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Doctoral thesis

A study of effects of river confluences on plant diversity in river ecosystems.

(河川性植物の多様性に合流が及ぼす影響に関する研究)

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Contents

Summary

In this thesis, I hypothesized that river confluences have high vegetation and plant species diversity in river ecosystems and tested that using several spatial scales and approaches. In the Chapter II, I tested the hypothesis that around river confluences, frequent disturbances create heterogeneous habitats and consequently increase biodiversity using the data set from all river systems of Hyogo Prefecture. In the Chapter III, I further tested the confluence effects on functional vegetation groups that were likely to be more influenced by flood disturbances than other vegetation types using the data set from Kakogawa river basin system. In the Chapter IV, I tested confluence effects on plant species diversity in 11 river confluences within the Mukogawa river basin system. In the Chapter V, I tested validity of both neutral theory and niche theory as potential explanations for the assembly and diversity of plant communities in 11 river confluences within the Mukogawa river basin system. It the Chapter VI, I found that the numbers of both threatened species and artificial constructions increased with the number of confluences and the degree of meandering per unit area using the data set from all river systems of Hyogo Prefecture. These studies together suggest that flooding disturbances which occur more frequently around river confluences, played important roles in maintaining biodiversity. According to the results, I discuss how to apply my findings to conservation plans for riparian plant species diversity.

摘要

１．　本博士論文は、河川の合流点に注目して、河川生態系における生物多様性の維持機構を明らかにすること、並びにその知見を利用して生物多様性の保全を達成するための具体的なアイディアを示すことを目的とした。

２．　２章では、兵庫県全域の河川を対象に、合流点の周辺では多様な物理環境が成立していることを示した。

３．　３章では、兵庫県加古川水系全域の河川を対象に、合流点周辺では特に親水性植生の多様性が高いことを示し、合流点における多様性には単線に比べて活発な水の作用、すなわち洪水が関係していることを示した。

４．　４章では、兵庫県武庫川水系における１１箇所の合流点において合流の直前と直後における植物の種多様性を比較することで、合流がもたらす洪水が裸地を形成し、それが植物の種多様性に貢献していることを示した。

５．　５章では、兵庫県武庫川水系における１１箇所の合流点において、合流を含む組み合わせ、合流を含まない組み合わせそれぞれで植物群集の類似度を比較することで、合流周辺における群集の集合プロセスについて論じた。その結果、群集の集合プロセスは、夏は主に中立過程、春は種選別（ニッチ）過程に従うことが示唆された。

６．　６章では、単位面積あたりの合流点の数と蛇行の度合いが大きい地域は絶滅危惧種数が多く、同時に強い人為改変にさらされていることを示し、河川の合流点に迫る生物多様性損失の危機を明らかにした。さらにはその結果を、実際の保全の現場にどのようにして生かすかというアイディアを示した。

７．　終章では、得られた知見を再度概観し、その意義と生態学研究における位置づけをまとめた。得られた全ての成果から、河川生態系の保全に向けた提言を掲げ、博士論文としての哲学とした。

Chapter I

General introduction

General introduction

To understand how biodiversity is generated and maintained has been a central issue of various basic biological fields, such as ecology, taxonomy, biogeography, evolutionary biology and genetics. On the other hand, recent rapid biodiversity loss is recognized as one of important global issues. *Convention on Biological Diversity* (CBD) was adopted by United Nation at the 1992 Earth Summit in Rio de Janeiro, and entered into force at the end of 1993. It has three main objectives (CBD website: http://www.cbd.int/): (1) to conserve biological diversity, (2) the use biological diversity in a sustainable fashion, (3) to share the benefits of biological diversity fairly and equitably. Contracting parties are "*aware of the general lack of information and knowledge regarding biological diversity and of the urgent need to develop scientific, technical and institutional capacities to provide the basic understanding upon which to plan and implement appropriate measures*" in order to attain these objectives. Thus, biodiversity now becomes a target of various fields of applied and social science as well.

To conserve biological diversity on the present earth, we have to understand biological mechanisms maintaining biodiversity in various ecosystems. This is because to know mechanisms are important for restoration of degrade ecosystems as well as for keeping biodiversity in healthy ecosystems. Biologists often recognize three levels in biodiversity: genetic diversity, species diversity and ecological diversity (CBD website: http://www.cbd.int/). Mechanisms maintaining biodiversity are often species- and ecosystem-specific, intensive investigations on certain species or ecosystems would be necessary. Also, it is almost impossible for a person to examine all genetic and species diversity in all ecosystems. In this thesis, I focused mechanisms maintaining plant species diversity in riparian ecosystems. Plant species provides diverse habitats and foods for consumers and decomposers (Qian & Ricklefs 2008), so that ecosystems with highly diverse plant species should harbor high biodiversity (Burkart 2001; Whited *et al.* 2007). River ecosystems, where upland environments border streams, are among the most biologically diverse and productive ecosystems worldwide (Ward *et al.* 1999; Burkart 2001; Ward & Tockner 2001; Whited *et al.* 2007). To elucidate the mechanisms maintaining plant species diversity in river ecosystems should provide an important knowledge to understand mechanisms maintaining terrestrial biodiversity.

We would better understand dominant mechanisms in order to conserve biodiversity in given ecosystems. In other words, we have to find out most influential abiotic and/or biotic factors and their role in maintaining biodiversity of the ecosystems. In this thesis, I focus on the effect of river confluences (nodes of river networks), which are found in almost all river ecosystems, on vegetations and plant species diversity. A river ecosystem composed of many rivers, which join together at confluences to form larger networks and flowing into the sea (Lowe *et al.* 2006). Within a river system, river confluences are known to exhibit particular hydrodynamic traits (Rhoads & Kenworthy 1995; De Serres *et al.* 1999; Benda *et al.* 2004a; Benda *et al.* 2004b). For example, more frequent and/or strong flooding events take place around confluences than single-flow areas (Benda *et al.* 2004a; Benda *et al.* 2004b), creating diverse habitats such as pools of various depths and alluvial fans around confluences (Benda *et al.* 2004a; Benda *et al.* 2004b). Thus, river confluences are suggested to enhance biodiversity through various habitat creations (Benda *et al.* 2004b). Despite the suggested importance of river confluences for river biodiversity maintenance, their significance has not been examined.

In this thesis, I examine positive effects of river confluences on plant diversity (hereafter I refer to as confluence effects) in different scales (broad scale and small scale) in order to find out general patterns of confluence effects and to study mechanisms how they work. In Chapter 2, I examine confluence effects on habitat heterogeneity using data set from all river systems of Hyogo Prefecture in order to show the general patterns around river confluences. In Chapter 3, I examine confluence effects on 10 functional vegetation groups of Kakogawa river basin system where is the largest basin in Hyogo Prefecture. I try to examine a difference in confluence effects on colonization and establishment among different functional vegetation groups in these chapters. In Chapter 4, more detailed field observations around eleven confluences of Mukogawa river basin system are conducted in order to examine confluence effects on plant species diversity. In Chapter 5, I focused community composition in riparian ecosystems and how confluences affect communities structuring process. In Chapter 6, I again use broad scale data set and test confluence effects on rare species diversity in all river systems of Hyogo Prefecture. According to the results, I discuss how to apply my findings to conservation plans for riparian plant species diversity. In the final chapter, I briefly summarized my main findings and discussed the importance of understanding confluence effects in the light of disturbance-diversity relationships in basic and applied ecology, and then propose my ideas for biodiversity conservation in river ecosystems.

Chapter II

Landscape approach I:

Enhanced diversity at network nodes: river confluences increase vegetation-patch diversity.

Abstract

Although dendritic networks within ecosystems have typically been considered a special case of network topology, they have attracted a great deal of attention in recent years. These systems exhibit unique features in that both the nodes and branches provide distinct habitats. Within a river discontinuum context, river confluences, which are nodes of dendritic river networks, are hypothesized to have particular hydrodynamic traits that create heterogeneous habitats through a unique disturbance regime, although this hypothesis has not yet been tested. I tested this hypothesis using a vegetation data set collected from 14 river basin systems in Hyogo Prefecture, Japan. I compared vegetation-patch diversity between confluence and single-flow areas using hierarchical Bayesian models. My results demonstrated greater vegetation-patch diversity in confluence areas compared to single-flow areas. My findings support the hypothesis that confluences result in highly heterogeneous habitats. To the best of our knowledge, this is the first empirical report to demonstrate that river confluences have high vegetation-patch diversity. I conclude that network nodes play an important role in maintaining the biodiversity of river networks.

要約

ネットワークにおけるノードは一般に、そのネットワーク内において特殊な性質を示すことが多い。河川ネットワークのノードである合流点は、頻繁な洪水が起こることが知られており、その周辺では多様な物理環境が成立していると考えられる。その結果として生物多様性が高まっていることが予想されるが、この仮説について未だ検証した例はない。そこで本章では、兵庫県全14の主要水系における植生データを利用し、合流点と単線における植生の多様性を階層ベイズモデルによって比較した。その結果、仮説どおり合流点の周辺では物理環境の多様性が高まっていることが示された。河川ネットワークのノードである合流点は、河川生態系における生物多様性に重要な役割を持っている可能性が示唆された。

Introduction

Recent syntheses have used network theoretical analysis to understand the functioning of diverse sets of complex ecological systems (May 2006; Montoya *et al.* 2006). These analyses have suggested that emergent characteristics such as system-level responses to disturbance can be predicted from the structure of a network and the strength of interactions among network elements (Grant *et al.* 2007). Although dendritic networks within ecosystems are usually considered a special case of network topology (Grant *et al.* 2007), they have attracted a great deal of attention in recent years. Such systems exhibit the distinctive feature that both the nodes and branches provide unique habitats (Benda *et al.* 2004a; Benda *et al.* 2004b; Grant *et al.* 2007).

In dendritic networks, nodes provide high-quality habitats (Grant *et al.* 2007). River confluences, which correspond to the nodes of dendritic river networks, are known to exhibit particular hydrodynamic traits (Rhoads & Kenworthy 1995; De Serres *et al.* 1999; Benda *et al.* 2004a; Benda *et al.* 2004b; Rice *et al.* 2008) that result in many geomorphically diverse habitats (Benda *et al.* 2004b; Rice *et al.* 2008). In river ecosystems, flooding-induced disturbances, which provide the most dynamic and complex biophysical habitats (Naiman *et al.* 1993; Burkart 2001), occur more frequently at confluences (Benda *et al.* 2004b). Thus, confluences are considered to increase spatial and temporal habitat heterogeneity (Benda *et al.* 2004a; Benda *et al.* 2004b; Rice *et al.* 2008). Benda *et al*. (2004a,b) reviewed several cases of habitat creation by confluences, e.g., the formation of fans and erosion-resistant deposits, which may influence biodiversity. However, the roles of confluences in creating habitat heterogeneity (confluence effects) within river ecosystems have rarely been examined, but they should be investigated within a context of maintaining biodiversity in river ecosystems.

Habitats in river systems are characterised by differences in river streams and reaches, which join together to form larger networks (Lowe *et al.* 2006). Therefore, an effective analysis of the ecological importance of a river confluence as a component of the river channel network must incorporate the entire river channel network. Ideally, this kind of analysis applies data collected from many rivers that constitute various river channel networks (Benda *et al.* 2004b). This type of approach helps to minimise individual river system–specific “noise” when analysing confluence effects (Knick *et al.* 2008). However, few wide-area biodiversity data sets from many river systems are available, because data collection is often expensive and time-consuming (e.g.,Svensson *et al.* 2007; Haddad *et al.* 2008). From 2002 to 2006, the Hyogo Prefecture government in Japan conducted the Research about the Natural Environment of Rivers (RNER) program for all rivers within the prefecture. This program involved investigating riparian vegetation for 195 individual rivers in 14 river basin systems, over an area of 5105 ha. All data were digitised and then incorporated into a geographic information system (GIS) (Hyogo Prefecture 2007). I used the RNER riparian vegetation data to determine whether diversity in vegetation patches, which serve as potential habitat, increases around confluences of Hyogo Prefecture rivers. High physical heterogeneity may augment biological diversity via the well-established principle that biological diversity tends to increase with habitat variability (Benda *et al.* 2004b; Rice *et al.* 2008).

I analysed the RNER data set to determine how river confluences affect habitat heterogeneity using a hierarchical Bayesian model that included three hierarchical random effects (see “Methods” section). In the RNER vegetation data set, different vegetation types were illustrated as patches on a vegetation map. The 17 vegetation types correspond to different habitat types in the RNER (Hyogo Prefecture 2009; Table 1). I used Shannon and Simpson diversity indices of vegetation patches as indices of habitat diversity and compared these between confluence sites and non-confluence sites. The following sections present my findings and discuss the significance of river confluences in riparian ecosystems.

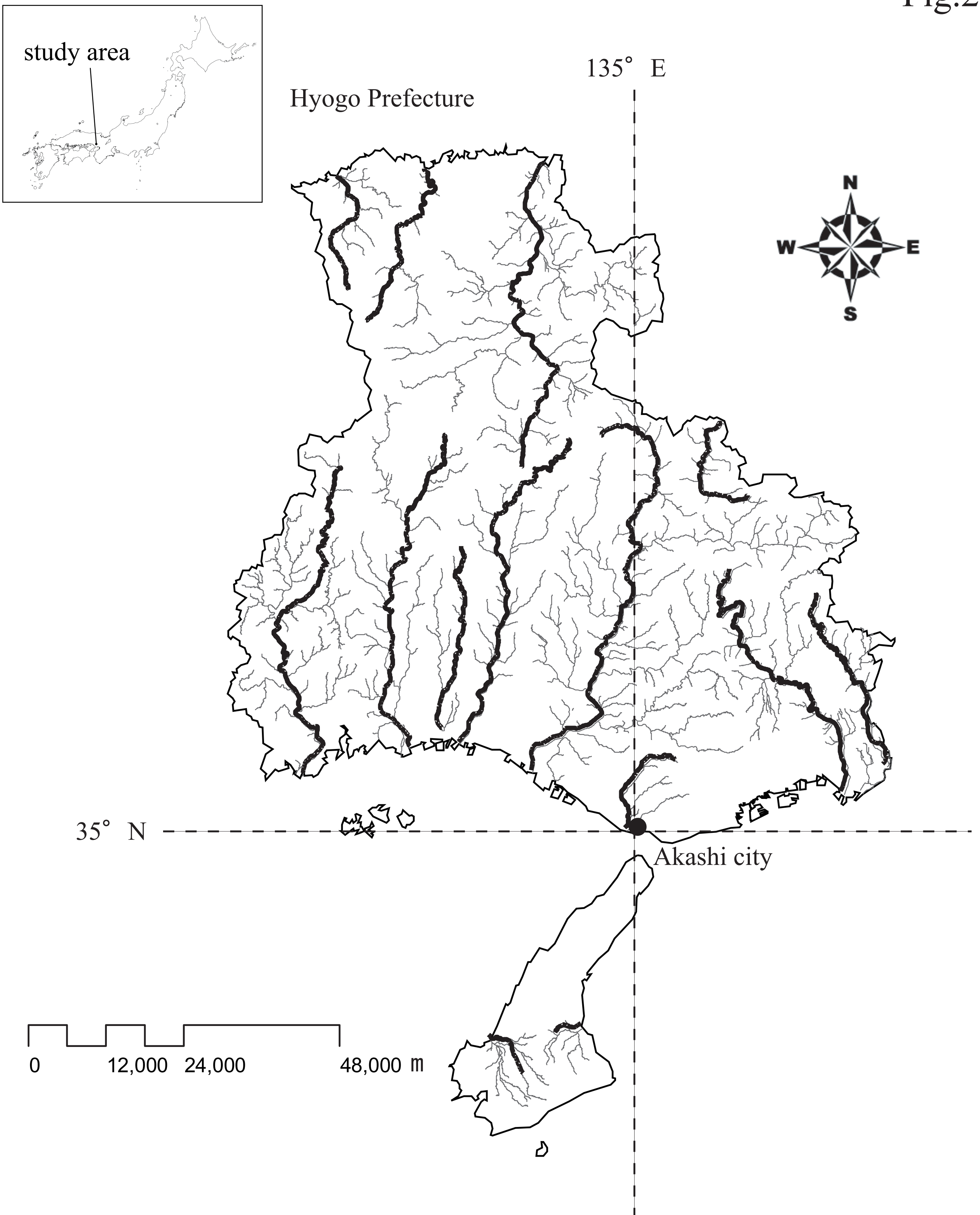
Methods

Research using the Natural Environment of Rivers (RNER) data set

I used the RNER vegetation data set from surveys conducted between 2002 and 2006 (Fig. 1) to investigate riparian vegetation in alluvial river sections (total length, 680 km). The RNER vegetation data set was created using two steps. The first step involved identification of the edges of vegetation patches from aerial photographs and digitalisation of vegetation patches on a 1/2500 contour map. Color photographs (scale: 1/10,000) taken by the Hyogo Prefecture government were used for patch identification. After the creation of the vegetation patch map, extensive field surveys using the Braun–Blanquet approach (i.e., phytosociological surveys) were conducted to classify the types of vegetation within the patches (Hyogo Prefecture 2007). Because surveying all vegetation patches would be prohibitively time-consuming, the phytosociological surveys were conducted on arbitrarily selected patches for each vegetation type. The data set first classified vegetation patches into 17 types based on habitat types that were estimated from dominant species and their life form (Table 1). In addition, land use and unvegetated areas (e.g., natural bare ground, open water, and artificial areas) were also classified into five types, and the vegetation/land-use types were summarised as patches on a vegetation map (Fig. 2). Vegetation was mainly distributed within 50 m of the river line, and each vegetation patch was entered as digital polygon data into GIS (ArcGIS version 9.1; ESRI Co., Tokyo, Japan).

In this study, I used the 17 vegetation types to evaluate habitat heterogeneity, as this vegetation classification system was intended to categorise habitats for plants along river lines of Hyogo Prefecture (Hyogo Prefecture 2009; Table 1).

