOC was only positively correlated with the height of *P. australis*. However, the EC showed a negative correlation with the stem diameter value, and the pH showed a negative relationship with the stem diameter and coverage of *P. australis*.

Imperviousness, representing the level of urbanization and accessibility of human disturbance, were negatively correlated with the stem diameter and coverage of *P. australis*.

Regression analysis was used to further ascertain how environmental factors affect the characteristics of *P. australis*, and the best explanatory factor and model with the lowest Akaike information criterion (AIC) value were selected and listed in Table 4-4. The regression analysis indicated the local factors as predictors for height, leaf area and stem diameter of *P. australis*, explained 7.9%–37.6% of the variation in the characteristics. Land cover type explained the 10.6%–41.4% of variation, was mainly related to the variation in coverage of *P. australis* and Shannon-Wiener index. The explanatory model with the lowest AIC value for each characteristic was the combination of local factors and land cover types, which explained 15.8%–57.4% of variation.

#### **4.3.4 Key factor affecting the characteristics of *P. australis***

To explore the determinants that affect the plant communities and characteristics of *P. australis*, redundant variables were deleted according to the explanation of fourteen variables determined using Monte Carlo forward selection in redundancy analysis. All of the environmental variables explained 50.1% of the total variance. Imperviousness, soil water content, total nitrogen, pH, electrical conductivity are regarded as the key factors ( $P < 0.05$ ) determining the traits of *P. australis* (Table 4-5). In these factors, soil water content accounted for the 40.9% of the explanation; land cover factors (imperviousness) accounted for the 22.9% of the explanation; soil chemical properties (pH and electrical conductivity) explained 18.4% of the total variance; soil nutrition (Total nitrogen) explained 9.9% of the total variance.



## 4.4 Discussion

### 4.4.1 Variation in the traits of *P.australis* in urban and suburban areas

Vegetation characteristics that change along the urbanization gradient have been well studied, with the majority of the research focusing on the community structure and taxonomic composition on plants (Ives et al. 2011). However, as for the aquatic plant community, the important aspect of the urban ecosystem, their response to urban ecosystem was still less understood. In this study, the variation of *P. australis* communities and individuals were described on an urbanization gradient. As a native aquatic plant species in the Japanese riparian area, *P. australis* has been proved that has strong adaptability to environmental change. However, in this study, the coverage of *P. australis* showed a decreasing trend from suburbs to urban sites, with increases in dominance of weeds or invasive species in urban riparian zones. The *P. australis* communities with high coverage of *P. australis* (community 1) tends to be distributed in the suburb area (sites B and C), where there are lower urbanization levels and anthropogenic disturbance. On the contrary, in the urbanized areas (sites A and D), the communities 5 and 6 with low coverage of *P. australis* were distributed, and accompanied by weeds and invasive species. The findings about *P. australis* from this study are consistent with many international studies that have revealed the links between urbanization and degradation of riparian vegetation.

The result of differences in the characteristics among the six groups of *P. australis* community suggests that generally, the dominance of *P. australis* had a positive correlation with their morphological characteristics. However, in communities 2 and 3, the values of the characteristic indices showed opposite trends with the similar coverage of *P. australis*, which indicates these communities had complicated interactions with the vegetation and environment, thus reflecting the complex factors. For example, spatial variation in soil characteristics has impact on vegetation growth (Tola et al. 2017; Li et al. 2018). Besides, interspecies competition might be a possible reason for the different performance in communities 2 and 3. When competitors are present, *P. australis* may not be vigorous enough to competitively displace existing species and may coexist with them (Aerts 1999). In this study, it was observed that when *P. australis* and *M. sacchariflorus* coexist, growth and individual size of *P. australis* were inhibited. Then, it suggests that competition will become more intense when species with

similar ecology appears, which will affect the growth and individual size of *P. australis*.

Species diversity is often used to describe the relationship between vegetation and the environment (Isbell et al. 2015). In current study, it was found that the diversity of vegetation with the increase of the urbanization level. Compared with community 1, the communities 5 and 6 that originate from the urban area have higher diversity value. This result was consistent with the findings that the diversity index was higher in the urban than suburb area in consequence of the increase the diversity invasive species and weeds. In addition, the dominance of *P. australis* may be a possible reason for the variation of diversity indices among six types of communities (Uddin and Robinson 2017). Compared with the communities dominated by a single species, the highly competitive species and the environment of low competition can balance the resource allocation, thus making the growth of various species possible (Marshall and Baltzer 2015). The results of species diversity in this study coincided with the previous research results, suggesting that the dominance of *P. australis* was negatively correlated with the diversity index of plant communities (Uddin and Robinson 2017). In the communities where the dominance of other species overtopped the *P. australis*, the diversity indices show a relatively higher value.

#### **4.4.2 Impact of environmental factors on *P. australis***

Plant responses to environmental factors are partly mediated by plant traits (Meng et al. 2014). In this study, it was found that the soil properties (e.g., electrical conductivity, total nitrogen, oil water content,) and the land cover (e.g., imperviousness) are the significant influencing factors for the variance in the traits of *P. australis* in the urban ecosystem.

The importance of soil moisture and nutrition in formation of the traits of *P. australis* has long been discussed (Saltonstall and Court Stevenson 2007; Mamat et al. 2016). This was also confirmed by the results of this study, showing that the coverage, height and stem diameter was positively correlated with soil water content. Adequate water supply promotes the nutrients absorption by plant roots and photosynthesis of plant leaves, which is conducive to the growth, nutrient storage and energy metabolism of *P. australis*. Water holding capacity is mainly dependent on soil texture, and result demonstrates that the percentage of silt was positively shaping the structure of *P. australis*, which is also in line with earlier observations, which it is related to smaller soil particle size and better structure of *P. australis* (Coops et al. 1994; Clevering et al. 2001). Total nitrogen can be an important driver of plant functional traits and

strategies (Orwin et al. 2010). As reported in previous studies, the increase in the nitrogen content could facilitate the acquisition of aboveground resources by the plants (Clevering and Lissner 1999). In the current study, the content of total nitrogen exhibited a significant positive relationship with the height and leaf area of *P. australis*, implying the *P. australis* distributed in the area with high-nutrition soils have appeared to be selected for high leaf area and plant height, presenting their acquisitive strategy (Uddin and Robinson 2018).