Fig.2-1


study area
135° E
Hyogo Prefecture
N
W
E
S
35° N
Akashi city
0
12,000
24,000
48,000 m
: Main streams of each basin systems
: Tributaries

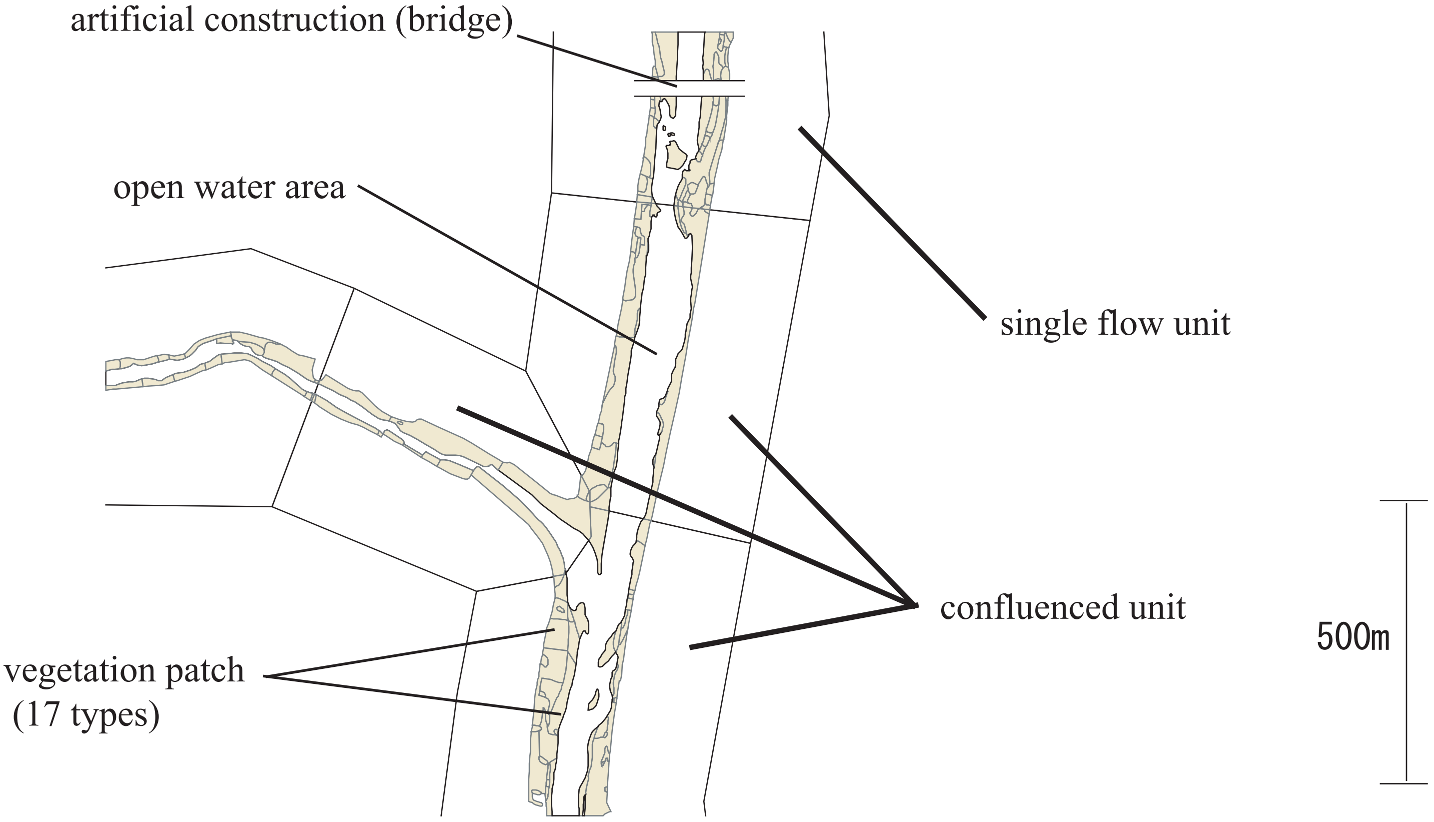


Fig. 2-2. Example of the Research about the Natural Environment of Rivers (RNER) geographic information system (GIS) data. Square polygons represent individual units. Confluence and single-flow units are defined as units adjacent to more than three other units and two other units, respectively. The central white polygon represents open water, and the other small polygons represent classified vegetation patches.

Data preparation

I used GIS software (ArcGIS) to divide river lines into 500-m units along all rivers of Hyogo Prefecture; each 500-m unit was a 500-m long and approximately 400-m wide polygon (Fig. 2). The first 500-m unit was placed at the mouth of each river, and the other 500-m units were then set automatically along river lines starting from the first unit using GIS. When a single vegetation patch was encompassed by two 500-m units, the patch was divided into two 500-m units. I defined a 500-m unit adjacent to more than three other units and including a river confluence as a “confluence unit”, whereas a 500-m unit adjacent to two or fewer other units and not including a river confluence was considered a “single-flow unit” (Fig. 2). A total of 190 units were classified as confluence units, and 1293 units were classified as single-flow units. I also calculated the area of all patches of vegetation within each 500-m unit. I then calculated Shannon (*H’*) and Simpson (*D*) diversity indices of vegetation patches for each unit as follows:

$$H'_x = -\sum_{i=1}^{N} (\mathrm{a}i / \mathrm{A}x) \ln(\mathrm{a}i / \mathrm{A}x),$$

$$D_x = 1 - \sum_{i=1}^{N} (\mathrm{a}i / \mathrm{A}x)^2,$$

where N is the number of vegetation types within the unit *x*, A*x* is the total vegetation area of the unit, and a*i* is the area of vegetation *i*. Finally, I calculated the total vegetation area and stream power index (SPI) per unit. SPI is the product of river-bed inclination and basin area and is generally used as an index of the erosive power of flowing water (Wilson & Gallant 2000). These two factors may affect vegetation diversity in riparian areas; therefore, I incorporated them into the models to control for their effects when determining confluence effects.

Pre-specified conditions

Data sets for river channel networks have a hierarchical construction: flows compose reaches, which link together to form larger stream networks (Lowe *et al.* 2006). Each of these components has unique traits. In addition, when a large-scale data set such as the RNER data set is analysed, the power of statistical analyses is often influenced by variation among data collectors, data sampling dates, and non-investigated site characteristics (Link 1999; Link & Sauer 2002; Clark *et al.* 2003; Thogmartin *et al.* 2004). Additionally, environmental factors are usually spatially autocorrelated (e.g.,(Keitt *et al.* 2002). To minimise these issues, multiple types of random effects should be incorporated into models (Link & Sauer 2002). The use of random effects is an effective method for data summarisation; i.e., the reduction of many parameters into simple summaries (Link 1999). The top-ranked random effect used in our analysis was river basin systems, which are related to variation in river length, catchment area, landform, and other traits. The second-ranked random effect is individual rivers, which are related to the diversity of types and scales of human land use and artificial constructions. The bottom-ranked rank random effect is individual 500-m units, which are related to unobserved micro-environmental factors such as observer error. Our models incorporated a nested structure of these three random effects, which were treated as mean zero normal random variables (Fig. 3).

Model establishment

I established hierarchical Bayesian models that included three hierarchical random effects. Shannon *H'* and Simpson *D* were assumed to have normal distributions. Our models can be expressed as:

$Y_{ijk} \sim Normal(\alpha_{k,}, {}_{V})$,

α_k = Intercept + $conf_k$ + SPI_k + $area_k$ + R_i + R_j + R_k, and

V = Variance of each diversity index,

where Y_{ijk} is Shannon *H'* or Simpson *D'* in a 500-m unit *k* on river *j* of river system *i*. I used the effects of three physical parameters as fixed effects: the presence of a river confluence (*conf*, 1, or 0); stream power index (*SPI*); and total vegetation area (*area*) of a unit. I also incorporated three random effects: river system, individual river, and individual unit (R_i, R_j, and R_k, respectively).

A necessary initial consideration in a Bayesian analysis is that prior distributions for each variable are informed (Link & Sauer 2002; Thogmartin *et al.* 2004). Because I had little empirical support for one distribution over another, our model was based on non-informative priors (Link & Sauer 2002; Thogmartin *et al.* 2004). All prior random and fixed effects were designed to have standard normal distributions (Fig. 3). In addition, the variance of each prior diversity index distribution (V) was also designed to have a standard normal distribution.

Fitting the hierarchical model

To fit the hierarchical models, I used WinBUGS and R version 2.4.1 software with the R2WinBUGS package to conduct a Markov Chain Monte Carlo (MCMC) analysis using Gibbs sampling. To use the MCMC results, the Markov Chain must change from the initial values into a stationary distribution. I conducted MCMC sampling for 100,000 counts and discarded the initial 30,000 as burn-in. In addition, to minimise results affected by the initial values, I conducted an analysis of three sets of initial values during MCMC sampling. I used R to generate random-sampling initial values and evaluated the contribution of fixed effects using a posterior predictive check based on a 95% confidence interval.

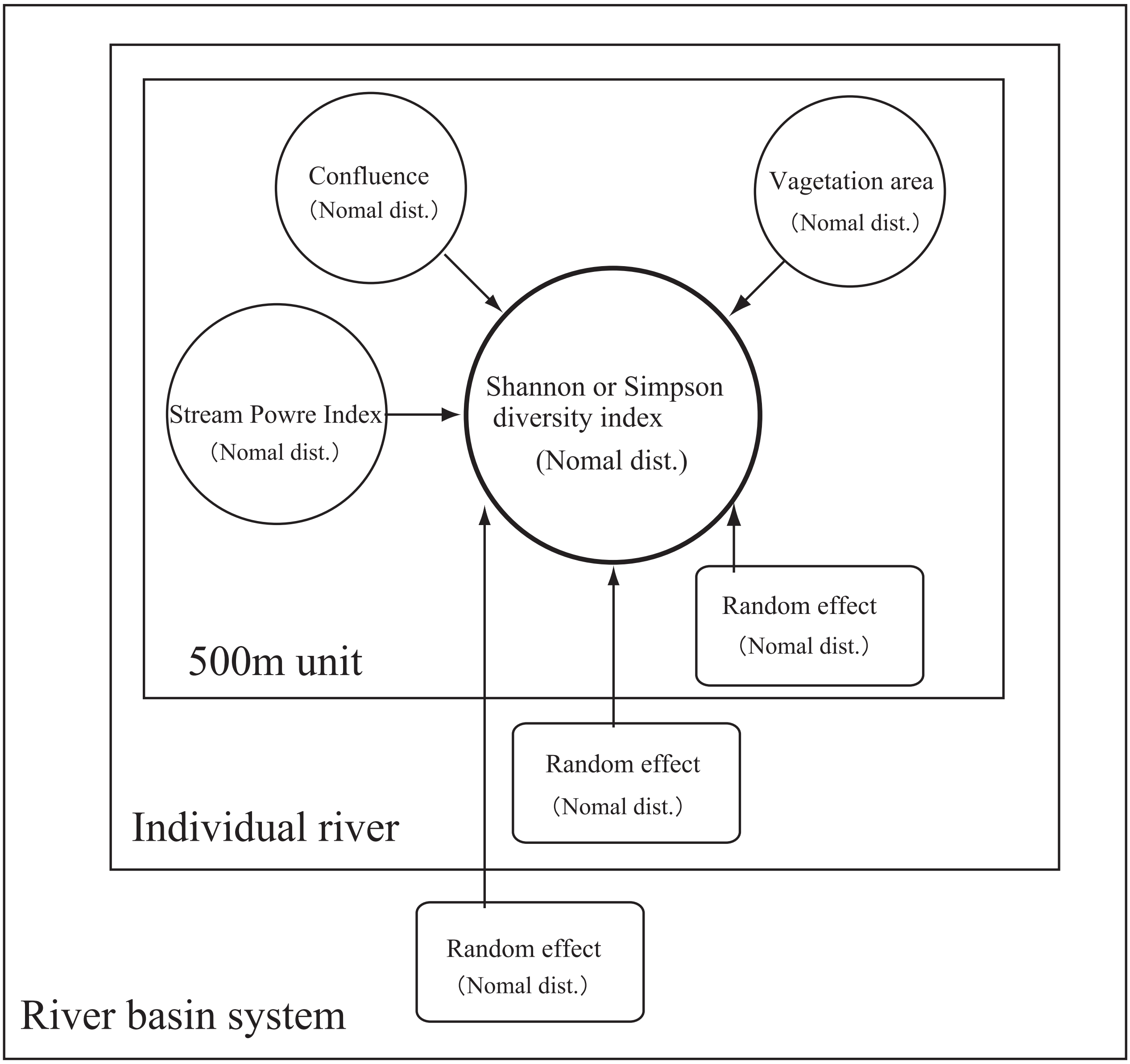


Fig. 2-3. Conceptual diagram of nested random effect models. The central circle represents the vegetation diversity index (patch number, Shannon H’ , or Simpson D’).
The surrounding circle represents fix effects, and the wavy square represents random effects.

Results

The means (±SD) of Shannon *H'* at confluence and single-flow units were 1.22 ± 0.32 and 1.07 ± 0.41, respectively, and the means of Simpson *D'* at confluence and single-flow units were 0.62 ± 0.15 and 0.52 ± 0.20, respectively. The mean values of SPI at confluence and single-flow units were 931.57 ± 808.00 and 631.11 ± 705.49, respectively. The mean areas of vegetation in confluence and single-flow units were 103,106.8 ± 53,742.2 m^2 and 90,994.7 ± 62,312.0 m^2, respectively.

My hierarchical Bayesian-model analysis revealed that all fixed effects had significant positive effects on Shannon *H'* (the 95% confidence interval did not include 0; Table 2). Simpson *D'* was positively affected by the presence of a confluence and area of vegetation but was not significantly affected by SPI (the 95% confidence interval included 0 for SPI; Table 3).

Table 2-1. Vegetation type in RNER data set and explain of indication habitats. Definitions were referred to Hyogo Prefecture (2009).

No.	Vegetation type	Habitat type that is indicated by the vegetation type
1	*Miscanthus sacchariflorus* dominant vegetation	Sandy habitats frequently found in relatively gentle river inclination (1/1000〜1/250) areas
2	*Phragmites communis* dominant vegetation	Muddy wetland habitats found in areas with low flow velocity
3	*Phragmites japonica* dominant vegetation	Frequently disturbed rudaceous habitats widely distributed in steeper river inclination (1/300〜) areas
4	*Salix gracilistyla* dominant vegetation	Usually flooded river-side habitats frequently found in steeper river inclination (1/200〜) areas
5	Floating-leaved and submerged plant vegetation	Stagnant water and slow-current habitats
6	Halophytic plant vegetation	Habitats preffered by halophytic plants
7	Sand dune vegetation	Habitats similar to coastal sand dune
8	Vegetation beside mountain stream	Stably wet habitats that is maintained by droplet of the flow and/or bubbles up water.
9	Riparian forest vegetation	Wet forest habitats higher from the river water surface
10	*Salix* species (other than *S. gracilistyla*) dominant vegetation	Wet forest habitats near the river line in the middle and lower strean areas
11	Annual plant vegetation just beside river channel	Frequently flooded and submerged habitats beside the river line
12	Low-moor vegetation	Wetland habitats around indentations and swaps with low flow velocity
13	Rudaceous grassland vegetation	Usually dry but infrequently flooded habitats higher from the river water surface
14	Floodplain grassland vegetation	Rarely flooded habitats far and higher from the river line
15	Floodplain woody plant vegetation	Floodplain habitats less frequently disturbed than low-moor vegetation
16	Hill forest vegetation	Rarely flooded hilly habitats
17	Roadside weed vegetation	Dry and treaded habitats

Table 2-2. Quantiles (2.5%, 50%, and 97.5%) of posterior distributions of Shannon diversity index (H').

			Values for the following percentiles		
Parameter	Mean	S.D	2.5%	50%	97.5%
Confluence	7.59×10^{-2}	2.50×10^{-2}	2.65×10^{-2}	7.61×10^{-2}	1.25×10^{-1}
SPI	4.10×10^{-5}	1.39×10^{-5}	1.38×10^{-5}	4.10×10^{-5}	6.83×10^{-5}
Vegetation area	1.27×10^{-6}	2.96×10^{-7}	6.82×10^{-7}	1.27×10^{-6}	1.84×10^{-6}
Deviance	-4.12×10^{2}	4.83×10^{2}	1.53×10^{3}	-3.37×10^{2}	3.04×10^{2}
Intercept	2.24×10^{0}	3.54×10^{0}	4.24×10^{-1}	6.37×10^{-1}	1.36×10^{1}

Table 2-3. Quantiles (2.5%, 50%, and 97.5%) of posterior distributions of Simpson diversity index (*D*).

			Values for the following percentiles		
Parameter	Mean	S.D	2.5%	50%	97.5%
Confluence	3.33×10^{-2}	1.27×10^{-2}	8.20×10^{-3}	3.33×10^{-2}	5.85×10^{-2}
SPI	1.32×10^{-5}	7.05×10^{-6}	-6.62×10^{-7}	1.32×10^{-5}	2.71×10^{-5}
Vegetation area	3.97×10^{-7}	1.53×10^{-7}	9.59×10^{-8}	3.98×10^{-7}	6.94×10^{-7}
Deviance	-2.38×10^{3}	2.58×10^{2}	-2.93×10^{3}	-2.36×10^{3}	-1.94×10^{3}
Intercept	1.15×10^{0}	1.06×10^{1}	2.55×10^{-1}	8.82×10^{0}	3.18×10^{1}

Discussion

My finding that confluence sites exhibited high vegetation-patch diversity in rivers in Hyogo Prefecture is the first empirical support of the existence of confluence effects related to biological habitat diversity within riparian areas. Both the Shannon and Simpson diversity indices for vegetation patches were higher for confluence units than for single-flow units. Even though my results revealed a diversity pattern for roughly classified vegetation types, this type of pattern still provides a useful basis for investigating and understanding the process by which habitat diversity is maintained in riparian ecosystems.

Channel disturbances are amplified at confluences because these locations are points that accumulate water, sediments, and woody debris (Benda *et al.* 2004a; Benda *et al.* 2004b; Rice *et al.* 2006; Rice *et al.* 2008). Water movement can strongly affect the distribution of vegetation types throughout floodplains, as such forces alter the physical structure and stability of the habitat through erosion and sedimentation (Salo *et al.* 1986). Debris flows and sediment deposits result in topographic heterogeneity around river confluences (Benda *et al.* 2004b). Together with my results, these findings suggest that habitat diversity increases around river confluences because these areas have unique hydrodynamic features and subsequently amplify disturbance regimes. High habitat diversity generally corresponds to high diversity in plant species (Wagner *et al.* 2000). In fact, I found that plant species diversity was enhanced by the flooding-induced creation of bare ground around confluences of the river systems in this study (Osawa *et al.* 2010). In turn, high plant diversity provides diverse habitats and food sources for animals (Qian & Ricklefs 2008). Thus, the highly diverse vegetation patches around river confluences may harbour many plant and animal species in river ecosystems. Future research should examine the detailed processes by which debris and sediment deposition and flooding disturbances enhance the establishment of diverse vegetation types and plant species.

In my analyses, I successfully regulated the effects of SPI and vegetation area in the models, and both factors affected vegetation diversity. For example, SPI positively affected the Shannon diversity index. SPI is conventionally used as an index of the erosive power of flowing water (Wilson & Gallant 2000) and can be used as a representation of disturbance intensity. Relatively strong disturbances likely occurred in high SPI areas, forming various types of vegetation patches, which points to the importance of disturbance for habitat diversity. Vegetation area positively affected both the Shannon and Simpson indices. The RNER program was conducted throughout alluvial (from mid to downstream) river areas that were surrounded by mainly urban and/or agricultural areas (Hyogo Prefecture 2007). One possible explanation for the positive relationship between diversity indices and vegetation area is that smaller vegetation areas are indicative of the intensification of artificial habitat alterations.

To the best of my knowledge, my study is the first to demonstrate that river confluences may generate habitat diversity for plants in riparian areas. A linear perspective on river networks (i.e., the river continuum concept; Vannote *et al.* 1980) has dominated much of river ecology over the last 20 years (Fisher 1997), despite the recognition that river networks are branched with tributaries that interrupt gradual downstream changes in channel and valley morphology (Benda *et al.* 2004a). Recently, the network dynamics hypothesis has articulated the relationships among key attributes of river networks and the patchy heterogeneity of the fluvial process and form (Benda *et al.* 2004a; Benda *et al.* 2004b). My results present empirical evidence of this more recent discontinuum perspective in river ecology, in which river confluences are considered key elements within a dendritic river network. Future research should examine confluence effects in a diversity of freshwater riverine systems (e.g. Fernandes *et al.* 2004), with particular focus on the fact that confluences vary in geomorphic features, such as shape and scale, within and among watersheds. Such variation in geomorphic features may produce different confluence effects on biodiversity (Benda *et al.* 2004b).