It is noteworthy that the effects of urbanization-related factors on colonization of *P. australis* were found in the current study. Compared with the suburban areas, urban areas harbor a significantly larger proportion of impervious surface. The percentage of impervious surface (IMP) was commonly used as an index to quantify the level of urban development (Su et al. 2019). We found the IMP is a key anthropogenic driver that affects the traits of *P. australis* in the urban ecosystem (Table 4-5). The increased IMP could reduce the coverage of *P. australis* (Table 4-4), which is consistent with previous studies (Dixon et al. 2012). This tendency could be explained by several factors. One aspect might be that the sharp increase in IMP has a potential to degrade riparian habitats due to the concentration of human activities and the increase of surface runoff. The soil ecosystem was affected by obstructing the exchange of gases, water, and materials between the atmosphere and the soil (Hu et al. 2018). The riparian species might be affected negatively by these alternations resulting from IMP and replaced by plant species distributed in moderate habitats. On the other hand, the IMP triggering the variation of the coverage of *P. australis* might be attributed to the introduction of the alien species by IMP. Human disturbance increased the chance of survival and growth for invasive plant species, which might also be attributed to the situation that the riparian soils surrounded by the impervious surface create the adverse environmental conditions for *P. australis*. This study has similar findings to the studies reported that there are positive correlations between the proportion of imperviousness and species richness of invasive species (Grella et al. 2018). In the plant communities that distributed in the urban area and surrounded by the large proportion of impervious surface, *P. australis* was accompanied by a large number of invasive species.

In this study area, the urban soils were more alkaline than suburban soils (Table 4-3), which is speculated to be caused by such conditions as the runoff from calcium carbonate-containing urban materials. In this study, it was revealed that the elevation of soil pH might contribute to the growth inhibition of *P. australis* by affecting their stem diameter (Table 4-4). Plant stem diameter is frequently regarded as an indicator of plant performance in the

assessment of competitive ability and resource supply (Wang et al. 2019). According to these results, the increased level of pH value might result in a competitive disadvantage in resource acquisition. Despite the report in previous studies that *P. australis* occurs on a wide range of substrates and can tolerate soil pH from 2.5 to 9.8 (Packer et al. 2017), it was observed in this study that *P. australis* with good performance in stem diameter occurs in suburban areas, where the pH is less than 6, indicating that *P. australis* has a preference for weakly acidic environments in the research area. Thus, it can be confirmed that *P. australis* can thrive in mildly acidic conditions (Packer et al. 2017; Uddin and Robinson 2018). In addition, soil pH is one of the major determinants of soil fertility. Mildly acid soil (i.e., pH 5.5-6) is usually considered as the optimal pH condition as most micronutrients are more available to plants than those in neutral-alkaline soils, which is generally conducive to plant growth (Zhao et al. 2015; Yin et al. 2016).

Electrical conductivity (EC) was the conventional determination standard for the soil salinity. A higher level of EC in urban areas can be achieved by intensive irrigation in urban riparian areas. The riparian area of Shonai River was occupied by parks, golf courses, and fields, which gives rise to the need for a considerable amount of irrigation water for the purpose of landscape management (Miyamoto and Chacon 2006). There are some studies demonstrating that salinity had a negative effect on the structure of *P. australis* (Mauchamp and Mésleard 2001; Soetaert et al. 2004). Besides, the negative relationship between the stem diameter of *P. australis* and the EC of soil was found to be significant in the current study. With Sites A and D in particular, the electrical conductivity of the soil was relatively high among the 4 sites, which is potentially affected by the way of irrigation or severe human disturbance, which causes the stem diameter of *P. australis* to be small (Wu et al. 2008) In addition, as a kind of salt-tolerance plant, *P. australis* is capable of adjusting its function depending on the salinity of the surrounding environment (Howard and Rafferty 2006). Therefore, in this study, the lower stem diameter of *P. australis* might also result from its self-adjustment to the relatively high level of EC in urban areas.

The traits of *P. australis* are associated with *P. australis*'s strategies to adapt to environmental changes. The traits of *P. australis* mainly include the most effective utilization of nutrients, light, and water resources dispersal strategies. The environmental factors will cause the traits of *P. australis* to vary. However, there exists an array of other environmental influencing factors in the traits of *P. australis*, such as flooding frequency, chemical, and physical water characteristics. These factors, as potential co-variates, might affect the variation

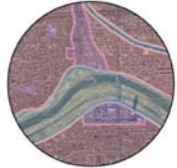



of *P. australis* in the urban ecosystem. In the future, it is necessary to further study more factors for disentangling the effect of artificial disturbance and urbanization from hydrological conditions on plant traits.

#### **4.4.3 Applications for management**

The population and diversity of native species have been reduced gradually in riparian areas worldwide (González et al. 2017). These trends may be accelerated by anthropogenic disturbance, and then it can be a progressive loss of natural resilience of urban ecosystems (Richardson et al. 2007; Schwoertzig et al. 2016). In this study, the ecology of *P. australis* in urban and suburban areas was explored, and the environmental factors that play an important role in *P. australis*' colonization and growth were identified. IMP was a major factor that could affect the dominance of *P. australis* in the current study. Thus, in riparian areas, restrictive approaches, such as restricting construction of public space in riverside, implementing legislation to prevent human activities within a certain area of riversides, and establishing protective zones for *P. australis* are recommended for ecological restoration in urban areas in the future. The increased content of soil pH and EC associated with urbanization also have a considerable influence on the traits of *P. australis*. Therefore, controlling urban runoff by strengthening supervision and rationally planning urban and river junction zones is suggested. In addition, it was noticed that riparian areas in urban included many golf courses and parks, and these public spaces were characterized by high water consumption. A large amount of irrigation might be related to the higher conductivity was assumed in this study. Hence, in order to maintain riparian areas resilience and prevent the reduction of native species diversity, it is recommended to apply such management methods as controlling the construction of golf land and developing water-saving irrigation for the urban ecosystem.

## 4.5 Tables

**Table 4-1.** The description and characteristics of each sampling site. Notes: the pink areas on the image represent settlement and urban areas; blue, river and riparian areas; dark green, forest areas; purple, others; light green, farmlands; brown, wastelands.

Sampling site	Quadrats surveyed	Sampling site description	Altitude variation(m)		Example image of the sampling site
			Min	Max	
Site A (urban)	10	Site A was located to the northwest of the densely built metropolitan city (Nagoya, Japan), in the lower reaches of the river section. The riparian area in Site A was transformed by a large number of recreational spaces and different levels of roads to meet the needs of residents.	7.4	11.3	 <p><b>SiteA</b> The proportion of settlement and urban area: 57.72%</p>
Site B (suburb)	10	Sites B was located in the suburban region of Nagoya city. The riparian area remains semi-natural state with continuous shrub and grassland, and a few small patches of farmland were embedded.	16.5	20.1	 <p><b>SiteB</b> The proportion of settlement and urban area: 32.17%</p>
Site C (suburb)	10	Site C was located in the middle reaches of the river section, which is characterized by a semi-natural landscape and hilly area. Because of few residents nearby, the riparian area was bordered by natural vegetation and relatively unaffected by human influence.	43.8	52.1	 <p><b>SiteC</b> The proportion of settlement and urban area: 13.95%</p>
Site D (urban)	10	Site D was located in the middle reaches of the river system. As the central part of Tajimi City, this area harbors a large number of local residents. And in order to everyone can easily access the river flow and enjoy river scenery, the loose inclination at the lower riverbed was designed.	89.3	97.1	 <p><b>SiteD</b> The proportion of settlement and urban area: 78.23%</p>

**Table 4-2.** Kruskal–Wallis ANOVA and significance results comparing local factors of soil samples collected in sampling sites A–D. Values represent means  $\pm$  SE. Notes: SWC, soil water content; TN, total nitrogen; TS, total sulfur; SOC, soil organic carbon; EC, electrical conductivity;

	Site A	Site B	Site C	Site D	Df	P-value
Gravel (%)	16.84 $\pm$ 4.30	15.68 $\pm$ 5.97	19.58 $\pm$ 5.71	20.53 $\pm$ 5.60	3	ns
Sand (%)	37.62 $\pm$ 5.45	36.87 $\pm$ 6.29	41.82 $\pm$ 1.66	41.39 $\pm$ 3.13	3	ns
Silt (%)	45.54 $\pm$ 5.45	47.43 $\pm$ 7.01	38.59 $\pm$ 5.41	38.09 $\pm$ 8.56	3	ns
pH	6.41 $\pm$ 0.14	5.71 $\pm$ 0.19	5.99 $\pm$ 0.21	6.52 $\pm$ 0.13	3	<0.001**
EC ( $\mu$ S/cm)	81.08 $\pm$ 7.41	37.53 $\pm$ 11.68	61.01 $\pm$ 22.21	91.64 $\pm$ 9.74	3	<0.001**
SWC (g/g)	0.24 $\pm$ 0.03	0.26 $\pm$ 0.03	0.21 $\pm$ 0.02	0.20 $\pm$ 0.05	3	ns
TN (%)	0.18 $\pm$ 0.05	0.18 $\pm$ 0.01	0.12 $\pm$ 0.02	0.13 $\pm$ 0.02	3	ns
SOC (%)	1.9 $\pm$ 0.58	2.14 $\pm$ 0.21	1.08 $\pm$ 0.02	1.63 $\pm$ 0.28	3	ns
TS (%)	0.06 $\pm$ 0.01	0.03 $\pm$ 0.02	0.05 $\pm$ 0.01	0.06 $\pm$ 0.04	3	ns

**Table 4-3.** Kruskal–Wallis ANOVA and significance results comparing local factors of soil samples collected in *P. australis* community 1–6. Values represent means  $\pm$  SE. Notes: C1–C6 represent community types 1–6; SWC, soil water content; TN, total nitrogen; TS, total sulfur; SOC, soil organic carbon; EC, electrical conductivity;

	C1	C2	C3	C4	C5	C6	Df	P-value
Gravel (%)	12.08 $\pm$ 4.30	19.47 $\pm$ 5.97	25.54 $\pm$ 5.71	9.15 $\pm$ 5.60	18.59 $\pm$ 5.54	25.94 $\pm$ 4.91	5	ns
Sand (%)	35.46 $\pm$ 5.45	54.22 $\pm$ 6.29	38.00 $\pm$ 1.66	34.67 $\pm$ 3.13	39.64 $\pm$ 5.12	36.13 $\pm$ 4.71	5	ns
Silt (%)	52.44 $\pm$ 5.45	26.33 $\pm$ 7.01	36.46 $\pm$ 5.41	56.17 $\pm$ 8.56	41.78 $\pm$ 8.83	37.93 $\pm$ 8.50	5	ns
pH	5.72 $\pm$ 0.14	6.11 $\pm$ 0.19	6.25 $\pm$ 0.21	6.12 $\pm$ 0.13	6.50 $\pm$ 0.06	6.37 $\pm$ 0.19	5	<0.05**
EC ( $\mu$ S/cm)	37.36 $\pm$ 7.41	43.21 $\pm$ 11.68	81.82 $\pm$ 22.21	73.72 $\pm$ 9.74	88.80 $\pm$ 5.61	86.10 $\pm$ 8.72	5	<0.05**
SWC (g/g)	0.26 $\pm$ 0.03	0.19 $\pm$ 0.03	0.22 $\pm$ 0.02	0.26 $\pm$ 0.05	0.21 $\pm$ 0.05	0.19 $\pm$ 0.03	5	ns
TN (%)	0.22 $\pm$ 0.05	0.08 $\pm$ 0.01	0.13 $\pm$ 0.02	0.20 $\pm$ 0.02	0.15 $\pm$ 0.04	0.09 $\pm$ 0.04	5	ns
SOC (%)	2.44 $\pm$ 0.58	0.71 $\pm$ 0.21	1.35 $\pm$ 0.02	2.55 $\pm$ 0.28	1.67 $\pm$ 0.5	1.12 $\pm$ 0.67	5	ns
TS (%)	0.04 $\pm$ 0.01	0.02 $\pm$ 0.02	0.02 $\pm$ 0.01	0.05 $\pm$ 0.04	0.07 $\pm$ 0.03	0.09 $\pm$ 0.01	5	ns