Appendix 2-1. List of dominant plants species in each vegetation types.
All scientific names are referred to YList, (http://bean.bio.chiba-u.jp/bgplants/ylist_main.html).

Vetation type	Dominant species name
Miscanthus sacchariflorus dominant vegetation	*Miscanthus sacchariflorus*
Phragmites communis dominant vegetation	*Phragmites australis*
Phragmites japonica dominant vegetation	*Phragmites japonica*
Salix gracilistyla dominant vegetation	*Salix gracilistyla*
Floating-leaved and submerged plant vegetation	*Nymphoides peltata* *Nymphoides indica* *Potamogeton wrightii* *Trapa japonica* *Nuphar subintegerrima* *Potamogeton octandrus* *Potamogeton crispus* *Hydrilla verticillata* *Vallisneria natans* *Potamogeton maackianus* *Ranunculus nipponicus* *Myriophyllum spicatum* *Potamogeton oxyphyllus* *Spirodela polyrhiza* and *Lemna aoukikusa* *Egeria densa and Elodea nuttallii* *Myriophyllum aquaticum* *Pistia stratiotes* *Eichhornia crassipes* *Azolla* spp.(exotic)

Appendix 2-1. Continued

Vetation type	Dominant species name
Halophytic plant vegetation	*Phacelurus latifolius*
	Aster tripolium
	Carex scabrifolia
	Limonium tetragonum
	Suaeda australis and *Atriplex gmelinii*
	Artemisia fukudo
Sand dune vegetation	*Carex pumila*
	Carex kobomugi and Wedelia prostrata
	Scutellaria strigillosa
	Calystegia soldanella and *Lathyrus japonicus*
	Vitex rotundifolia
Vegetation beside mountain stream	*Hosta montana,*
	Carex blepharicarpa and *Osmunda lancea*
	Acorus gramineus
	Carex curvicollis and *Sedum subtile*
	Carex teinogyna
	Carex persistens
	Carex forficula
	Carex heterolepis
Riparian forest vegetation	*Ulmus parvifolia*
	Celtis sinensis and *Aphananthe aspera*
	Juglans mandshurica
	Melia azedarach
	Zelkova serrata and *Acer palmatum*
	Euptelea polyandra
	Alnus japonica

Appendix 2-1. Continued

Vetation type	Dominant species name
Salix species dominant vegetation	*Salix chaenomeloides* and *Salix eriocarpa*
	Salix pierotii
	Salix udensis
	Salix miyabeana
	Salix jessoensis
	Salix triandra
Annual plant vegetation just beside river channel	*Lindernia procumbens*
	Persicaria lapathifolia and *Panicum dichotomiflorum*
	Microstegium vimineum
	Persicaria thunbergii
	Persicaria hydropiper
	Xanthium occidentale and *Chenopodium ficifolium*
	Bidens pilosa
Low-moor vegetation	*Leersia japonica*
	Carex thunbergii and *Isachne globosa*
	Leersia oryzoides
	Eleocharis mamillata
	Carex dispalata
	Typha latifolia and *Typha domingensis*
	Ischaemum aristatum
	Phalaris arundinacea and *Oenanthe javanica*
	Eleocharis kuroguwai
	Leersia sayanuka
	Schoenoplectus triqueter
	Coix lacryma-jobi
	Acorus calamus
	Lycopus lucidus

Appendix 2-1. Continued

Vetation type	Dominant species name
	Persicaria japonica
	Penthorum chinense
	Sparganium japonicum
	Schoenoplectus tabernaemontani
	Zizania latifolia and *Bolboschoenus fluviatilis*
	Sparganium erectum
	Lythrum anceps
	Nasturtium officinale
	Paspalum distichum
	Iris pseudacorus
	Alternanthera philoxeroides
	Gymnocoronis spilanthoides
	Cyperus eragrostis
	Stachys aspera
	Humulus scandens and *Lactuca indica*
	Matteuccia struthiopteris
	Phragmites vallatoria
	Sambucus chinensis
	Arundo donax
Rudaceous grassland	*Anaphalis margaritacea*
	Potentilla chinensis
	Artemisia capillaris
Grassland vegetation on flood channel	*Fallopia japonica*
	Boehmeria nivea
	Rumex japonicus
	Miscanthus sinensis
	Imperata cylindrica and *Erigeron annuus*
	Glycine max

Appendix 2-1. Continued

Vetation type	Dominant species name
	Arundinella hirta
	Heracleum sphondylium
	Digitaria ciliaris
	Cayratia japonica
	Boehmeria japonica
	Artemisia indica
	Sicyos angulatus
	Verbena brasiliensis
	Conyza sumatrensis
	Artemisia indica
	Coreopsis lanceolata
	Ambrosia trifida
	Festuca arundinacea
	Helianthus tuberosus
	Eragrostis curvula
	Paspalum dilatatum
	Fagopyrum dibotrys
	Solidago altissima
	Sorghum halepense
	Lolium multiflorum
	Crassocephalum crepidioides
	Ipomoea triloba
	Andropogon virginicus
Floodplain woody plant vegetation	*Deutzia crenata*
	Lycium chinense
	Aralia elata and *Rubus hirsutus*
	Rosa multiflora
	Sasa palmata
	Pleioblastus argenteostriatus and *Pleioblastus shibuyanus*

Appendix 2-1. Continued

Vetation type	Dominant species name
	Pleioblastus simonii
	Pueraria lobata
	Ampelopsis glandulosa
Hill forest	*Quercus acutissima*
	Quercus serrata and *Quercus variabilis*
	Quercus aliena
	Quercus glauca
	Quercus phillyraeoides
	Castanopsis cuspidata and *Photinia glabra*
	Quercus myrsinifolia
	Castanopsis sieboldii
Roadside weed vegetation	*Digitaria violascens* and *Eleusine indica*
	Eragrostis ferruginea
	Cynodon dactylon
	Pennisetum alopecuroides

Chapter III

Landscape approach II: Key components in river ecosystems: river confluences maintain diversity of hydrophilic vegetation.

Abstract

In riparian areas, the distribution patterns of plant species are generally considered to depend on their flooding tolerance. Areas around river confluences are known to experience frequent and/or strong flooding events in riparian areas. Thus, I hypothesized that areas around river confluences exhibit many hydrophilic vegetation types associated with flooding regimes. To test this hypothesis, I compared patch numbers and total areas of 10 functional vegetation groups between confluences and single-flow areas. The vegetation groups were classified on the basis of functional groups of dominant species. I found that patch numbers of annual grass, forb, and vine, perennial grass and forb, and riparian forest vegetations, as well as total areas of annual forb and vine, perennial grass and forb, bamboo and riparian forest vegetations, and natural bare ground, were greater around river confluences than single-flow areas. These results suggest that more frequent and/or strong disturbances occur around confluences, providing habitat for these functional vegetation types. Thus, river confluences are a key element in maintaining diverse riparian vegetation.

要約

河川敷における植物の分布は、撹乱に対する抵抗性に大きく影響される。河川の合流点周辺は洪水が頻発することが知られており、そこには撹乱抵抗性の高い親水性の植物が特に多くみられると予想できる。そこで本章は、10 の植物機能群について、その分布を合流点の周辺と単線で比較した。その結果、合流点の周辺では、一年生イネ、スゲ植物群、広葉草本群、つる植物群、多年生イネ、スゲ植物群、広葉草本群、河畔林木本のパッチ数、並びに一年生広葉草本群、つる植物群、多年生イネ、スゲ植物群、広葉草本群、タケ類、河畔林木本の成立面積が大きいことが示された。同時に自然裸地面積も合流点周辺で大きくなっていた。以上のことから、合流点の周辺では頻繁な洪水が発生し、一部の植物機能群に好適な環境が作り出されていると考えられた。河川の合流点は、頻繁な洪水が発生することによって、親水性植生の多様性に貢献している可能性が示唆された。

Introduction

Among terrestrial ecosystems, natural riparian corridors provide the most diverse, dynamic, and complex biophysical habitats, as they are shaped by frequent disturbances due to flooding (Burkart 2001; Naiman *et al.* 1993; Whited *et al.* 2007). Riparian corridors are characterized by dynamic landscape changing events such as lateral channel migration, creation of oxbow lakes in old river channels, and erosion and accumulation of sediments (Naiman *et al.* 1993; Salo *et al.* 1986). These dynamic landscape changes, which are often promoted by flooding, influence the establishment of various types of hydrophilic vegetation, which in turn influences diversity in consumer taxa by providing a variety of foods and habitats (Burkart 2001; Qian & Ricklefs 2008).

Within a river system, river confluences, which are the nodes of the river network, exhibit particular hydrodynamic traits (Benda *et al.* 2004a; Benda *et al.* 2004b; De Serres *et al.* 1999; Rhoads & Kenworthy 1995). Many types of disturbance events occur at river confluences, including more frequent and/or strong flooding events (Benda *et al*. 2004b), creating wide and diverse wetland conditions such as pools of various depths and alluvial fans (Benda *et al.* 2004a; Benda *et al.* 2004b).

Generally, the size of the stream, its position within the river network, the local hydrologic regime, and geomorphology all influence the establishment of streamside vegetation (Naiman & Decamps 1997; Naiman *et al.* 1993; Salo *et al.* 1986). Within riparian corridors, the distribution patterns of plant species differently along the flooding gradient, which experiences large variations in flooding duration, depth, and frequency (Vervuren *et al*. 2003). Species distribution patterns are thought to depend on their flooding tolerance (He *et al*. 1999; van Eck *et al*. 2004). Thus, if confluences provide a wide range of flooding regimes, as suggested by Benda *et al*. (2004b), I can hypothesize that vegetation types that prefer hydrophilic habitats are more frequently found around river confluences than in other areas within riparian systems. However, this hypothesis has not yet been tested (Benda *et al*. 2004b).

In this chapter, I tested the hypothesis predicting the effects of river confluences on floodplain vegetation patterns using a data set provided by the Research on Natural Environments of Rivers (RNER), Hyogo Prefecture, Japan (Hyogo Prefecture 2007). In the RNER data set, floodplain vegetation was classified into 91 types based on the dominant species. Natural bare ground areas were also recorded. These vegetation types and natural bare ground areas were summarized as patches on a vegetation map. I selected 59 vegetation types that are likely related to flooding and organized these into

10 functional vegetation groups. I then compared the distribution patterns of the 10 functional vegetation groups and natural bare ground areas between confluence and non-confluence areas. I discuss the importance of river confluences in maintaining various hydrophilic vegetations and the relationship between disturbance regimes and vegetation distribution in riparian ecosystems on the basis of my results.

Methods

RNER data set

I used the RNER vegetation data set from surveys conducted between 2002 and 2006 (Fig. 3-1) to investigate riparian vegetation in alluvial river sections (total length, 680 km). RNER identified the edges of vegetation patches from aerial photographs. Subsequently, extensive field surveys were conducted to classify the types of vegetation in the patches (Hyogo Prefecture 2007). The data set coarsely classified vegetation patches into 17 types based on dominant species and their life-form and/or habitat type, as well as more finely classifying patches into 91 types based on the dominant species. Land use and unvegetated areas (e.g., natural bare ground, open water, and artificial areas) were also coarsely classified into five types, and the vegetation/land use types were summarized as patches on a vegetation map (Fig. 3-2). Vegetation was mainly distributed within 50 m of the river line and each vegetation patch was input as digital polygon data into GIS (ArcGIS version 9.1; ESRI Co., Tokyo, Japan).

I used the Kakogawa River basin system data set from RNER (Fig. 3-1). The Kakogawa River basin system is the largest basin system in Hyogo Prefecture (Hyogo Prefecture 2007), with 96 km of main river lines and basin areas covering approximately 1,730 km^2 (Hyogo Prefecture 2007). Moreover, the Kakogawa River basin system contains more confluences and vegetation types than other river systems in Hyogo Prefecture, enabling us to test my hypothesis. In all, RNER reports 57 confluences of alluvial river sections (i.e. researched section) in the Kakogawa River basin (Fig. 3-1).

Fig.3-1

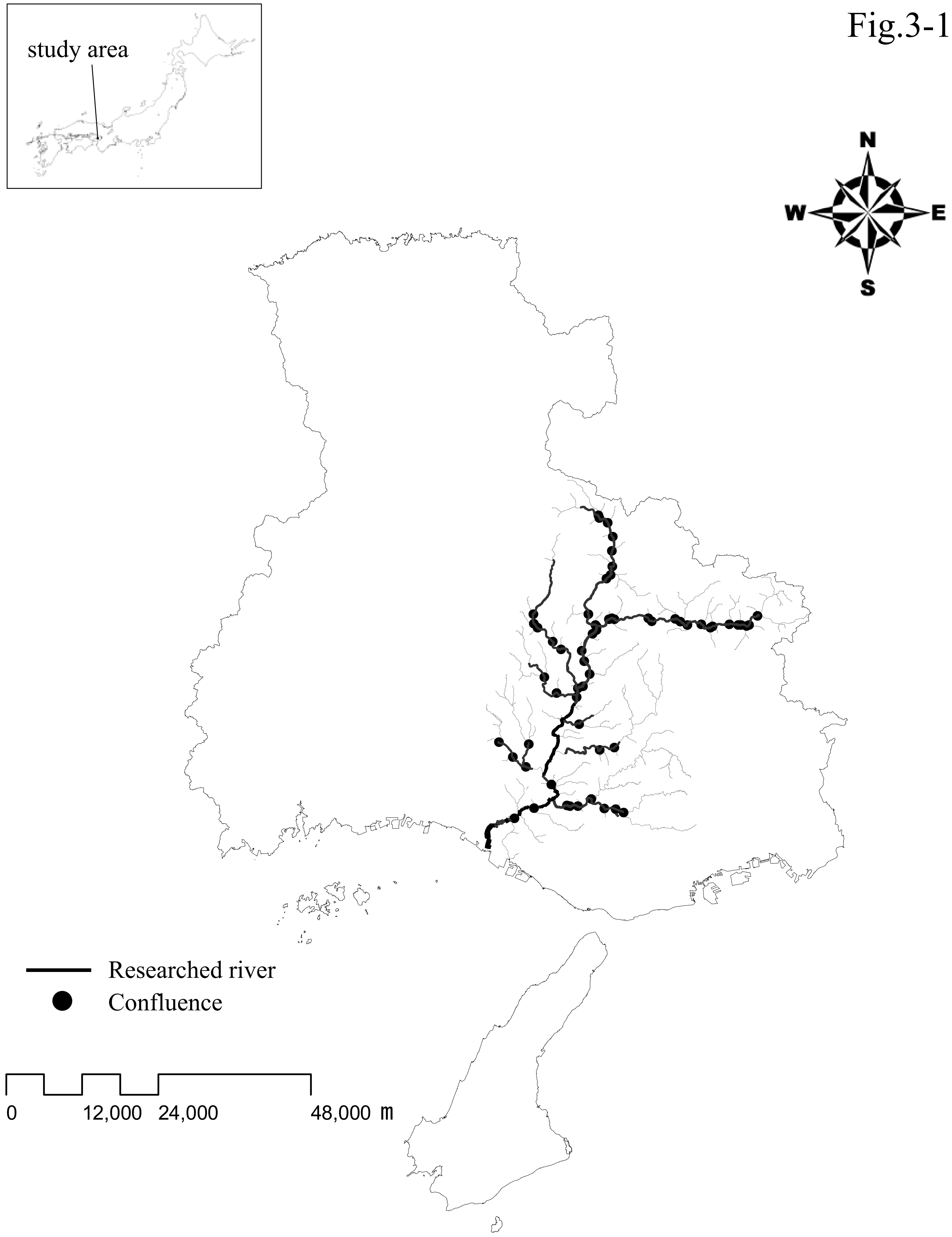


Fig. 3-1. Locations of streams on the Kakogawa river basin system in the Hyogo Prefecture. The thick line indicates the researched areas. The black points indicated the focused confluence.

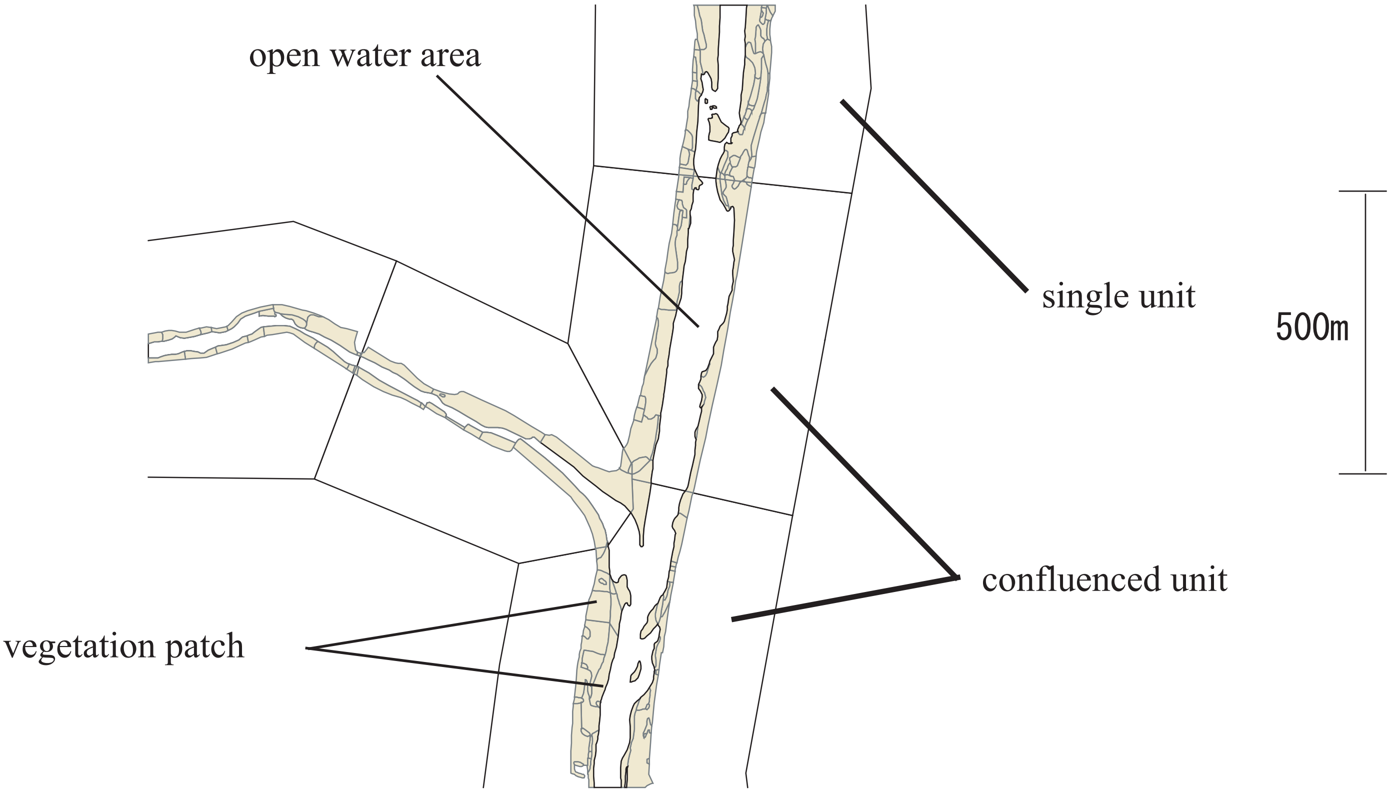


Fig. 3-2. Summary of RNER GIS data. Squares indicate individual units. Confluence and single-flow units are defined as units adjacent to more than three other units and to two or fewer other units, respectively. The central white square indicates open water area, and other small squares indicate classified vegetation patches.