**Table 4-4.** Step multiple linear regression of the characteristics of *P.australis* with environmental factors.

Notes: IMP, imperviousness; SWC, soil water content; TN, total nitrogen; TS, total sulfur; SOC, soil organic carbon; EC, electrical conductivity;

	<b>Predictor</b>	<b>AIC</b>	<b>Adjusted R<sup>2</sup></b>	<b>P-value</b>
<b>Coverage</b>	IMP	56.86	0.414	< 0.001
	SWC + EC+ silt + IMP	56.40	0.574	< 0.001
<b>Leaf area</b>	TN	83.22	0.079	< 0.05
	gravel + TN + SOC + green space	83.01	0.158	< 0.05
<b>Height</b>	SWC	49.42	0.376	< 0.001
	SWC+ TN	49.09	0.402	< 0.001
<b>Stem diameter</b>	SWC	57.64	0.299	< 0.001
	pH + EC + SWC + farmland	57.15	0.531	< 0.001
<b>Shannon-Wiener index</b>	IMP	78.43	0.106	< 0.05
	gravel + sand + silt + pH + IMP	77.96	0.243	< 0.05



**Table 4-5.** Key influencing factors selected based on the redundancy analysis obtained from the Monte Carlo test of forward selection.

Environmental factors	Percentage of variance explained (Marginal)	Percentage of variance explained (conditional)	<i>P</i> -value	Relative explanation (%)
soil water content	22.1	19.1	<0.01	40.9
Imperviousness	13.3	10.7	< 0.01	22.9
Total nitrogen	9.1	4.6	<0.05	9.9
Soil organic carbon	8.8	1	ns	2.1
pH	8.5	4.4	<0.05	9.4
Silt	7.1	1	ns	2.1
Sand	6.7	1	ns	2.1
Electrical conductivity	6.1	4.2	<0.05	9
Farmland	5.7	0.5	ns	1.1
Gravel	4.8	0	ns	0
Green space	4.7	0.2	ns	0
Water bodies	0.3	0	ns	0
Sulfur	2.8	0	ns	0
total		46.7		