Hydrophilic vegetation

I selected 59 vegetation types that are strongly related to flooding from the RNER data set and divided these into 10 functional vegetation groups based on the dominant species (Van der Maarel 2005). Annual plants were divided into three functional vegetation groups: grass, forb, and vine vegetations. Because both the annual forb *Bidens pilosa* var. *pilosa* and the grass *Setaria faberi* dominated patches of *B. pilosa* var. *pilosa–S. faberi* to a similar extent, all of the patches were divided into two different functional vegetation group patches (annual grass and forb vegetation patches), each of which had half the area of the original patch. Perennial plants were divided into three functional vegetation groups: grass, forb, and vine vegetations. All patches of the perennial grass *Imperata cylindrica* var. *koenigii* and the annual forb *Erigeron annuus* were also divided into two different functional patches (perennial grass and annual forb vegetation patches), each of which had half the area of the original patch. Four functional woody plant vegetation groups were recognized: willow, bamboo, riparian forest, and other woody vegetations. I referred to the *Wild Flowers of Japan* series (Satake *et al.* 1989a, b; Satake *et al.* 1981, 1982a, b) to categorize the functional groups of dominant species.

Data generation

I used GIS software (ArcGIS) to divide river lines into 500-m units along all rivers of the Kakogawa system; each 500-m unit was a polygon 500 m long and approximately 400 m wide (Fig. 2). The first 500-m unit was placed at the mouth of the Kakogawa River, and then the other 500-m units were set automatically along river lines starting from the first unit using GIS. When a single vegetation patch was encompassed by two 500-m units, I divided the patch into two 500-m units. I defined a 500-m unit adjacent to more than three other units and including a river confluence as a “confluence unit” and a 500-m unit adjacent to two or fewer other units and not including a river confluence as a “single-flow unit” (Fig. 2). I then calculated the patch numbers and total areas of each of the 10 functional vegetation groups for each unit.

I also calculated the total area of natural bare ground patches in each 500-m unit. As direct measurements of the degree of disturbance are usually difficult (Pollock *et al.* 1998), I used the area of bare ground as an index of flood disturbance, assuming that large bare ground areas indicated strong flooding disturbance.

Finally, I calculated the total vegetation area, flow accumulation (Jenson & Domingue 1988), and riverbed inclination using a 30-m digital elevation model (DEM) per unit. I used flow accumulation, the accumulated number of grid cells along the flow direction, which therefore increases in a downstream direction (Jenson & Domingue 1988), as the index of basin area. Riverbed inclination is the average inclination of the river line in each unit and tends to be higher in upstream areas. Flow accumulation and inclination are thought to positively affect flooding intensity (Wilson & Gallant 2000). As these three variables could influence hydrophilic vegetation distribution and abundance, I incorporated them into the models to control for their effects when determining confluence effects.

Statistical analysis

I used generalized linear mix effects models (GLMMs) and model selection based on Akaike's information criterion (AIC; Burnham & Anderson 2002) with round-robin modeling combinations. Specifically, I established GLMMs with possible combinations of variables and selected the model with the lowest AIC. I applied a Poisson error distribution (log link) to the patch number of each vegetation type, and Gaussian error distribution (identity link) to the total area of each vegetation type and bare ground. My primary GLMM that included all explanatory variables was represented as

$$Y_{ij} \sim exp(X_{ij}),$$

$$y_{ij} \sim f(X_{ij}),$$

$$X_{ij} = \beta_0 + \beta_1 \text{ Confluence}_i + \beta_2 \text{ Vegetation area}_i + \beta_3 \text{ Flow accumulation}_i + \beta_4 \text{ Inclination}_i + \sigma_j ,$$

where Y_{ij} is the number of patches of each functional vegetation group, and y_{ij} is the total area of focused vegetation type and bare ground. The suffixes $_i$ and $_j$ indicate unit ID and individual river ID, respectively. β_0 is the intercept (constant), and $\beta_{1\sim4}$ are the coefficients of the respective variables. Unit ID, σ_j, was incorporated into the model as a random term to regulate the effect of river size variations and the degree of artificial modification of the 500-m units on the number and total area of each vegetation type.

All statistical analysis were conducted using statistical package R ver. 2.7.1 (R Development Team 2008)

Results

I found 67 confluence units and 385 single-flow units in my data set. The mean vegetation areas of confluence and single units were $1.53 \times 10^5 \pm 4.61 \times 10^4$ m^2 and $1.70 \times 10^5 \pm 6.88 \times 10^4$ m^2 (mean ± SD) respectively. For confluence and single units, the mean flow accumulation values were $4.20 \times 10^5 \pm 4.50 \times 10^5$ and $3.96 \times 10^5 \pm 5.60 \times 10^5$, respectively, and the inclination values were $4.97 \times 10^{-3} \pm 4.52 \times 10^{-3}$ and $7.10 \times 10^{-3} \pm 6.66 \times 10^{-3}$, respectively.

The mean patch number and total area of annual grass vegetations were 1.72 ± 2.07 and $6.91 \times 10^2 \pm 1.50 \times 10^3$ m^2, respectively, in confluence units and 1.24 ± 1.88 and $7.98 \times 10^2 \pm 1.82 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of annual forb vegetations were 9.76 ± 6.67 and $5.14 \times 10^3 \pm 4.92 \times 10^3$ m^2, respectively, in confluence units and 6.42 ± 5.64 and $3.59 \times 10^3 \pm 4.82 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of annual vine vegetations were 2.91 ± 3.05 and $1.22 \times 10^3 \pm 2.33 \times 10^3$ m^2, respectively, in confluence units and 2.16 ± 2.89 and $9.14 \times 10^2 \pm 1.79 \times 10^3$ m^2, respectively, in single-flow units.

The mean patch number and total area of perennial grass vegetations were 11.7 ±

10.1 and $4.97 \times 10^3 \pm 4.87 \times 10^3$ m^2, respectively, in confluence units and 9.25 ± 10.5 and $5.23 \times 10^3 \pm 7.32 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of perennial forb vegetations were 6.94 ± 5.05 and $3.32 \times 10^3 \pm 4.16 \times 10^3$ m^2, respectively, in confluence units and 4.98 ± 5.06 and $2.70 \times 10^3 \pm 3.79 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of perennial vine vegetations were 2.45 ± 2.61 and $1.89 \times 10^3 \pm 2.72 \times 10^3$ m^2, respectively, in confluence units and 2.03 ± 2.32 and $1.44 \times 10^3 \pm 2.18 \times 10^3$ m^2, respectively, in single-flow units.

The mean patch number and total area of willow vegetations were 2.45 ± 4.54 and $7.26 \times 10^2 \pm 1.96 \times 10^3$ m^2, respectively, in confluence units and 2.22 ± 5.12 and $8.51 \times 10^2 \pm 2.66 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of bamboo vegetations were 1.06 ± 1.84 and $5.496 \times 10^2 \pm 1.48 \times 10^3$ m^2, respectively, in confluence units and 1.02 ± 1.72 and $5.17 \times 10^2 \pm 1.18 \times 10^3$ m^2, respectively, in single-flow units. The mean patch number and total area of riparian forest vegetations were $6.57 \times 10^{-1} \pm 1.297$ and $2.99 \times 10^2 \pm 7.44 \times 10^2$ m^2, respectively, in confluence units and $3.44 \times 10^{-1} \pm 9.58 \times 10^{-1}$ and $1.53 \times 10^2 \pm 6.59 \times 10^2$ m^2, respectively, in single-flow units. The mean patch number and total area of other woody vegetations were $5.97 \times 10^{-2} \pm 2.38 \times 10^{-1}$ and $4.13 \pm 1.99 \times 10$ m^2, respectively, in confluence units and $1.84 \times 10^{-1} \pm 7.07 \times 10^{-1}$ and $6.59 \times 10 \pm 3.38 \times 10^{2}$ m^2, respectively, in single-flow units.

The mean area of natural bare ground was $3.29 \times 10^{3} \pm 5.42 \times 10^{3}$ m^2 in confluence units and $2.66 \times 10^{3} \pm 5.18 \times 10^{3}$ m^2 in single-flow units.

Lowest AIC models

Among all possible models, I chose those with the lowest AIC as the best. Explanatory variables in the best models differed among functional vegetation groups and between patch number and total area (Table 1). The existence of confluences was incorporated in all of the best models, except patch numbers of perennial vine, willow, and bamboo vegetations (Table 1). Vegetation area was incorporated in the best models for patch numbers of annual grass and forb, perennial grass and vine, willow, riparian forest, and other woody vegetations, and the total area of perennial grass vegetations (Table 1). Flow accumulation was incorporated in the best models for patch numbers of annual grass, all perennial, willow, riparian forest, and other woody vegetations, as well as the total areas of annual and perennial grass, perennial vine, and willow vegetations (Table 1). Inclination was incorporated in all of the best models for patch numbers and total areas, except patch numbers of perennial vine and willow vegetations (Table 1).

The best model of natural bare ground area incorporated confluence, flow accumulation, and inclination (Table 1).

Contribution of variables to the best models

The presence of a confluence had a positive effect on patch numbers in the best models, which all, except other woody vegetations, incorporated this explanatory variable (Table 2). Vegetation area had a positive effect on patch numbers of annual grass and forb, perennial grass and vine, and other woody vegetations, whereas patch numbers of willow and riparian forest vegetations decreased with vegetation area (Table 2). Flow accumulation had a positive effect on patch numbers of annual grass, perennial grass, forb, willow, riparian forest, and other woody vegetations, but a negative effect on perennial vine vegetation patch numbers (Table 2). Inclination had a negative effect on patch numbers of herb vegetations that incorporated this explanatory variable, but a positive effect on woody vegetation patch numbers using this variable.

The total areas of annual forb and vine, perennial grass and forb, bamboo, and riparian forest vegetations increased in the presence of a confluence, whereas total annual grass, perennial vine, willow, and other woody vegetation areas decreased (Table 3). Vegetation area had a positive effect on the total area of perennial grass vegetations

(Table 3). Flow accumulation had a positive effect on the total areas of annual grass, perennial grass and forb, and willow vegetations, but was negatively correlated with the total area of perennial vine vegetations (Table 3). Inclination had a negative effect on the total areas of all herbaceous vegetations, but had a positive effect on those of all woody vegetations (Table 3).

Confluence presence, flow accumulation, and inclination had positive effects on the total area of natural bare ground ($\beta_1 = 6.399 \times 10^2 \pm 5.87 \times 10^2$, $\beta_3 = 5.37 \times 10^{-3} \pm 4.08 \times 10^{-4}$, $\beta_4 = 6.54 \times 10^4 \pm 3.47 \times 10^4$, and $\beta_0 = 6.81 \times 10 \pm 4.07 \times 10^2$).

Table 3-1: Results of model selections with AIC. Variables in the best models are shown. Confluence indicates confluence unit or not, Varea indicates the total vegetation area of each unit, FlowA indicates flow accumulation and Inclination indicates river bed inclination. Variables in black and grey indicate that the variable had positive and negagitive effects, respecitvely, on the patch number or total area.

Dependent variables	Functional vegetaiton group	Variables in the best model	BM AIC	PM AIC
Patch numer	Annual grass	Confluence + Varea + FlowA + Inclination	-	995.3
	Annual forb	Confluence + Varea + Inclination	1626.5	1628.1
	Annual vine	Confluence + Inclination	1232.5	1235.8
	Perennial grass	Confluence + Varea + FlowA + Inclination	2380.0	-
	Perennial forb	Confluence + FlowA + Inclination	1393.1	1394.9
	Perennial vine	Varea + FlowA	935.4	932.7
	Willow	Varea + FlowA	1397.1	1400.8
	Bamboo	Inclination	917.9	932.8
	Forest	Confluence + Varea + FlowA + Inclination	542.1	-
	Other woody	Confluence + Varea + FlowA + Inclination	334.8	-
Total area	Annual grass	Confluence + FlowA + Inclination	7993.2	8006.6
	Annual forb	Confluence + Inclination	8842.5	8866.0
	Annual vine	Confluence + Inclination	8015.8	8031.5
	Perennial grass	Confluence + Varea + FlowA + Inclination	9097.6	-
	Perennial forb	Confluence + FlowA + Inclination	8563.0	8573.5
	Perennial vine	Confluence + FlowA + Inclination	8186.7	8191.7
	Willow	Confluence + FlowA + Inclination	8181.7	8193.7
	Bamboo	Confluence + Inclination	7671.0	7696.0
	Forest	Confluence + Inclination	7131.0	7139.0
	Other woody	Confluence + Inclination	6432.0	6459.0
	Natural bare ground	Confluence + FlowA + Inclination	8839.6	8848.1

Note: BM and PM AICs mean AICs for the best models and primary models, respectively. BM AICs are not indicated when primary models are best models.

Table 3-2 . Results of GLMMs with the lowest AIC for the patch numbers of 10 functional vegetation groups. Estimated coefficients (SEs) are shown.

Vegetation type	Confluence (β_1)	Vegetation area (β_2)	Flow accumulation (β_3)	Inclination ($\beta 4$)	Intercept
Annual grass	2.39×10^{-1} (1.09×10^{-1})	1.38×10^{-6} (5.90×10^{-7})	2.21×10^{-7} (1.03×10^{-7})	-2.74×10 (8.81)	-9.25×10^{-1} (3.51×10^{-1})
Annual forb	2.98×10^{-1} (4.60×10^{-2})	7.84×10^{-7} (2.68×10^{-7})	-	-1.63×10 (3.61)	5.85×10^{-1} (1.75×10^{-1})
Annual vine	1.50×10^{-1} (8.08×10^{-2})	-	-	-3.49×10 (7.39)	-1.25×10^{-2} (2.295×10^{-1})
Perennial grass	1.89×10^{-1} (4.095×10^{-2})	1.62×10^{-6} (1.71×10^{-7})	5.48×10^{-7} (3.53×10^{-8})	-3.71×10 (3.74)	1.98×10^{-1} (2.75×10^{-1})
Perennial forb	1.59×10^{-1} (5.296×10^{-2})	-	2.02×10^{-7} (4.26×10^{-8})	-4.57×10 (4.99)	6.29×10^{-2} (2.88×10^{-1})
Perennial vine	-	3.05×10^{-6} (7.46×10^{-7})	-1.04×10^{-6} (1.09×10^{-7})	-	-1.35 (3.92×10^{-1})
Willow	-	-2.20×10^{-6} (3.53×10^{-7})	1.19×10^{-6} (6.18×10^{-8})	-	-1.84 (4.50×10^{-1})
Bamboo	-	-	-	3.68×10 (7.18)	-2.93 (4.30×10^{-1})
Riparian forest	7.23×10^{-1} (1.71×10^{-1})	-4.65×10^{-6} (1.45×10^{-6})	5.19×10^{-7} (1.73×10^{-7})	7.79×10 (9.01)	-1.56 (2.86×10^{-1})
Other woody	-8.76×10^{1} (5.20×10^{1})	4.14×10^{-6} (1.37×10^{-6})	5.91×10^{-7} (2.96×10^{-7})	7.04×10 (1.41×10)	-3.52 (3.28×10^{-1})

Table 3-3 . Results of GLMMs with the lowest AIC for the total area of 10 functional vegetation groups. Estimated coefficients (SEs) are shown.

Vegetation type	Confluence (β_1)	Vegetation area (β_2)	Flow accumulation (β_3)	Inclination ($\beta 4$)	Intercept
Annual grass	-1.53×10^{2} (2.28×10^{2})	-	8.23×10^{-4} (1.59×10^{-4})	-1.23×10^{4} (1.35×10^{4})	5.59×10^{2} (1.58×10^{2})
Annual forb	1.05×10^{3} (5.96×10^{2})	-	-	-1.08×10^{5} (3.58×10^{4})	2.86×10^{3} (5.31×10^{2})
Annual vine	1.19×10^{2} (2.39×10^{2})	-	-	-3.36×10^{4} (1.41×10^{4})	8.29×10^{2} (1.89×10^{2})
Perennial grass	1.16×10 (7.83×10^{2})	3.74×10^{-2} (4.84×10^{-3})	3.44×10^{-3} (6.95×10^{-4})	-1.06×10^{5} (4.73×10^{4})	-1.55×10^{3} (9.62×10^{2})
Perennial forb	1.84×10^{2} (4.32×10^{2})	-	2.17×10^{-3} (3.66×10^{-4})	-1.10×10^{5} (2.62×10^{4})	2.02×10^{3} (3.65×10^{2})
Perennial vine	-2.47×10 (2.81×10^{2})	-	-1.49×10^{-3} (2.46×10^{-4})	-5.35×10^{4} (1.74×10^{4})	1.40×10^{3} (2.96×10^{2})
Willow	-1.78×10^{2} (2.82×10^{2})	-	2.72×10^{-3} (1.96×10^{-4})	6.36×10^{3} (1.67×10^{4})	-2.69×10^{2} (1.95×10^{2})
Bamboo	2.21×10 (1.63×10^{2})	-	-	2.94×10^{3} (9.56×10^{3})	3.15×10^{2} (1.21×10^{2})
Riparian forest	1.32×10^{2} (8.92×10)	-	-	8.098×10^{3} (5.199×10^{3})	3.46×10 (6.24×10)
Other woody	-5.43×10 (4.096×10)	-	-	8.82×10^{3} (2.37×10^{3})	-9.96 (2.75×10)

Discussion

I found that the area of natural bare ground was greater in confluence units than in single-flow units, suggesting that more frequent and/or strong disturbances occurred around confluences than single-flow areas. My vegetation analyses revealed that patch numbers and total areas of almost all herbaceous and riparian forest vegetations were more frequently higher in confluence units than in single-flow units, although the total areas of annual grass and perennial vine vegetations decreased in confluence units. Thus, the hypothesis that river confluences provide wide and diverse flooding-induced wetland conditions, which in turn promote the establishment of various hydrophilic vegetation types, was basically supported. Although my data set was insufficient to elucidate the detailed processes determining the vegetation patterns, it provides a useful starting point for investigating these processes.

Effects of flooding disturbance on patch numbers and total areas of functional vegetation groups

The influence of confluence, flow accumulation, and riverbed inclination on patch number and total area differed among the 10 functional vegetation groups. This suggests that these functional vegetation groups prefer different flooding disturbance regimes in the Kakogawa River system.

Patch numbers and total areas of annual forbs and vines increased in confluence units and decreased with riverbed inclination, suggesting that these vegetation types are frequently established in regularly but not strongly disturbed areas. Annual forbs, such as *Crassocephalum crepidioides* and *Persicaria* and *Erigeron* species, are believed to invade open areas created by disturbances (Cho & Cho 2005; Ohtsuka *et al.* 1993). Confluences may frequently create bare ground and thus promote the establishment of annual forbs. However, the annual vines *Humulus japonicus* and *Sicyos angulatus* have been reported on disturbed areas far from river lines in Japan and Korea (Baek *et al.* 1997; Kamada & Okabe 1998). This finding and my results suggest that annual vine vegetations prefer relatively weakly disturbed riparian zones.

Annual and perennial grass and forb vegetations increased in area, and all of these except annual grass vegetations increased in patch number in confluence and high-flow accumulation units; however, all decreased with inclination, suggesting that these herbaceous vegetation types prefer regularly and strongly disturbed downstream areas. Some riparian perennial forbs and grasses, such as *Artemisia*, *Miscanthus*, *Phalaris*, and *Phragmites* species, are highly flood-tolerant and are often distributed in downstream areas (Aguiar *et al.* 2005; Baek *et al.* 1997; Cho & Cho 2005; Ohtsuka *et al.* 1993). My results are consistent with these findings.

Perennial vine vegetations were more frequently distributed in single-flow areas with low-flow accumulation and inclination. Nakagoshi and Kondo (2002) also reported that *Pueraria lobata* was not distributed in steep riparian areas of other Japanese rivers (Nakagoshi & Kondo 2002). Together with my results, this suggests that perennial vines prefer relatively stable riparian areas with infrequent and/or weak disturbances.

All woody vegetations increased in patch number and/or total area with flow accumulation and riverbed inclination, suggesting that woody vegetations have higher flooding tolerance than herbaceous vegetation. In fact, riparian forest vegetations are generally distributed in strongly disturbed areas (Johnson *et al.* 2000; Kozlowski 1997; Nakamura *et al.* 2007). The total area of all woody vegetations increased with inclination, suggesting that woody vegetation generally prefers upstream riparian areas in the Kakogawa River system. However, the effects of confluences differed among functional woody vegetation types.

In confluence units, bamboo and riparian forest vegetations increased in patch numbers and/or total area, but the total area of willow and other woody vegetations decreased. I cannot fully explain this surprising result, as willows are well adapted to regularly and strongly disturbed habitats (Niiyama 1987, 1990). One possible explanation is that floods are too frequent at confluences for these vegetation types to establish. The colonization and establishment of all woody vegetations around confluences requires field investigations to explain differences among woody vegetation groups.

Species distribution patterns often depend on the flooding tolerance of riparian vegetation (He et al. 1999; van Eck et al. 2004). Floristic composition along the flood-level gradient of floodplain vegetation represents serial stages of succession, such that pioneer annual and willow communities establish along riversides, perennial communities on lowlands, and forests on uplands (Bunn & Arthington 2002; Campbell *et al.* 1992; Niiyama 1990). My results indicate that confluences promote the establishment and colonization of many herbaceous vegetation types, as well as some types of woody vegetation. Thus, river confluences appear to provide frequently and/or strongly disturbed habitats. Disturbance intensity may also depend on flow accumulation and riverbed inclination (Wilson & Gallant 2000), and disturbed riparian environments may be formed by a combination of these factors. The relationship between flooding tolerance and the distribution of riparian vegetation types should be investigated via detailed field surveys and experiments within a wide range of flooding regimes provided by confluence, flow accumulation, and inclination.

Effect of vegetation area on hydrophilic vegetation

Total vegetation area was positively associated with patch numbers of five vegetation types (annual grass and forb, perennial grass and vine, and other woody vegetations) and total area of perennial grass vegetations. These results are not surprising because vegetation area is representative of the total area of potential habitats (MacArthur & Wilson 1976). However, the patch numbers of willow and riparian forest vegetations were negatively affected by vegetation area. A possible explanation for this result is that these trees prefer upstream areas with narrow riparian vegetation zones.

Conclusions

My results indicate that river confluences provide frequently and/or strongly disturbed habitats associated with flooding regimes and increased habitats for many functional vegetation groups. Thus, river confluences may play important roles in maintaining various vegetation types in river ecosystems. However frequent flooding is a problem for human settlement and activity near rivers. Therefore, many riparian zones have been heavily modified to control the impact of flooding (Poff *et al.* 1997; Rinaldi & Johnson

1997; Washitani 2001). In fact, areas around river confluences are more often artificially modified with hardscape compared to single-flow areas (Osawa *et al*. unpublished data). Future studies should evaluate river confluences as key habitats for riparian plant species diversity, and policy makers should strive to keep ecological processes around confluences free of anthropogenic effects.

Appendix 3-1. 59 vegetation types and functional group of dominant species in this study.

Life form	Vegetation name	Functional group
Annual plants		
	Ambrosia trifida Community	Forb
	Conyza canadensis Community	Forb
	Crassocephalum crepidioides Community	Forb
	Lindernia procumbens Community	Forb
	Melilotus officinalis Community	Forb
	Persicaria thunbergii Community	Forb
	P. hydropiper Community	Forb
	Xanthium canadense - *Chenopodium ficifolium* Community	Forb
	Bidens pilosa var. *pilosa* - *Setaria faberi* Community	Forb, Grass
	Coix lacryma-jobi Community	Grass
	Digitaria ciliaris Community	Grass
	Lolium multiflorum Community	Grass
	Humulus japonicus - *Lactuca indica* var. *laciniata* Community	Vine
	Sicyos angulatus Community	Vine
	Imperata cylindrica var. *koenigii* - *Erigeron annuus* Community	Perennial Grass/Annual Forb
Perrenial plants		
	Artemisia indica Community	Forb
	Boehmeria nivea Community	Forb
	Fallopia japonica Community	Forb
	Helianthus tuberosus Community	Forb
	Lycopus lucidus Community	Forb
	Matteuccia struthiopteris Community	Forb
	Nasturtium officinal Community	Forb
	Sambucus chinensis Community	Forb
	Solidago altissima Community	Forb
	Sparganium erectum Community	Forb
	Typha latifolia Community	Forb
	Andropogon virginicus Community	Grass
	Carex dispalata Community	Grass
	Eragrostis curvula Community	Grass
	Festuca arundinacea Community	Grass
	Juncus effusus Community	Grass
	Leersia oryzoides Community	Grass
	Miscanthus sacchariflorus Community	Grass
	Miscanthus sinensis Community	Grass
	Phragmites communis Community	Grass
	P. japonica Community	Grass
	P. karka Community	Grass
	Paspalum dilatatum Community	Grass
	P. distichum Community	Grass
	P. urvillei Steud. Community	Grass
	Phalaris arundinacea - *Oenanthe javanica* Community	Grass
	Sorghum halepense Community	Grass
	Verbena brasiliensis Community	Grass
	Zizania latifolia and *Scirpus yagara* Community	Grass
	Cayratia japonica Community	Vine
	Pueraria lobata Community	Vine
Woody plants		
	Salix gracilistyla Community	Willow
	S. chaenomeloides - *S. eriocarpa* Community	Willow
	S. gilgiana Community	Willow
	S. serissaefolia Community	Willow
	Pleioblastus chino var. *viridis* Community	Bamboo
	Pleioblastus Simonii Community	Bamboo
	Pseudosasa japonica Community	Bamboo
	Celtis sinensis var. *japonica* - *Aphananthe aspera* Community	Forest
	Juglans mandshurica Maxim. var. *sieboldiana* Community	Forest
	Ulmus parvifolia Community	Forest
	Zelkova serrata - *Acer palmatum* Community	Forest
	Aralia elata - *Rubus hirsutus* Community	Others
	Rosa multiflora Community	Others

All scientific names were reffered to ylist (http://bean.bio.chiba-u.jp/bgplants/ylist_main.html)

Chapter IV

Field research approach I:

River confluences enhance riparian plant species diversity.

Abstract

In riparian zones along the banks of streams and rivers, flooding often causes large changes in environmental conditions immediately downstream of confluences. In turn, spatial heterogeneity in flooding along rivers and streams likely affects local species diversity. Furthermore, flooding during the plant growing season can strongly affect plant survival. In this chapter, I hypothesized that confluences have impacts on plant species diversity, and that these impacts are larger during the plant growing season. To test this hypothesis, I measured plant species diversity and the extent of natural bare ground at 11 river confluences during two different seasons (summer and spring) within the Mukogawa River basin system, Japan. Species diversity was highest at down-confluence areas in the summer. I linked the pattern of species diversity to that of bare ground creation by floods around the confluences and to the seasonality of annual plant recruitment. The extent of bare ground was significantly greater at down-confluence areas than at up-confluence areas. The recruitment of annual species was higher in the summer than in the spring and included rapid occupancy of bare ground in the summer. I suggest that within river systems, spatial and seasonal differences in patterns of flooding function together to regulate plant species diversity.

要約

河川の合流点直下は、洪水によって物理環境が急激に変化し、その場所に生育する植物の種多様性に影響を及ぼしていると考えられる。さらに、植物の生育期に発生する洪水は、植物の生存率に強く影響すると考えられる。本章では、１）河川の合流が植物の多様性に影響するのか　２）その影響は、植物の生育期大きくなるのか　という仮説を検証した。調査は、兵庫県武庫川水系における１１箇所の合流点の前後において、春と夏の２回、合流の直前と直後における植物の多様性および裸地面積を調査した。その結果、植物の多様性は夏の合流直下で最も高くなった。植物を生活系に分けたところ、一年生草本は夏の合流下で多様性が最大になる傾向に従った。裸地面積は春夏とも合流直下で広く、夏は春に比べて小さくなっていた。以上のことから、合流直下では、春から夏にかけて裸地に一年生草本が旺盛に侵入することで、多様性が高まっていると考えられた。河川生態系における撹乱発生の空間的、時間的な違いは共に植物の種多様性に影響していることが示唆された。

Introduction

Natural riparian zones, where terrestrial environments border streams, provide some of the most diverse, dynamic, and complex biophysical habitats among terrestrial ecosystems (Naiman *et al.* 1993; Burkart 2001; Whited *et al.* 2007). Riparian zones exhibit sharp environmental gradients (Naiman *et al.* 1993; Ward *et al.* 2002; Iwata *et al.* 2003) that harbour varying plant and animal diversity (Burkart 2001; Whited *et al.* 2007). In these systems, flooding constitutes a major abiotic mechanism generating habitat and species diversity (Ferreira & Stohlgren 1999; Silvertown *et al.* 1999; Vervuren *et al.* 2003; van Eck *et al.* 2004; Beltman *et al.* 2007).

Although hydrologic and geomorphic conditions in riparian zones were once thought to change gradually along the lengths of rivers or streams (Harding *et al.* 1999; Sekiguchi *et al.* 2002), the recent river discontinuum perspective highlights the non-uniform or patchy distribution of physical conditions along river ecosystems (Benda *et al.* 2004b). When heavy rains occur, sequential freshets (flooding) alter physical environments around confluences much more than along unbranched river banks, such that patchy sediment deposits frequently accumulate around river confluences (Benda *et al.* 2004b).

Areas downstream of confluences (down-confluence areas) are likely to be much more strongly disturbed by flooding than upstream areas (up-confluence areas), as the contributory volume of river and stream water abruptly increase immediately downstream of confluences (Rhoads & Kenworthy 1995; De Serres *et al.* 1999; Benda *et al.* 2004b). Moreover, the distribution and diversity of plants in riparian areas can be greatly affected by disturbance in the form of floodings (Ferreira & Stohlgren 1999; Burkart 2001; Vervuren *et al.* 2003; van Eck *et al.* 2004; Archaux & Wolters 2006). Thus, I hypothesized that the increased incidence of flooding in down-confluence areas would result in different patterns of plant distribution and diversity relative to up-confluence areas (hereafter, we refer to this as the confluence effect).

In this chapter, I sought to conduct the first field test of the confluence-effect hypothesis, which proposes that amplified flooding affects species diversity in down-confluence areas of river ecosystems. I compared plant species diversity and the area of bare ground (an index of flooding disturbance) between up- and down-confluence areas and between the spring (the plant pre-growing season after snowmelt) and summer (the plant growing season after the rainy season) in 11 river confluences within the Mukogawa River basin system, Japan. In general, flooding during the growing season most strongly affects plant survival (Ferreira & Stohlgren 1999; Vervuren *et al.* 2003; van Eck *et al.* 2004). Based on my hypothesis, I predicted that plant diversity would differ between up- and down-confluence areas and that these difference would be larger in the summer than in the spring because of temporal synchrony with the plant growing season (Vervuren *et al.* 2003; van Eck *et al.* 2004). In light of our results, we discuss the general importance of the confluence effect and flooding seasonality on riparian plant diversity.

Methods

Confluences, sites, and quadrats

The study was conducted around 11 vegetated confluences within the Mukogawa River basin system (Fig. 4-1). The basin area is 500 km^2, and the total river length is 65.7 km (Hyogo Prefecture, 2007). The study confluences are all located within approximately the middle of the Mukogawa River basin system and are surrounded by mainly suburban and/or agricultural areas. Many of the river banks are constructed of concrete. Although the tributaries of the 11 study confluences varied in size (the smallest being a few meters wide and traversable by foot, and the largest being almost the same width as the main stream), I accounted for this variation in the statistical analyses (see *Data analysis* section). At each confluence, I established up-confluence (up-C) and down-confluence (down-C) sites (Fig. 4-2). Four belt transects consisting of five 1.4 × 1.4 m quadrats each were laid out perpendicular to the flow direction at each site (Fig. 4-2). The four belts were established on one side of the river because access was often only possible from one side. If both sides were accessible, we selected the more easily accessible side. In total, 440 quadrats were established.

The distance between upper and lower transects was the same among belts at each confluence but varied among confluences (the mean and range were ~60 m and ~40-90 m, respectively). Within each confluence site, the sizes of conglomerate sand (ø: 0.063~2.0 mm) and gravel (ø: 2.0~64 mm) underlying the vegetation were almost identical. Three native perennials, *Artemisia indica* Willd. var. *maximowiczii* (Nakai) H.Hara (*A. indica*), *Phragmites australis* (Cav.) Trin. ex Steud (*P. australis*), and *Phragmites japonica* Steud (*P. japonica*) were found most frequently within the 440 quadrats.

Species richness and area of bare ground

We investigated species diversity and the area of bare ground in the summer (from late August to late September 2007) and spring (from early May to early June 2008). In the Mukogawa River basin system, peaks of flow volume occur in early spring (ca. March-April) and early summer (ca. July-August) almost every year (Appendix. 4-2). Sampling was conducted immediately following these periods. We listed all plant species found in each quadrat and recorded the proportion of quadrat area covered by each species. The proportion of area covered by all species was <1.00 in all quadrats. We categorized listed species based on life form (annual, perennial herb, or woody plant), flowering season, and origin (native or non-native) (Appendix. 4-1). Our categories followed the "Wild flowers of Japan" series (Satake *et al.* 1981, 1982a, b) and "Plant invader 600" (Shimizu *et al.* 2001). We also recorded the proportion of bare ground in each quadrat. Because directly measuring the degree of disturbance is often difficult (Pollock *et al.* 1998), we used the area of bare ground as an index of flood disturbance, i.e., we assumed that a large area of bare ground indicated the occurrence of strong flood disturbance.

Fig.4-1

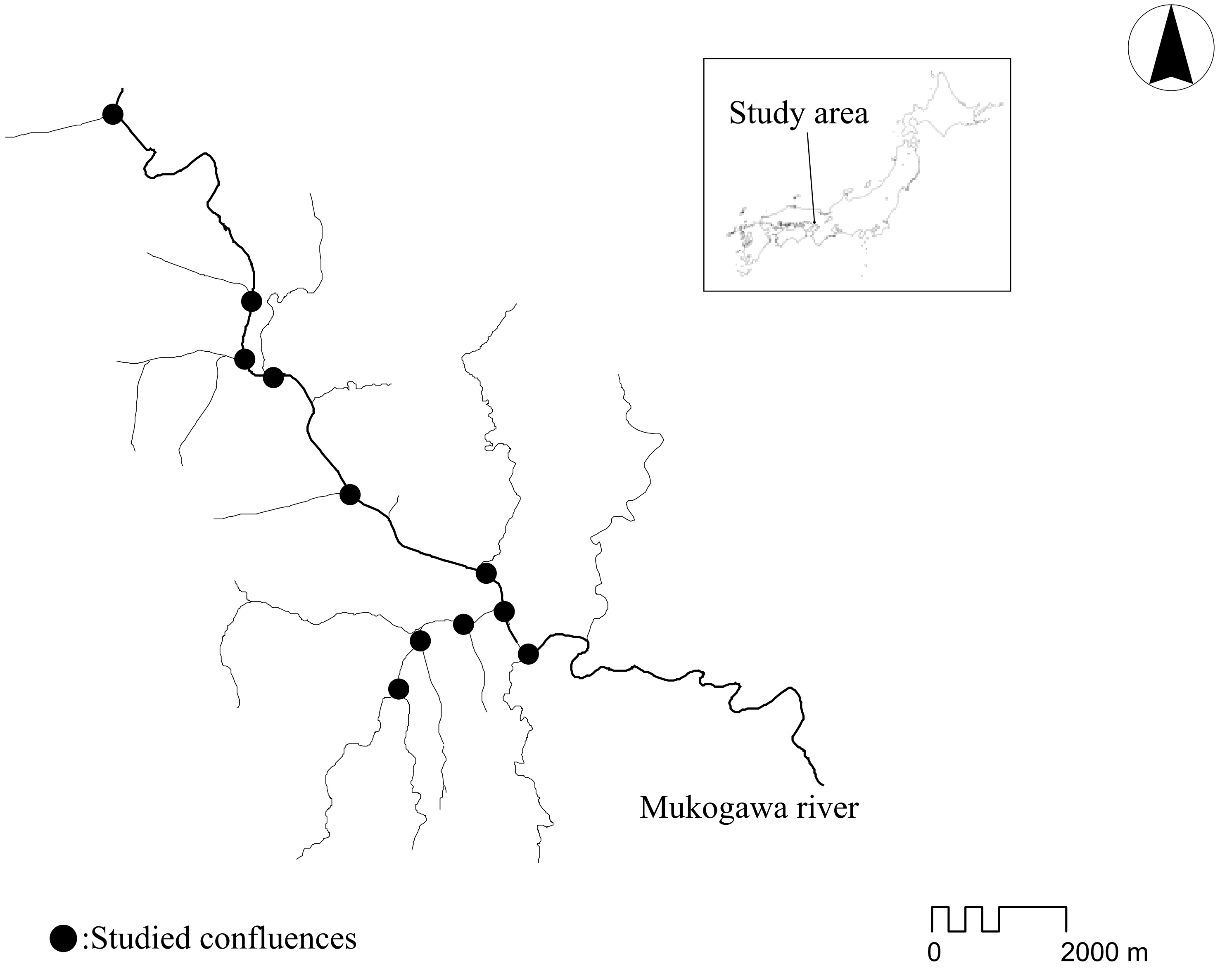


Fig. 4-1 Locations of the 11 study confluences.
The thick line indicates the main stream of the Mukogawa River.