## 4.6 Figures

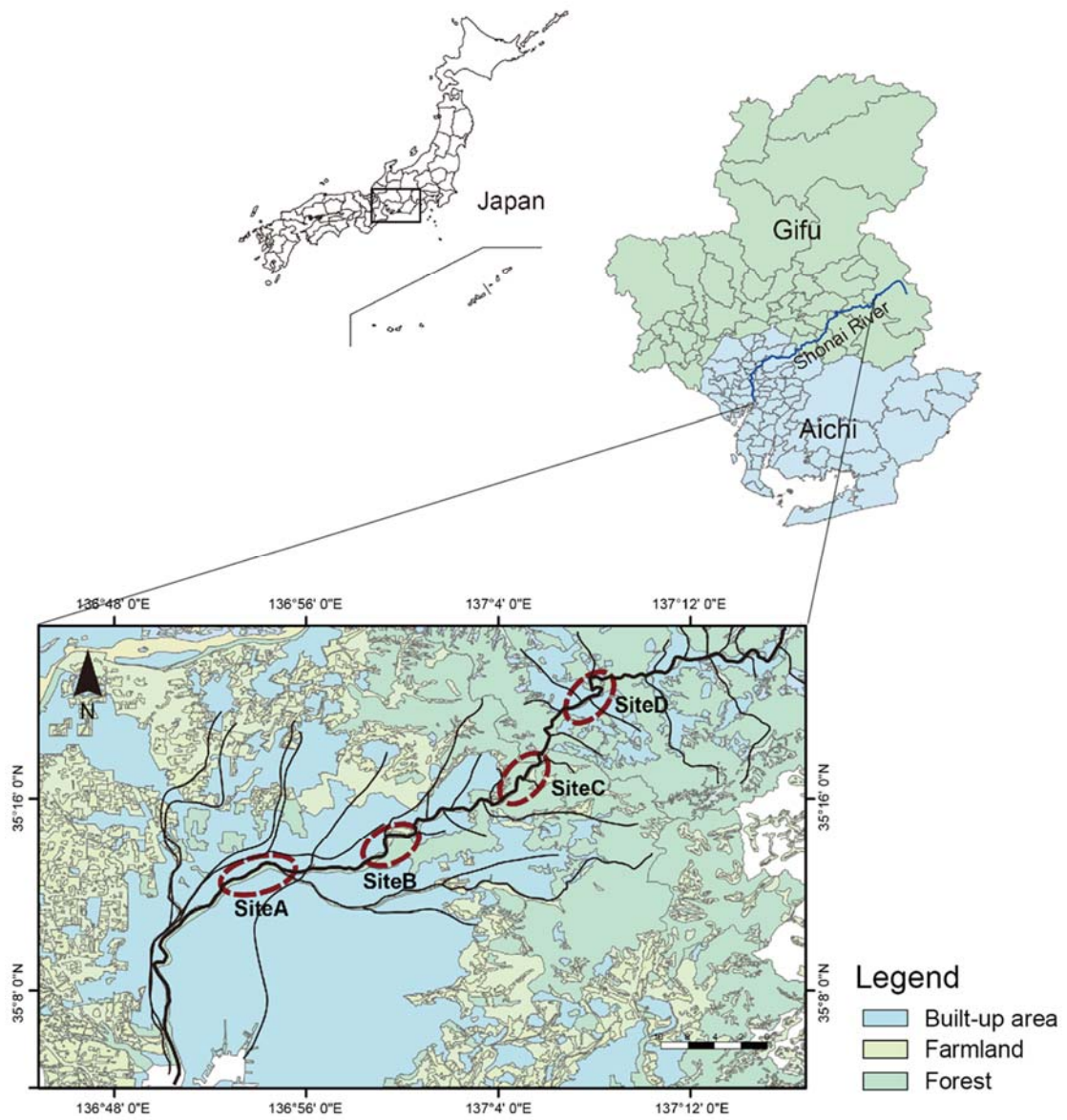
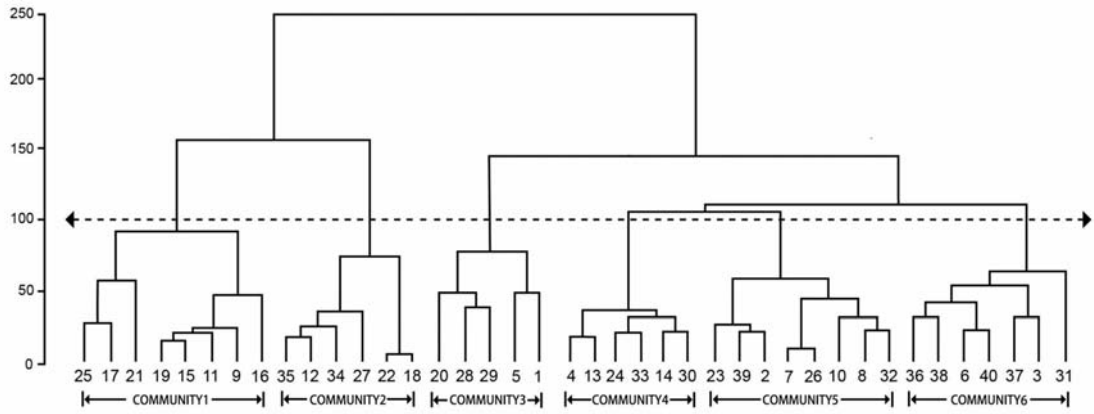
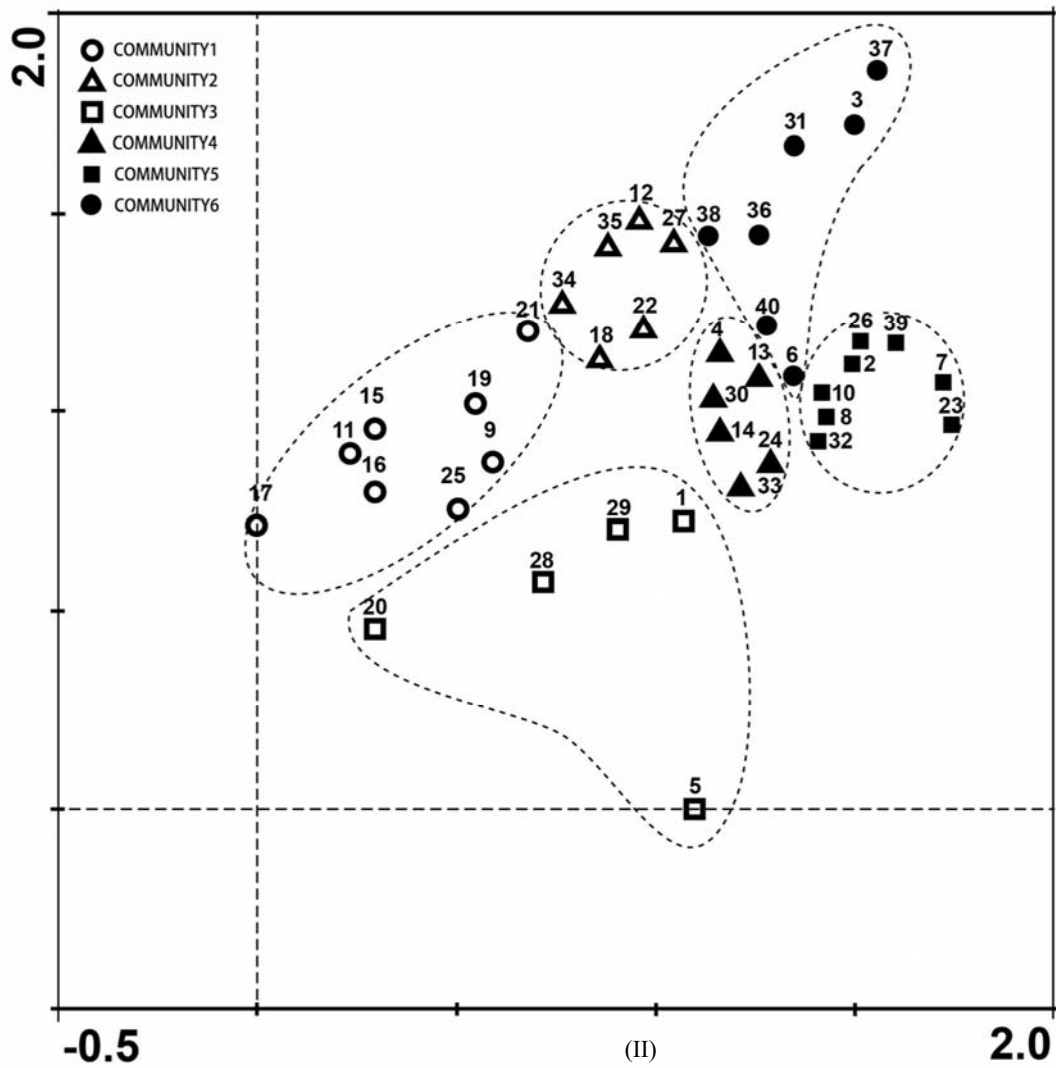


Fig. 4-1. Locations of the study sites and an overview of the Shonai River system in Japan.