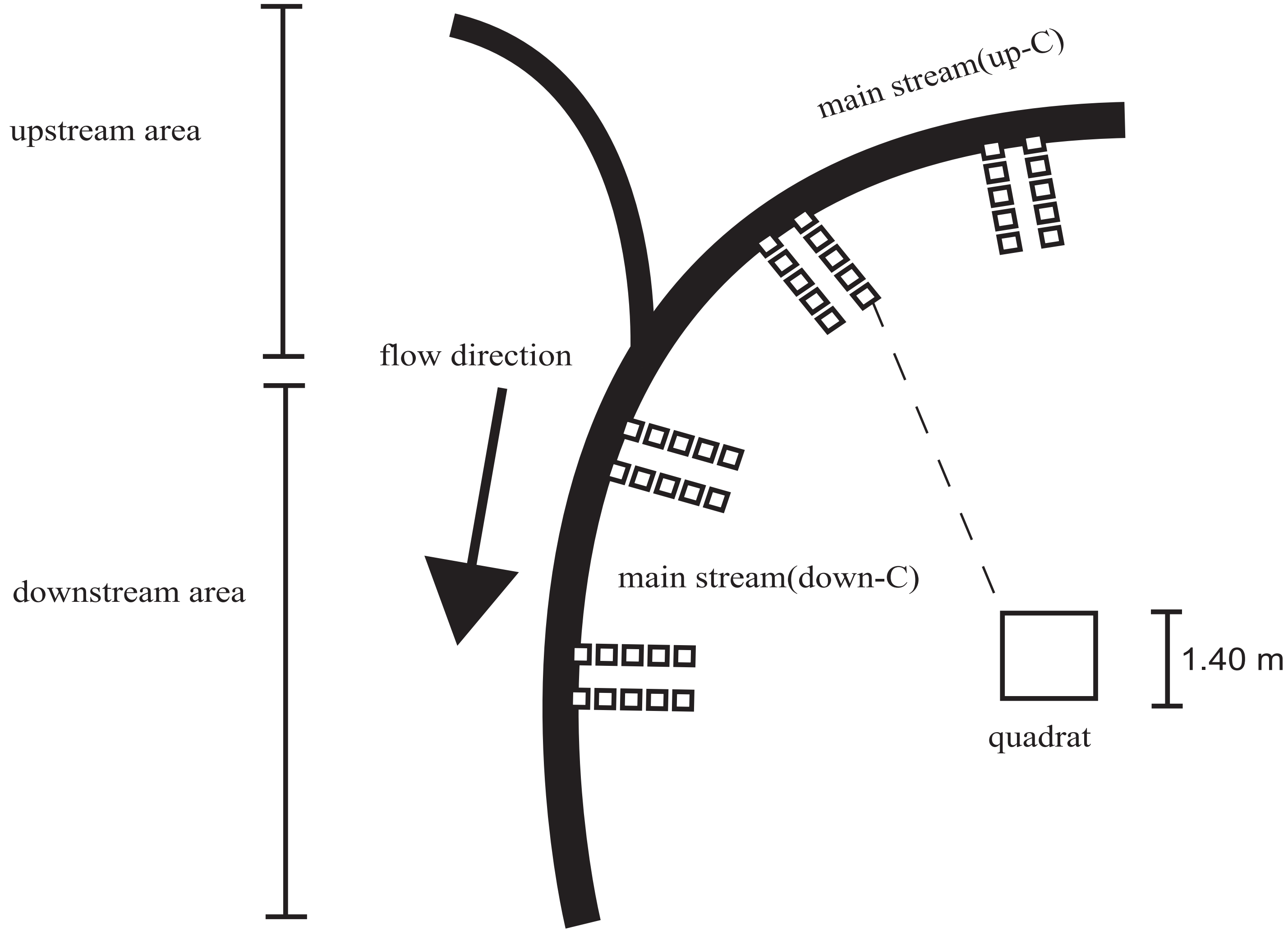


Fig. 4-2 Study areas and quadrats within a confluence. One up-confluence (up-C) and one down-confluence (down-C) site were established at each confluence. Four belt transects consisting of five quadrats (1.4 × 1.4 m) each were laid out perpendicular to the flow direction at each site. The thick and thin lines indicate the main streams and tributaries, respectively. Quadrats within transects were numbered 1, 2, 3, 4, and 5 from the river bank landwards.

Data analysis

For each quadrat, species richness (total species number) and the numbers of annual, perennial (herb), native, and non-native species were calculated. Although I could not identify several Poaceae and Cyperaceae and small seedlings (approximately five species in the spring and 14 in the summer) to the species level, I included these individuals in analyses of species richness when I was able to determine morphospecies. I excluded data for these unidentified species in analyses of life form and origin. Perennial species did not include woody plants. Shannon (*H*') and Simpson (*D*) diversity indices for total species in each quadrat based on species cover (proportion of area). Diversity indices were calculated as follows:

$$H'_x = -\sum_{i=1}^{\mathrm{N}} (\mathrm{a}i / \mathrm{A}x) \ln(\mathrm{a}i / \mathrm{A}x)$$

$$D_x = 1 - \sum_{i=1}^{\mathrm{N}} (\mathrm{a}i / \mathrm{A}x)^2$$

where *x* is the identifier for each quadrat, N is the species number within the quadrat, A is the total area covered by all species in the quadrat, and a*i* is the area covered by species *i*. The cover area for each species in each quadrat was calculated as the proportion of covered area for each species multiplied by 1.96 (1.4 × 1.4 m). For each quadrat, I also calculated the area of bare ground, which was the proportion of bare ground multiplied by 1.96.

I used generalized linear mixed effect models (GLMM) with Poisson errors and a Wald test to examine the effects of site position (up-C or down-C), study season (spring or summer), quadrat position (from riverside landward: 1, 2, 3, 4, and 5 on an ordinal scale), and their interactions on species richness and the numbers of annual, perennial, native, and non-native species. I also applied GLMMs with Gaussian errors and a Wald test to examine site, season, quadrat position, and their interactions on Shannon (H') and Simpson (D) diversity indices and the area of bare ground. Areas of bare ground were log transformed. Data from up-C and the spring were used in the GLMMs as baselines for comparisons. I incorporated confluence identity into the models as a random term to account for differences among confluences in non-measured environmental factors such as tributary size and the number of artificial constructions around the confluence.

All analyses were conducted using the statistical package R ver. 2.6.1 (R Development Core Team 2008).

Results

I identified 121 and 105 plant species in the spring and summer, respectively, for a total of 164 (110 native and 54 non-native) species (Appendix1). The numbers of annual, perennial, and woody species were 85, 72, and seven, respectively (Appendix1). Thirty-eight (23%) species were found at more than five confluences (Appendix1).

GLMM analyses indicated that species richness, Shannon's *H*', and Simpson's *D* were significantly higher at down-C sites in the summer compared to other sites and seasons (Fig. 4-3a, b, c, Table 4-1). The two diversity indices were significantly lower at down-C sites than at up-C sites (Table 4-1) and were lowest at down-C sites in the spring (Fig. 4-3b, c).

The numbers of annual and native species were highest at down-C sites in the summer (Fig. 4-4a, c, Table 4-1), corresponding to the pattern of species richness. The number of perennial species was significantly lower at down-C sites and in the summer than at up-C sites and in the spring, respectively (Table 4-1), although the differences were very small (Fig. 4-4b). The number of non-native species was higher at up-C sites in the spring and at down-C sites in the summer than for other combinations of site and season (Fig. 4-4d, Table 4-1). Quadrat position significantly negatively affected the number of native species (Table 1), indicating by high native species diversity near the waterline.

The area of bare ground at down-C sites was significantly larger than at up-C sites both in the spring and summer and was significantly smaller in the summer (Fig. 4-5, Table 4-1) and in quadrats farthest from the river waterline (Table 4-1). The interaction between down-C sites and quadrat position significantly negatively affected the area of bare ground (Table 4-1).

Neither species richness nor the area of bare ground at up-C sites was correlated with the distance from the nearest upstream confluence (species richness: $F = 0.41$, $df = 358$, $p = 0.52$; area of bare ground: $F = 2.66$, $df = 358$, $p = 0.10$), indicating that the physical environment of each confluence was not affected by the nearest upstream confluence.

Table4-1. GLMM tests for the effects of site position, study season, quadrat position, and their interactions on species richness, two diversity indices, the numbers of annual, perennial, native, and non-native species, and the area of bare ground. Values are estimated coefficients and standard errors (in parentheses). Summer refers to August/September 2007, and Significant effects identified by Wald tests are provided (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$).

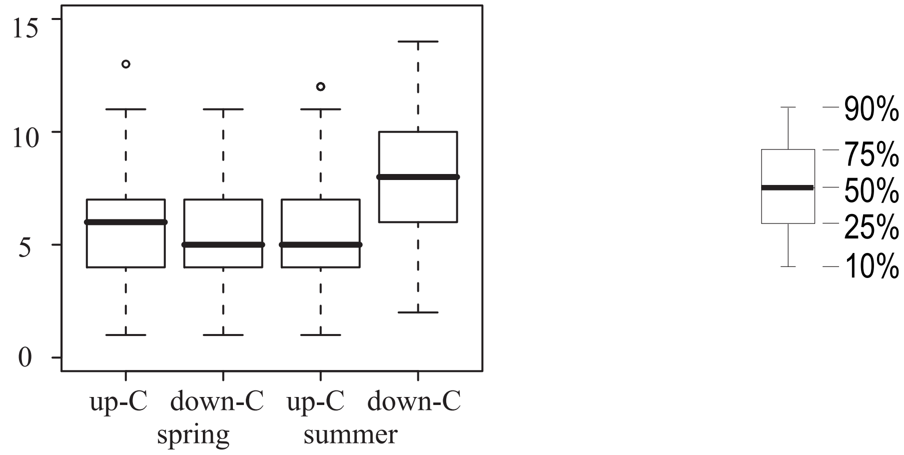
Response variables	Site (down-C)[a]	Season (summer)[b]	Quadrat[c]	Site x Season[d]	Site x Quadrat	Season x Quadrat	Site x Season x Quadrat
Species richness	-0.14	-0.016	-0.019	0.46 ***	0.031	-0.0046	-0.022
	(0.094)	(0.092)	(0.019)	(0.13)	(0.028)	(0.028)	(0.039)
Shannon *H′*	-0.33 ***	-0.10	0.0018	0.60 ***	0.044	-0.0046	-0.019
	(0.096)	(0.096)	(0.021)	(0.14)	(0.029)	(0.029)	(0.041)
Simpson *D*	-0.15 ***	-0.034	-0.0024	0.19 ***	0.015	-0.0021	0.0019
	(0.036)	(0.036)	(0.0077)	(0.051)	(0.011)	(0.011)	(0.015)
Annual species	-0.019	0.34 *	-0.047	0.46 *	0.034	0.015	-0.082
	(0.15)	(0.14)	(0.033)	(0.19)	(0.045)	(0.042)	(0.058)
Perennial species	-0.30 *	-0.48 ***	-0.014	0.37	0.048	-0.00067	0.034
	(0.13)	(0.14)	(0.026)	(0.196)	(0.039)	(0.043)	(0.059)
Native species	-0.057	0.053	-0.058 *	0.34 *	0.038	0.00036	-0.017
	(0.12)	(0.12)	(0.027)	(0.16)	(0.037)	(0.037)	(0.050)
Non-native species	-0.24	-0.29	-0.036	0.65 **	0.0044	-0.022	-0.035
	(0.17)	(0.18)	(0.034)	(0.25)	(0.051)	(0.053)	(0.074)
Bare ground area	5378.86 ***	-2277.16 **	-461.05 **	-1043.70	-839.68	266.38	110.03
	(766.57)	(766.58)	(163.43)	(1084.10)	(231.13)	(231.13)	(326.87)

[a] A positive value for coefficient indicates that the response valiable is higher at down-C sites than at up-C sites.

[b] A positive value for coefficient indicates that the response valiable is higher in summer than in spring.

Fig.4-3

(a) Total species number



(b) Shannon (H’) diversity index

(c) Simpson (D) diversity index

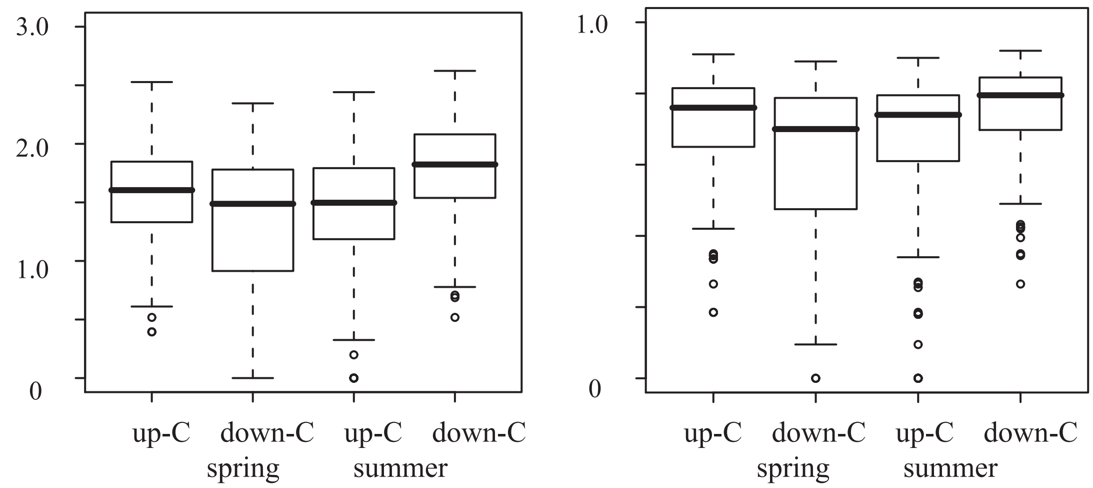
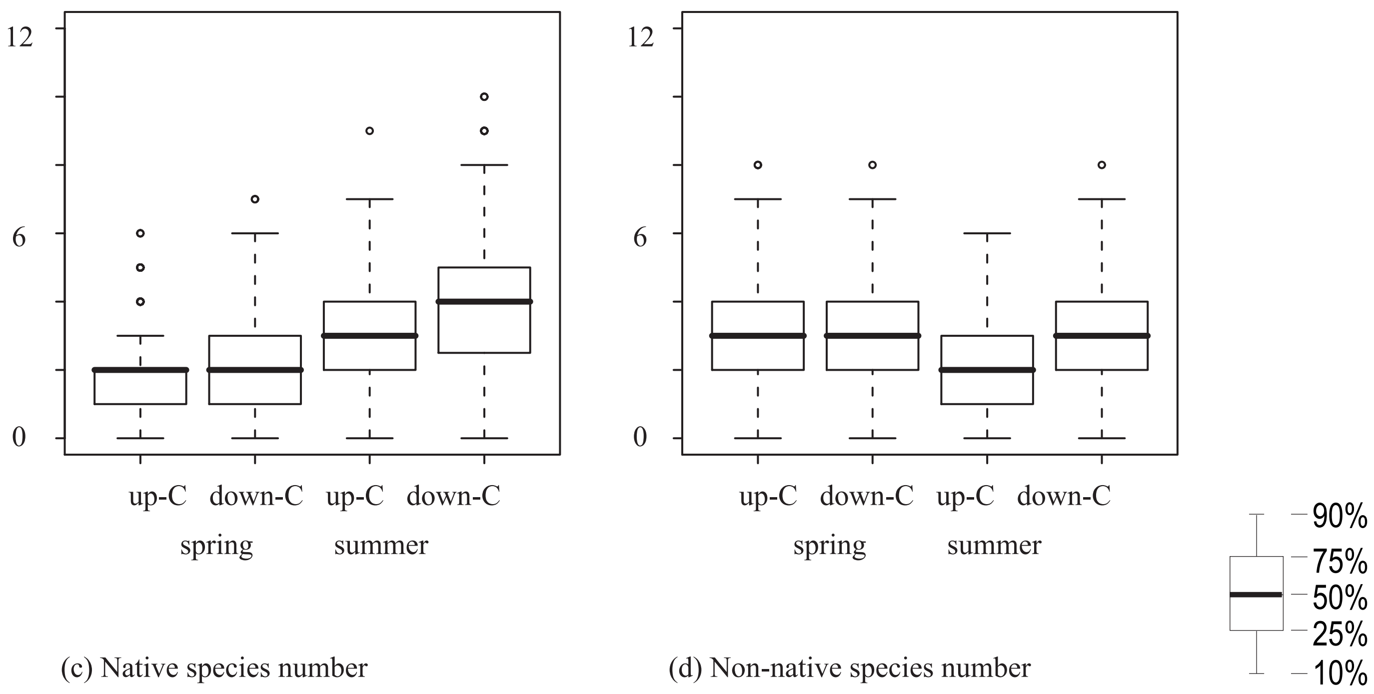


Fig. 4-3 Plant species richness and plant diversity indices [Shannon (*H'*) and Simpson (*D*)] for the 440 quadrats in the 11 confluences. The box plot represents the 75th, 50th, and 25th percentiles; the top bar ranges from the 75th to the 90th percentile, and the bottom bar from the 25th to the 10th percentile. Open circles represents outlier values from the 10th to 90th percentiles. Up-C and down-C indicate positions upstream and downstream of confluences, respectively. Spring and summer data were collected from early May to early June 2008 and from late August to late September 2007, respectively.

Fig.4-4

(a) Annual species number

(b) Perennial species number



(c) Native species number

(d) Non-native species number

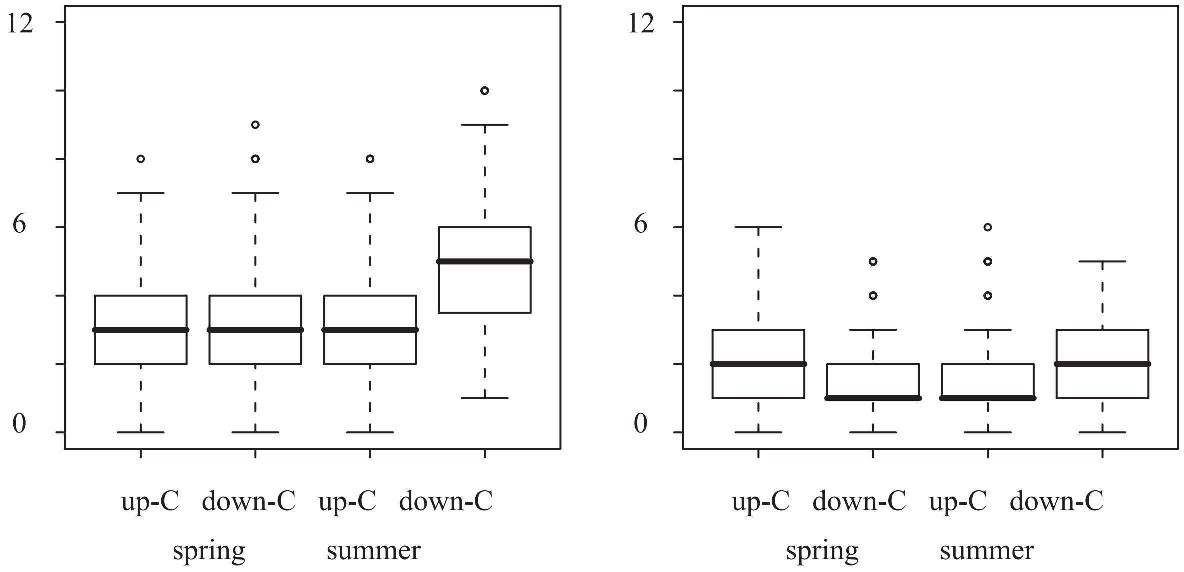


Fig. 4-4 Numbers of annual, perennial, native, and non-native species in the 440 quadrats at the 11 confluences. The box plot represents the 75th, 50th, and 25th percentiles; the top bar ranges from the 75th to the 90th percentile, and the bottom bar from the 25th to the 10th percentile. Open circles represents outlier values from the 10th to 90th percentiles. Up-C and down-C indicate positions upstream and downstream of confluences, respectively. Spring and summer data were collected from early May to early June 2008 and from late August to late September 2007, respectively.