(I)



(II)

Fig. 4-2. Dendrogram of sampling sites based on the cluster analysis (I) and detrended correspondence analysis (DCA) ordination diagram (II). Numbers 1–40 represent the sampling sites.

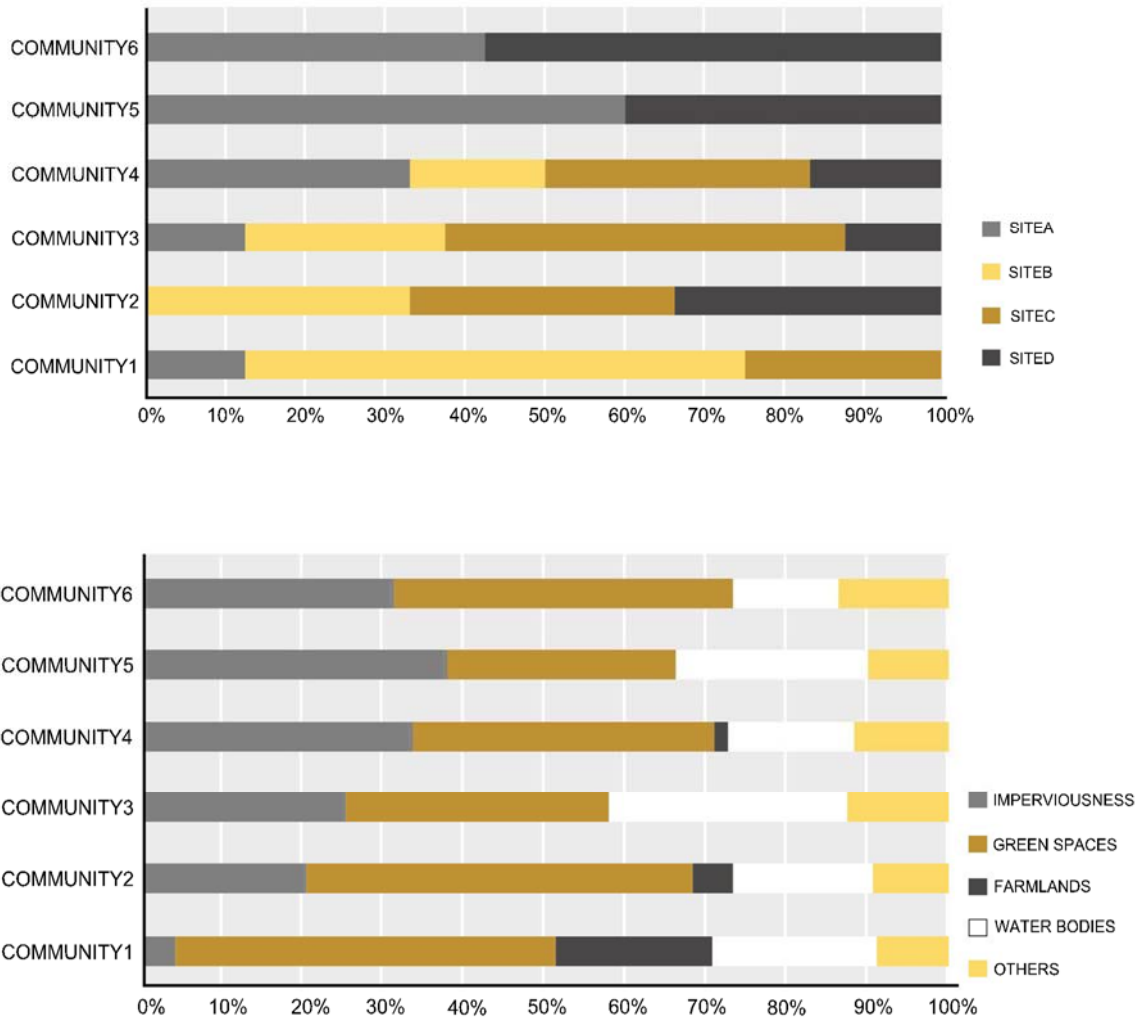


Fig. 4-3. Originated sites (I) and land cover types (II) among six *P. australis* communities.

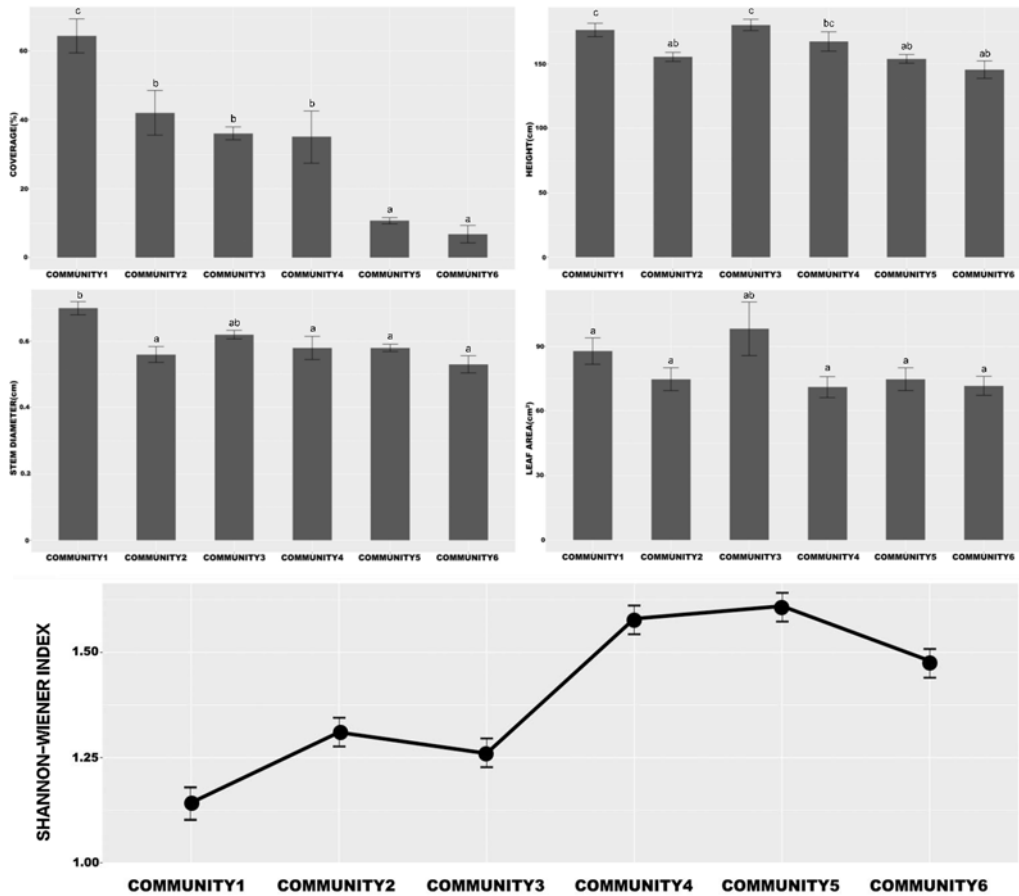


Fig. 4-4. Differences in the coverage (I), height (II), stem diameter (III), and leaf area (IV) of *P. australis* and diversity indices (V) in the six groups of *P. australis* community. Values represent means  $\pm$  SE. Values with the same letter are not significantly different at the 0.05 significance level.

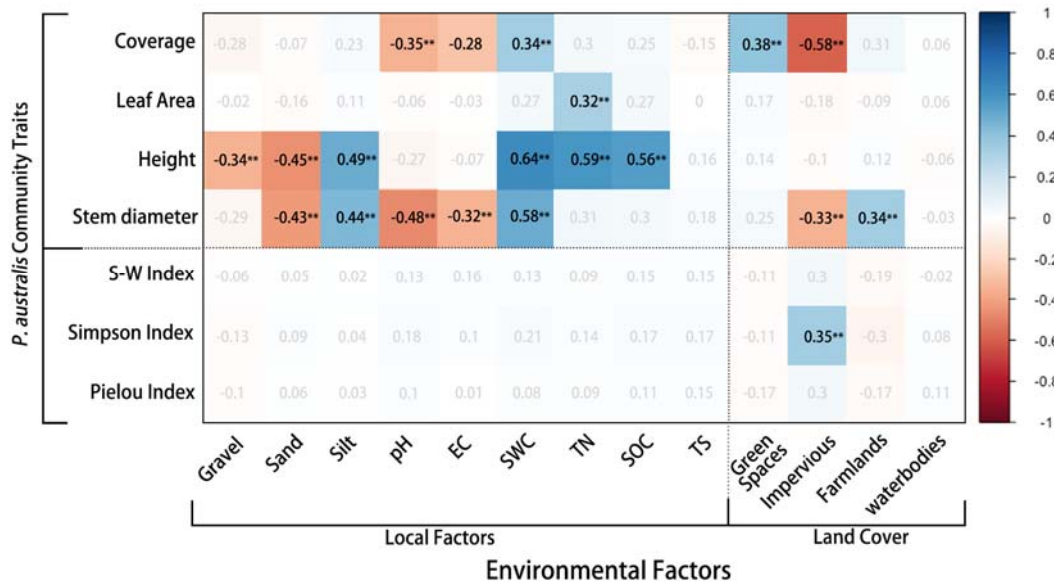


Fig. 4-5. Pearson correlation analysis of the relationship between community characteristics and environmental factors.

## Chapter 5: Conclusion

This dissertation investigated the effects of anthropogenic disturbance on riparian habitats in the central Japan area. As assumed in the research questions and hypotheses, the degradation of the riparian landscape caused by urban forced growth and human disturbances has seriously affected plant diversity along the Shonai and Miya rivers. Particularly, the consequences of human disturbances affected total and alien species  $\alpha$ -diversity, native species  $\alpha$ -diversity, specialist species  $\alpha$ -diversity, plant species  $\beta$ -diversity, and plant functional traits  $\beta$ -diversity.

### **Total species $\alpha$ -diversity**

In **Chapter 2**, I investigated whether plant  $\alpha$ -diversity (expressed as species richness) of two rivers was altered under the impacts of urbanization factors and local environmental variables. I found the response of total species richness to urbanization was observed to vary according to the types of habitat. In the artificial habitat, the total species were positively associated with urbanization intensity. These results were explained by the human disturbance and long historical development in the highly urbanized areas and both native and foreign species tend to be introduced in highly urbanized areas (Kühn and Klotz 2006). On contrary, the results in the semi-natural habitat presented a negative relationship between total species richness and urbanization intensity, which can be explained by the habitat heterogeneity in undisturbed riparian areas and promotes the coexistence of various types of plants. In **Chapter 3** I found that the total species richness decreased significantly as habitat degradation intensified, owing to a smaller number of native species in the highly disturbed area compared to those in undisturbed areas. The results exhibited in the **Chapter 4** underlined the positive effect of a large proportion of impervious surface as a component of anthropogenic on the total species  $\alpha$ -diversity as a result of the increase of alien species. I concluded that the response of total species to urbanization and human disturbance is unpredictable and changeable. Although this study found a reduction of species richness in urbanized areas, in some cases, some urbanization parameters led to the increase of alien species in some cases, resulting in an overall rise in total species richness.