Fig.4-5

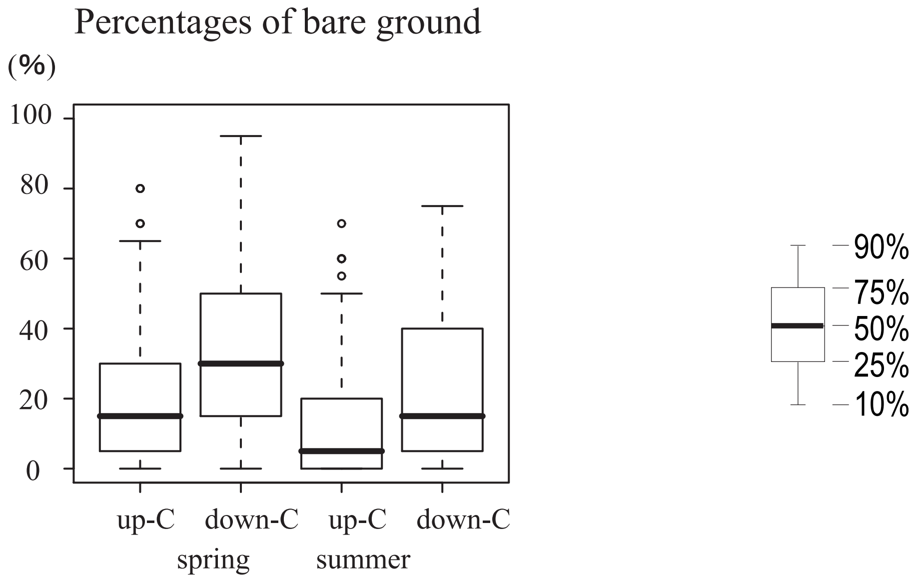


Fig. 4-5 Percentages of natural bare ground in the 440 quadrats at the 11 confluences. The box plot represents the 75th, 50th, and 25th percentiles; the top bar ranges from the 75th to the 90th percentile, and the bottom bar from the 25th to the 10th percentile. Open circles represents outlier values from the 10th to 90th percentiles. Up-C and down-C indicate positions upstream and downstream of confluences, respectively. Spring and summer data were collected from early May to early June 2008 and from late August to late September 2007, respectively.

Discussion

Species richness and the two diversity indices were highest at down-confluence areas in the summer in the Mukogawa river basin system (Fig. 4-3, Table 4-1). This finding supports my hypothesis that plant species diversity is associated with confluences and with the flooding season in riparian areas. For riparian plant communities, this study is the first to support the river discontinuum perspective, which emphasizes the importance of river confluences for biodiversity (Benda *et al.* 2004b).

Mechanisms by which plant diversity increases at down-confluence areas in the summer

Based on my results, the mechanisms by which plant species diversity increases at down-C sites in the summer in the Mukogawa river basin system likely include the extensive creation of bare ground by flooding disturbance at down-C sites as well as the strong recruitment of annual plant species in the summer. My results suggest that the extent of natural bare ground reflects the amount of active water movement (i.e., floodings), thus providing an appropriate index of flooding disturbance. According to the results for the area of bare ground, flooding effects varied spatially around confluences, with down-C sites suffering more severely (Fig. 4-5). Additionally, the area of natural bare ground increased with decreasing distance from the waterline (Table 1: the negative value of the estimated coefficient for quadrat position). Moreover, the interaction between site and quadrat position influenced the area of natural bare ground (Table 4-1: the negative value of the estimated coefficient of site × quadrat), indicating a large gradient of flooding effects immediately downstream of confluences. Thus, the existence of confluences appears to provide a non-uniform distribution of bare ground along the river line.

At down-confluence areas, species richness, Shannon (*H'*) and Simpson (*D*) diversity indices significantly increased only in the summer and tended to be lower in the spring (Fig. 4-3, Table 4-1). Thus, the confluence effect enhanced species diversity only during the plant growing season (i.e., summer). The number of annual species increased in the summer, especially at down-C sites, in synchrony with species richness (Fig. 4-4a), whereas perennial species did not increase at down-C sites or in the summer (Fig. 4-4b). These results suggest that increased species richness in the summer was due to the high recruitment of annual species. Most annual species at the study sites bloom during the summer and autumn (Appendix. 4-1); therefore, their growth activity likely increases in the summer. The decreased area of bare ground in the summer might imply high growth activity of annual plants in the summer. Annual species may originate from both seed banks and seeds carried by flooding water (Naiman & Decamps 1997; Washitani 2001), although demographic information for these species is very limited in Japan (cf. Washitani 2001). To better develop myunderstanding of the mechanisms affecting plant diversity around confluences, additional research should examine differences in recruitment and establishment between annual and perennial species and between up- and down- confluence areas.

My data revealed that very few species were found only at down-C sites in the summer (Appendix. 4-1), suggesting that summer disturbances do not create unique habitats within down-C sites. Hence, the temporal and seasonal matching between the creation of wide areas of bare ground and the peak growth season of annual species led to high species diversity at down-confluence areas in the summer in the Mukogawa river basin system. Because my study was conducted at spatially and temporally limited scales, further studies should be conducted in other riparian ecosystems to improve the generality of the confluence effect hypothesis.

Conservation of flooding disturbance around confluences

In this chapter, I demonstrated that flooding disturbances contribute more to plant species diversity immediately downstream of confluences. Although non-native species, especially annuals, often dominate after disturbances in riparian zones (Naiman & Decamps 1997; Brooks 1999; Miyawaki & Washitani 2004; Richardson *et al.* 2007), our results indicated that the confluence effect led to increases in the diversity of native annual species rather than that of non-native species (Fig. 4-4a, c, d). Thus, river confluences may generally play an important role in increasing and maintaining native plant diversity. Despite this role, river confluences are often artificially modified with concrete constructions (see chapter 6). Such habitat alteration typically results in the breakdown of many ecological processes (Ward *et al.* 1999; Nilsson & Berggren 2000; Ward & Tockner 2001; Washitani 2001). So following study, I evaluate river confluences as key habitats for riparian plant diversity and should strive to keep the ecological processes of these systems free of anthropogenic effects (see Chapter 6).

Appendix 4-1. List of plants species found in the study transects. Data for the origin, life form, and flowering season are provided. All scientific names follow the Ylist (http://bean.bio.chiba-u.jp/bgplants/ylist_main.html). The numbers of sites at which the species were found are also presented. N, native; Non-N, non-native, A, annual herb; P, perennial herb; W, woody plant; Sp, Spring; Su, summer; Au, autumn. Up-C and Down-C indicate up- and down-confluence sites, respectively.

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Aeschynomene indica L.	Non-N	A	Su/Au	0	0	4	6
Ambrosia artemisiifolia L.	Non-N	A	Su/Au	0	0	2	1
Ambrosia trifida L.	Non-N	A	Su/Au	1	0	0	0
Artemisia annua L.	Non-N	A	Su/Au	1	0	0	0
Arthraxon hispidus (Thunb.) Makino	Non-N	A	Su/Au	0	0	0	1
Aster subulatus Michx. var. *subulatus*	Non-N	A	Su/Au	0	0	3	4
Astragalus sinicus L.	Non-N	A	Sp/Su	2	1	0	0
Avena fatua L.	N	A	Su	6	5	0	0
Bidens biternata (Lour.) Merr. et Sherff	N	A	Su/Au	8	8	0	0
Bidens frondosa L.	Non-N	A	Su/Au	3	5	4	5
Brassica juncea (L.) Czern.	Non-N	A	Sp	7	9	1	4
Briza maxima L.	Non-N	A	Su	1	0	0	0
Cardamine scutata Thunb.	N	A	Sp/Su	7	8	2	6
Cerastium fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter et Burdet var. *angustifolium*	N	A	Su	2	4	0	0
Chamaesyce maculata (L.) Small	Non-N	A	Su/Au	1	1	1	3
Chamaesyce nutans (Lag.) Small	Non-N	A	Su/Au	0	0	6	7

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Chenopodium album L.	N	A	Su/Au	0	2	0	1
Chenopodium ambrosioides L.	Non-N	A	Su/Au	1	2	4	6
Coix lacryma-jobi L.	N	A	Su/Au	0	0	0	1
Commelina communis L.	N	A	Su/Au	2	1	11	11
Conyza canadensis (L.) Cronquist	Non-N	A	Su/Au	0	0	6	8
Conyza sumatrensis (Retz.) E.Walker	Non-N	A	Su/Au	7	8	6	9
Cosmos sulphureus Cav.	Non-N	A	Su/Au	0	0	0	1
Crassocephalum crepidioides (Benth.) S.Moore	Non-N	A	Su/Au	0	0	1	1
Cuscuta campestris Yuncker	Non-N	A	Su/Au	0	1	0	0
Cyperaceae sp	N	A	Su	0	0	6	7
Desmodium paniculatum (L.) DC.	Non-N	A	Su/Au	0	0	4	3
Digitaria ciliaris (Retz.) Koeler	N	A	Su/Au	1	4	3	3
Draba nemorosa L.	N	A	Sp/Su	1	0	2	2
Eclipta thermalis Bunge	N	A	Su/Au	1	2	2	4
Eleusine indica (L.) Gaertn.	N	A	Su/Au	0	0	4	0
Eragrostis multicaulis Steud.	N	A	Su/Au	0	1	0	0
Erigeron annuus (L.) Pers.	Non-N	A	Su/Au	5	1	1	1
Galium spurium L. var. *echinospermon* (Wallr.) Hayek	N	A	Su	0	2	0	0

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Glycine max (L.) Merr. subsp. *soja* (Siebold et Zucc.) H.Ohashi	N	A	Su/Au	5	5	7	9
Gnaphalium affine D.Don	N	A	Sp/Su	0	2	0	0
Hemistepta lyrata Bunge	N	A	Su	0	1	0	0
Humulus scandens (Lour.) Merr.	N	A	Su/Au	7	4	8	9
Ipomoea triloba L.	Non-N	A	Su/Au	0	0	0	1
Justicia procumbens L. var. *procumbens*	N	A	Su/Au	0	0	1	2
Kummerowia striata (Thunb.) Schindl.	N	A	Su/Au	0	0	0	1
Lactuca indica L.	N	A	Su/Au	0	0	1	4
Lamium amplexicaule L.	N	A	Sp/Su	1	0	0	0
Lamium purpureum L.	Non-N	A	Su	2	2	0	0
Lindernia procumbens (Krock.) Borb?s	N	A	Su/Au	1	0	2	3
Lolium multiflorum Lam.	Non-N	A	Su	2	2	0	0
Ludwigia epilobioides Maxim.	N	A	Su/Au	2	2	1	6
Mazus pumilus (Burm.f.) Steenis	N	A	Sp/Su/Au	2	1	0	0
Monochoria vaginalis (Burm.f.) C.Presl	N	A	Su/Au	0	0	1	1
Mosla scabra (Thunb.) C.Y.Wu et H.W.Li	N	A	Su/Au	0	0	0	1
Myosotis scorpioides L.	Non-N	A	Sp/Su	0	1	1	0
Oenothera biennis L.	Non-N	A	Su/Au	0	1	4	2
Oenothera glazioviana Micheli	Non-N	A	Su/Au	1	0	0	0

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Oxalis dillenii Jacq.	N	A	Su/Au	4	3	1	0
Panicum bisulcatum Thunb.	N	A	Su/Au	0	0	1	0
Papaver dubium L.	Non-N	A	Sp/Su	0	3	0	0
Perilla frutescens (L.) Britton var. *crispa* (Thunb.) H.Deane	N	A	Su/Au	2	0	0	1
Persicaria lapathifolia (L.) Delarbre	N	A	Su/Au	3	0	2	7
Persicaria longiseta (Bruijn) Kitag.	N	A	Su/Au	2	5	10	11
Persicaria sagittata (L.) H.Gross var. sibirica (Meisn.) Miyabe	N	A	Su/Au	0	0	1	1
Persicaria senticosa (Meisn.) H.Gross	N	A	Su/Au	0	0	1	2
Persicaria thunbergii (Siebold et Zucc.) H.Gross	N	A	Su/Au	6	8	5	8
Picris hieracioides L. subsp. ja*ponica* (Thunb.) Krylov	N	A	Su/Au	0	0	1	3
Poa annua L.	Non-N	A	Sp/Su/Au	1	4	0	1
Portulaca oleracea L.	N	A	Su/Au	0	0	2	2
Ranunculus sceleratus L.	N	A	Sp	0	2	0	0
Sagina japonica (Sw.) Ohwi	N	A	Sp/Su	1	1	0	0
Senecio vulgaris L.	Non-N	A	Su/Au	1	0	0	0
Setaria pumila (Poir.) Roem. et Schult.	N	A	Su/Au	0	0	3	3

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Setaria viridis (L.) P.Beauv.	N	A	Su/Au	0	0	8	8
Sicyos angulatus L.	Non-N	A	Su	0	0	0	1
Sisyrinchium rosulatum E.P.Bicknell	Non-N	A	Sp/Su	0	2	0	0
Solanum ptychanthum Dunal	Non-N	A	Su/Au	0	0	0	1
Sonchus oleraceus L.	N	A	Sp/Su	3	6	0	0
Stellaria media (L.) Vill.	N	A	Sp/Su/Au	4	4	0	0
Stellaria uliginosa Murray var. undulata (Thunb.) Fenzl	N	A	Sp/Su/Au	0	1	0	0
Torilis japonica (Houtt.) DC.	N	A	Su	8	6	0	0
Trapa japonica Flerow	N	A	Su/Au	0	1	0	0
Trifolium dubium Sibth.	Non-N	A	Su	6	6	0	0
Trigonotis peduncularis (Trevir.) Benth. ex Hemsl.	N	A	Sp	2	1	0	0
Veronica arvensis L.	Non-N	A	Sp/Su	0	2	0	0
Veronica persica Poir.	Non-N	A	Sp	4	2	0	0
Vicia hirsuta (L.) Gray	N	A	Sp/Su	3	7	0	0
Vicia sativa L. subsp. *nigra* (L.) Ehrh.	N	A	Sp/Su	5	6	0	0
Xanthium occidentale Bertol.	Non-N	A	Su/Au	2	2	7	7
Achyranthes bidentata Blume var. *fauriei* (H.Lev. et Vaniot)	N	P	Su/Au	4	3	7	9

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Agrimonia pilosa Ledeb. var. *japonica* (Miq.) Nakai	N	P	Su/Au	0	0	0	1
Artemisia capillaris Thunb.	N	P	Su/Au	0	0	3	4
Artemisia indica Willd. var. *maximowiczii* (Nakai) H.Hara	N	P	Su/Au	11	11	10	10
Boehmeria silvestrii (Pamp.) W.T.Wang	N	P	Su/Au	3	6	10	11
Boehmeria spicata (Thunb.) Thunb.	N	P	Su/Au	0	0	1	0
Calystegia hederacea Wall.	N	P	Su	0	0	1	0
Calystegia pubescens Lindl.	N	P	Su	0	0	1	0
Carex dimorpholepis Steud.	N	P	Su	1	0	0	0
Carex kobomugi Ohwi	N	P	Sp/Su	1	0	0	0
Cayratia japonica (Thunb.) Gagnep.	N	P	Su	4	1	3	3
Cicuta virosa L.	N	P	Su	1	0	0	0
Clinopodium gracile (Benth.) Kuntze	N	P	Su	0	0	1	1
Desmodium podocarpum DC. subsp. *oxyphyllum* (DC.) H.Ohashi	N	P	Su/Au	0	0	0	1
Dioscorea japonica Thunb.	N	P	Su	0	2	0	1
Duchesnea chrysantha (Zoll. et Moritzi) Miq.	N	P	Sp	1	0	0	0
Dunbaria villosa (Thunb.) Makino	N	P	Su/Au	1	0	0	2

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Elymus tsukushiensis Honda var. *transiens* (Hack.) Osada	N	P	Su	3	2	0	0
Epilobium pyrricholophum Franch. et Sav.	N	P	Su/Au	2	2	0	0
Equisetum arvense L.	N	P	Sp	5	4	2	4
Equisetum hyemale L.	N	P	Sp	0	0	0	1
Eragrostis ferruginea (Thunb.) P.Beauv.	Non-N	P	Su/Au	3	1	0	0
Erigeron philadelphicus L.	Non-N	P	Sp/Su	4	5	0	0
Fallopia japonica (Houtt.) Ronse Decr.	N	P	Su/Au	0	1	0	0
Galium japonicum Makin	N	P	Su	7	7	0	1
Geranium thunbergii Siebold ex Lindl. et Paxton	N	P	Su/Au	2	4	0	2
Geum japonicum Thunb.	N	P	Su	1	0	0	0
Helianthus tuberosus L.	Non-N	P	Su/Au	5	2	3	4
Houttuynia cordata Thunb.	N	P	Su	1	0	0	1
Hydrocotyle sibthorpioides Lam.	N	P	Su/Au	2	2	1	1
Iris pseudacorus L.	Non-N	P	Su	3	2	0	0
Ixeridium dentatum (Thunb.) Tzvelev	N	P	Su	3	2	0	0
Juncus decipiens (Buchenau) Nakai	N	P	Su/Au	0	2	1	2
Leersia japonica (Honda) Makino ex Honda	N	P	Su/Au	0	1	0	0
Lespedeza cuneata (Dum.Cours.) G.Don	N	P	Su/Au	1	5	3	8