### **Alien species $\alpha$ -diversity**

An increased number of alien species in urban areas was revealed in the present dissertation (**Chapters 2, 3, and 4**). The effect of urbanity enhancing the diversity of alien

plant species was implicated in the influence of urbanization factors. A large proportion of impervious surfaces converting from natural riparian habitat positively influenced the colonization of alien species (**Chapters 2 and 4**). My dissertation demonstrated the construction of impervious surfaces can cause changes in hydrological conditions and load intense human activities. Once introduced and established in a place with a large proportion of impervious surface, alien species can take advantage of the opportunities provided by hydrological and anthropogenic disturbances. Furthermore, the sites with a short distance to the city center induced the high species richness of aliens in the study area (**Chapter 2**). In the places near the city core, alien species invasions were increased directly or indirectly by various types of human-driven disturbances such as land-use conversion, habitat fragmentation, and recreational activities. This result was consistent with previous studies, revealing a declining trend of alien species from the city center to the suburbs or rural surroundings (Burton et al. 2005). Alien species are tolerate various stressful environments and occupy new niches in city center areas (Lake and Leishman 2004).

#### **Specialist and generalist plants $\alpha$ -diversity**

The distribution pattern of plant assemblages along the urbanization gradient could be reflected by the ecological specialization of plant species. Specialist species are closely related to a certain environment while generalist species can colonize in various environments (Denelle et al. 2020). In this dissertation, riparian and ruderal species were used as the surrogates of the specialist and generalist species to explore their response to urbanization, and the results were presented in **Chapters 2 and 4**. Besides, the richness of riparian species was suffering from the construction of impervious surfaces. By following artificial construction, riparian areas are strongly linked to hydrological alteration, riparian degradation, and intense human recreational activities. Due to hydrological alteration, riparian areas are being inundated less frequently and exist for shorter durations, facilitating the establishment of numerous terrestrial species. Ruderal species seemed to benefit from anthropogenic disturbance and land-use conversion in my study area, which was consistent with previous studies. Furthermore, I observed a decrease in ruderal species richness with increasing forest area, demonstrating that a large forest cover can resist the colonization of ruderal species.

#### **Taxonomic $\beta$ -diversity**

Considering the declines of specialist species and increase of generalist species due to anthropogenic disturbance, the floristic homogenization might occur as the replacement of specialist species by generalists (Büchi and Vuilleumier 2014). This dissertation revealed that

human disturbance could induce taxonomic homogenization in riparian areas (**Chapter 3**). Contrasting findings of the floristic differentiation in highly urbanized areas were reported in other studies. The results in my dissertation were explained by alien species propagate in most of the sites within the highly disturbed area, suggesting that alien species invasion was responsible for the homogenization in the highly disturbed riparian area. Regarding the environmental filtering process, I found environmental factors significantly affect the taxonomic  $\beta$ -diversity of riparian plant assemblages. The result of my study indicated that the habitat surrounded by a large proportion of impervious surface exhibited a relatively low  $\beta$ -diversity. Construction and expansion of impervious surfaces exert multiple disturbances, such as pollution, erosion, and frequent scouring flows. Following these disturbances, riparian areas might be subjected to a shift in plant community composition towards alien and tolerant species, inducing the increase of similarity of plant assemblages. Furthermore, NDVI and the proportion of forest cover were positively related to the taxonomic  $\beta$ -diversity of plant assemblages, indicating the importance of natural riparian forests on biodiversity conservation.

#### **Functional $\beta$ -diversity**

As a crucial component of floristic homogenization, the functional  $\beta$ -diversity of riparian plant assemblages was assessed in different levels of anthropogenic disturbance (**Chapter 3**). I observed that there were no significant differences in functional  $\beta$ -diversity in different levels of human disturbance. However, my study reported that anthropogenic disturbance indirectly induced functional homogenization for the introduction of alien species in the native flora. Moreover, the environmental factors were critical for the functional  $\beta$ -diversity pattern of plant assemblages. The artificial management of riparian areas was the strongest predictor for the variation of functional  $\beta$ -diversity in my study. By following artificial construction, riparian areas are strongly linked to hydrological alteration, riparian degradation, and intense human recreational activities, facilitating the establishment of numerous terrestrial species (Groffman et al. 2003; Pennington et al. 2010), and promoting the alteration of vegetation composition; as a typical result, plant trait convergence was generated. Furthermore, I found functional  $\beta$ -diversity was significantly correlated with the proportion of forests. I explained this result with two reasons. First, forests constitute a heterogeneous landscape, namely floodplain–grassland–forest mosaics (Erdős et al. 2018). This heterogeneous landscape could hold more specialist species with different functional traits. Second, environmental heterogeneity in forest habitat might critically affect the  $\beta$ -diversity of herbaceous and shrubs owing to the effects of forest type, forest structure, and forest size (Chávez and Macdonald 2012).



## **Implications and Outlook**

As urbanization is an inevitable process of human development and is unlikely to stop, many measures have been recently taken to formulate strategies to protect biodiversity from urbanization and anthropogenic disturbance. Based on my principal findings, I propose some suggestions to prevent further degradation of riparian habitats in central Japan:

- Management of the semi-natural habitats should include a designation of selected plots as nature reserves;
- It is necessary to consider urban riparian areas when planning urban expansion;
- Controlling the constructions of impervious surface that separate the floodplain habitat from the river (e.g., public open spaces, embankments) along the riverside. Since they are a necessary infrastructure in the scenario of bridges or dams, so they cannot be avoided;
- Maintaining several continuous strips of vegetation as a corridor along rivers should be considered;
- Planting native trees around impervious surfaces for the conservation of understory species and colonization of native plant species;
- Considering riparian 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 riparian forests.

These suggestions aimed to smooth the path towards further sustainable development of riparian habitat against urbanization and anthropogenic disturbances. The main information of this dissertation is that there is an urgent need to reduce the impact of anthropogenic disturbance on plant diversity. Indeed, urbanization and human disturbance have harmed the riparian ecosystem. However, "ecological sustainable urbanization" may become a reality and bring benefits to humanities through the implementation of some protective measures.

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