Appendix4-1. Continued

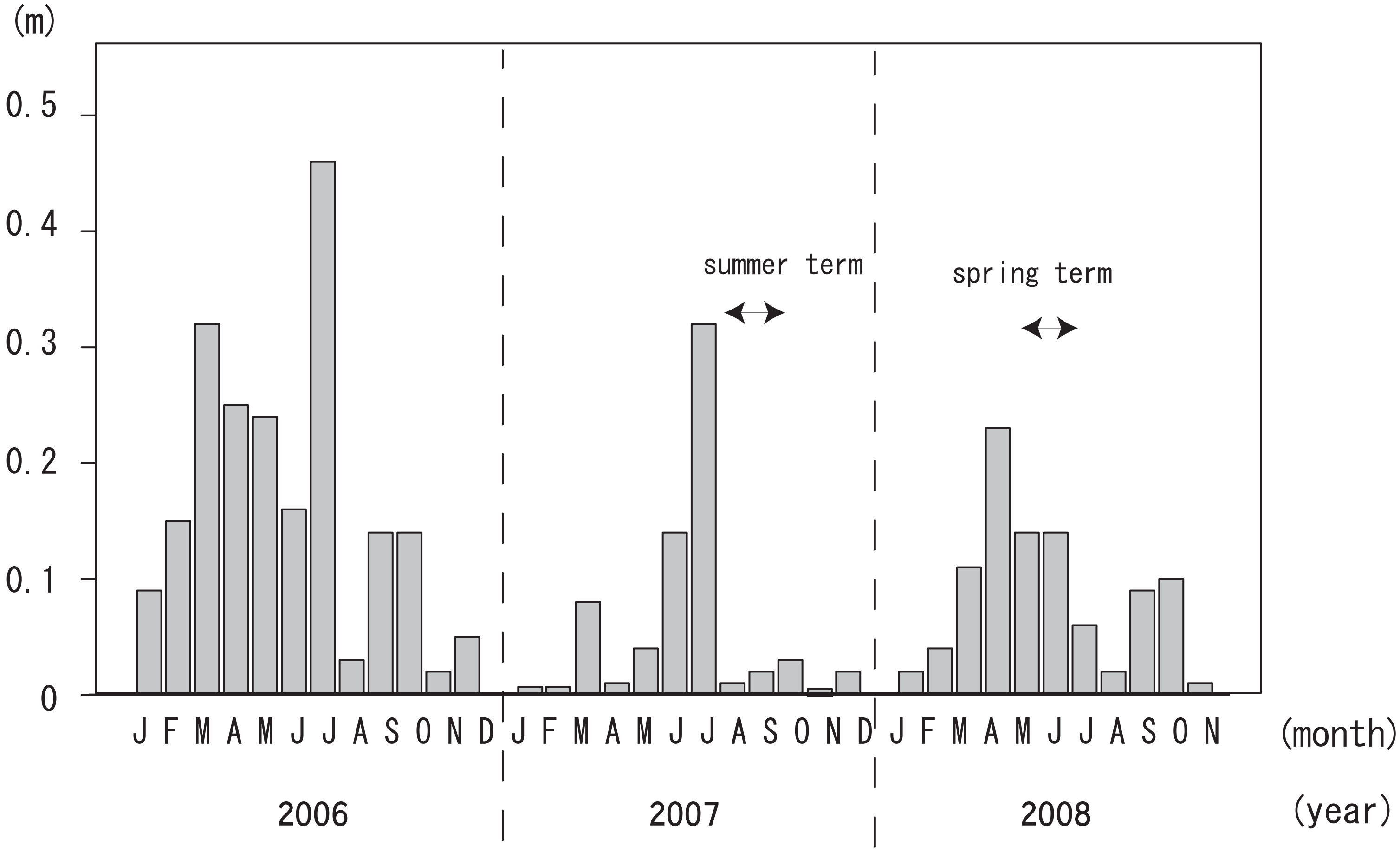
Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Lobelia chinensis Lour.	N	P	Su/Au	0	0	1	0
Luzula kjellmanniana Miyabe et Kud?	N	P	Su/Au	7	7	0	0
Lycopus lucidus Turcz. ex Benth.	N	P	Su/Au	1	2	1	2
Lythrum anceps (Koehne) Makino	N	P	Su/Au	0	0	1	0
Mentha arvensis L. subsp. *arvensis*	N	P	Su/Au	2	2	0	0
Metaplexis japonica (Thunb.) Makino	N	P	Su	0	2	1	2
Miscanthus sinensis Andersson	N	P	Su/Au	1	0	2	2
Oenanthe javanica (Blume) DC.	N	P	Su	4	4	3	5
Oenothera speciosa Nutt.	Non-N	P	Su	2	0	0	0
Oxalis corniculata L.	N	P	Su/Au	0	2	3	6
Paederia scandens (Lour.) Merr.	N	P	Su/Au	1	0	1	2
Paspalum distichum L.	Non-N	P	Su/Au	4	2	6	6
Phragmites australis (Cav.) Trin. ex Steud.	N	P	Su/Au	10	10	6	8
Phragmites japonica Steud.	N	P	Su/Au	3	6	5	6
Phytolacca americana L.	Non-N	P	Su/Au	0	1	0	1
Plantago asiatica L.	N	P	Sp/Su/Au	1	1	1	1
Plantago lanceolata L.	Non-N	P	Sp/Su	2	2	2	1
Potentilla freyniana Bornm.	N	P	Sp	2	2	1	1
Pueraria lobata (Willd.) Ohwi	N	P	Su/Au	5	5	3	6

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Ranunculus silerifolius H.Lev. var. *glaber* (H.Boissieu) Tamura	N	P	Sp/Su	1	4	0	0
Rorippa indica (L.) Hiern	N	P	Sp/Su/Au	0	3	0	0
Rubia argyi (H.Lev. et Vaniot) H.Hara ex Lauener	N	P	Su/Au	1	0	0	0
Rumex acetosa L.	N	P	Su	3	3	0	1
Rumex japonicus Houtt.	N	P	Su	3	4	3	0
Sagittaria pygmaea Miq.	N	P	Su/Au	0	0	0	1
Sanicula chinensis Bunge	N	P	Su/Au	0	0	0	1
Schoenoplectus triqueter (L.) Palla	N	P	Su/Au	1	1	0	0
Sedum sarmentosum Bunge	Non-N	P	Su	0	1	0	0
Sedum sarmentosum Bunge	Non-N	P	Su	0	2	0	0
Solidago altissima L.	Non-N	P	Au	6	4	1	1
Taraxacum officinale Weber ex F.H.Wigg.	Non-N	P	Sp/Su	2	1	0	0
Trifolium pratense L.	Non-N	P	Su/Au	4	2	3	1
Trifolium repens L.	Non-N	P	Sp/Su/Au	6	4	3	4
Typha latifolia L.	N	P	Su	0	0	1	1
Verbena bonariensis L.	Non-N	P	Su/Au	0	0	2	0
Verbena brasiliensis Vell.	Non-N	P	Su/Au	1	0	0	0
Veronica anagallis-aquatica L.	Non-N	P	Sp/Su	7	7	0	0

Appendix4-1. Continued

Species name	**Origin**	**Life form**	**Flowering season**	**Up-C in spring**	**Down-C in spring**	**Up-C in summer**	**Down-C in summer**
Albizia julibrissin Durazz.	N	W	Su	1	0	1	1
Ampelopsis glandulosa (Wall.) Momiy. var. *heterophylla* (Thunb.) Momiy.	N	W	Su	2	0	0	1
Deutzia crenata Siebold et Zucc.	N	W	Su	0	0	0	2
Indigofera pseudotinctoria Matsum.	N	W	Su	0	0	0	2
Robinia pseudoacacia L.	Non-N	W	Su	1	1	0	0
Rosa multiflora Thunb.	N	W	Su	1	1	1	3
Salix miyabeana Seemen subsp. *gymnolepis* (H.Lev. et Vaniot) H.Ohashi et Yonek.	N	W	Sp	5	2	3	5



Water level variation in the Mukogawa River from January 2006 to November 2008.
Mean monthly water heights are presented. Arrows indicate the terms when our research was undertaken. Water heights observation was taken every day. The data set was provided by the government of Hyogo Prefecture.

Chapter V

Field research approach II: Relative importance of neutral and niche process on plant community assemblage is seasonally changes around downside river confluences.

Abstract

The study of mechanisms structuring community has been a central issue in ecology. In this chapter, I examined similarities of riparian plant communities around eleven confluences of Mukogawa river basin system to test neutral and niche hypotheses on community structuring. I found that the community similarity was not different between two up-confluence area pairs and up- and down-confluence area pairs in summer, supporting the neutral theory. On the other hand, the community similarity significantly decreased in up- and down-confluence areas in spring, supporting the niche theory. Natural bare grounds were more widely distributed at down-confluence areas than up-confluence areas, and more widely in spring than in summer, suggesting that there was a difference in disturbance regime between these areas and seasons. My results showed that neutral process becomes obvious in plant growing season and in frequently disturbed riparian areas, suggesting that spatial and seasonal matching between open space creation and dispersal activity is the key to promote neutrality.

要約

生物群集がどのように集合しているのかを明らかにすることは、群集生態学の根本的な疑問の一つである。本章では兵庫県武庫川水系における１１箇所の合流点で、合流をはさむ組み合わせ、はさまない組み合わせそれぞれの類似度を比較することで、群集集合が中立説に従うのか、ニッチ説に従うのかを検証した。その結果、植物の生育シーズンにあたる夏の群集組成は合流をはさむ組み合わせ、はさまない組み合わせで類似度に差がなく、中立説に従っていることが示唆された。対して春には、合流をはさむ組み合わせ、はさまない組み合わせで類似度に差があり、ニッチ説に従っていることが示唆された。自然裸地の面積は、合流後、春でそれぞれ合流前、春より広いことが示された。以上の結果から、河川敷における植物群集の集合における中立過程は、植物の生育シーズンで、かつ頻繁に撹乱が起こる場所が両立する条件下において強く作用することが示唆された。

Introduction

The study of mechanisms structuring community has been a central issue in ecology. Two well-known theories, neutral and niche theories, have been proposed to explain how community assembly is structured in natural ecosystems (Gilbert & Lechowicz 2004; Thompson & Townsend 2006; Paine & Harms 2009; Rominger *et al.* 2009). The neutral theory assumes no difference in ecological traits among species and emphasizes the role of random dispersal processes in structuring local communities and speciation-extinction events in structuring large-scale meta-communities (Hubbell 2001, 2003; Thompson & Townsend 2006; Paine & Harms 2009; Rominger *et al.* 2009). In contrast, the niche theory describes local communities as non-random sets of species sorted based on their physiologically and competitively defined niches (Silvertown 2004; Thompson & Townsend 2006; Paine & Harms 2009; Rominger *et al.* 2009). Evaluating which of these alternative theories best explains the assembly of natural biological communities is a source of debate (e.g., (Gilbert & Lechowicz 2004; Silvertown 2004; Etienne 2005; Etienne & Olff 2005; Alonso *et al.* 2006; McGill *et al.* 2006; Thompson & Townsend 2006; Paine & Harms 2009; Rominger *et al.* 2009).

The neutral and niche theories make diametrically opposed assumptions about the importance of species traits in determining species composition, abundance and diversity patterns (Hubbell 2001; Silvertown 2004). Under the neutral theory assuming that random extinction and dispersal limitation dominate the spatial distribution of species, the similarity of species composition and abundance between two sample points is predicted to decrease with the distance between them, irrespective of any co-varying environmental factors (Condit *et al.* 2002; Thompson & Townsend 2006; Morlon *et al.* 2008). Under the niche theory, local-scale species composition and abundance should remain relatively constant across environmentally uniform distance gradients (e.g., transects through homogeneous space), but should change along gradients where environmental change is autocorrelated with distance (Condit *et al.* 2002; Thompson & Townsend 2006; Morlon *et al.* 2008; Rominger *et al.* 2009). Because of this difference in the predicted distance-community similarity pattern between neutral and niche theories, examining spatial variation in community structure (i.e., species composition and abundance) is an increasingly popular approach to understanding the relative importance of neutral and niche processes ((Condit *et al.* 2002; Gilbert & Lechowicz 2004; Thompson & Townsend 2006).

Spatial variation in community structure has been examined both for experimental (Stanley Harpole & Tilman 2006; Paine & Harms 2009) and natural communities (Thompson & Townsend 2006; Rominger *et al.* 2009), but it is often difficult to divide the effects of distance and the environmental changes along the distance because the distance between sites is often positively correlated with differences in local ecological conditions (Gilbert & Lechowicz 2004). Although such an approach is only valid when local conditions and spatial separation are independent of one another, it is very difficult in practice (Thompson & Townsend 2006). To understand the relative importance of neutral and niche processes, thus, the communities establishing very close to each other but on different environmental conditions should be examined in the fields.

River confluences, which are nodes of river networks, provide the ideal system to test the neutral and niche hypotheses. Although basal ecological conditions change gradually along the streams, the conditions drastically change around river confluences within a short distance (Benda *et al.* 2004). For instance, contributory area of the river and stream water volume abruptly increases and water temperature may rise or drop drastically below the confluences when tributary streams have a large flow and different water temperature from the main stream. When we have heavy rain and sequent freshet, dramatic change in stream conditions, that is, flooding and subsequent habitat alternation would occur more frequently at just downstream areas of confluences (down-confluence areas) than at upstream areas (up-confluence areas). Under these conditions, neutral theory predicts that similarities of plant communities between two different up-confluence areas and between up- and down-confluence areas are equal to each other. On the other hands, niche theory predicts that a lower community similarity is found between up- and down-confluence areas than between two up-confluence areas because of difference in local ecological conditions between up- and down–confluence areas. These predictions are worth testing in order to elucidate the relative importance of neutral and niche processes in riparian communities.

Recently, some studies indicate that both the neutral and niche theories explain local community structure simultaneously and that the relative importance of neutral and niche processes is different among functional groups within communities (Thompson & Townsend 2006); Rominger et al 2009). These studies imply that the mechanism of structuring community assembly was different among species with different traits within communities (Paine & Harms 2009). Thus, I should examine a difference in sensitivity to neutral and niche processes pool and divide among functional groups of the community.

In this chapter, I examined similarities of riparian plant communities around eleven confluences of Mukogawa river basin system in Hyogo Prefecture, Japan to test neutral and niche hypotheses on community structuring. Species richness differed between up- and down-confluence areas in these confluences (Osawa et al. unpublished data). First, I compared a similarity of whole plant communities between two up-confluence areas to that between up- and down-confluence areas within each confluence to examine relative importance of neutral and niche processes. Second, I divide plant species into 8 functional groups (Van der Maarel 2005), and compared similarities of each functional group between two up-confluence area pair and up- and down-confluence area pair to examine differences in community structuring mechanism among functional groups. I then discuss the role of neutral and niche processes in shaping riparian plant communities around confluences.

Methods

Confluences, sites, and quadrats

The study was conducted around 11 vegetated confluences within the Mukogawa River basin system (Fig. 5-1). The basin area is 500 km^2, and the total river length is 65.7 km (Hyogo Prefecture, 2007). The study confluences are all located within approximately the middle of the Mukogawa River basin system and are surrounded by mainly suburban and/or agricultural areas. Many of the river banks are constructed of concrete. Although the tributaries of the 11 study confluences varied in size (the smallest being a few meters wide and traversable by foot, and the largest being almost the same width as the main stream), I accounted for this variation as random effects in the statistical method (see *Statistical analysis* section).

At each confluence, I established two up-confluence sites (up-Ca and up-Cb) and a single down-confluence (down-C) sites (Fig. 5-2). Two belt transects consisting of five 1.4 × 1.4 m quadrats each were laid out perpendicular to the flow direction at each site and total 6 belt transects were set at each confluence (Fig. 5-2). All belts were established primarily on the main stream side. If mainstream sides were not accessible, I selected the tributary side. Consequently, I set sites on the mainstream side in 5 confluences and the tributary side in 6 confluences. In these 6 confluences where study sites were set on tributary side, tributary size were not extremely small compare to main streams. In total, I set up 330 quadrats around 11 confluences. The distances between up-Ca and up-Cb belt transects and between up-Cb and down-C belt transects were the same at each confluence but varied among confluences (the mean and range were ~60 m and ~40-90 m, respectively). Within each confluence, the sizes of conglomerate sand (ø: 0.063~2.0 mm) and gravel (ø: 2.0~64 mm) underlying the vegetation were almost identical.

Fig. 5-1

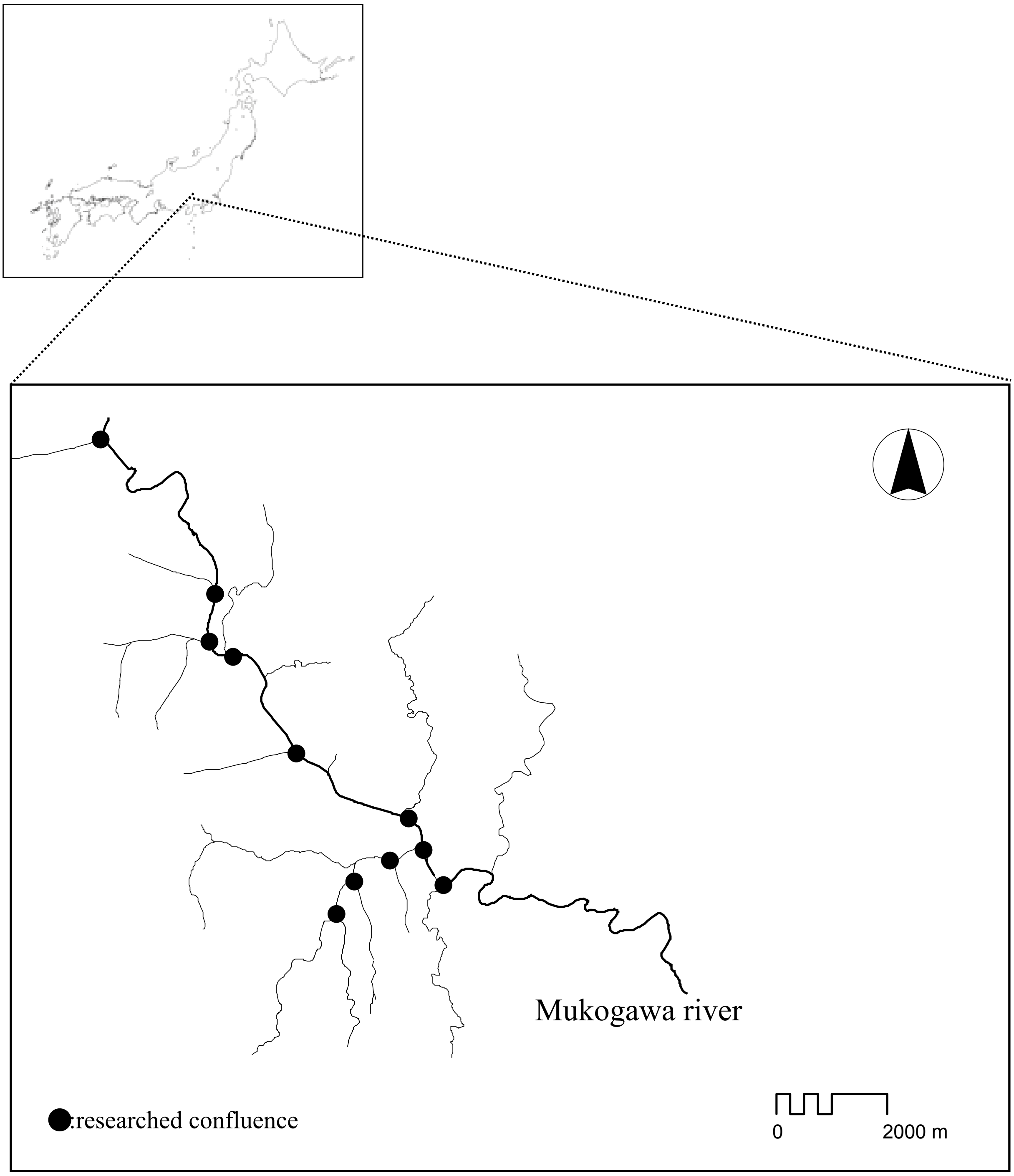


Fig. 5-1. Locations of the 11 studied confluences. The thick line indicates the main stream of the Mukogawa River.

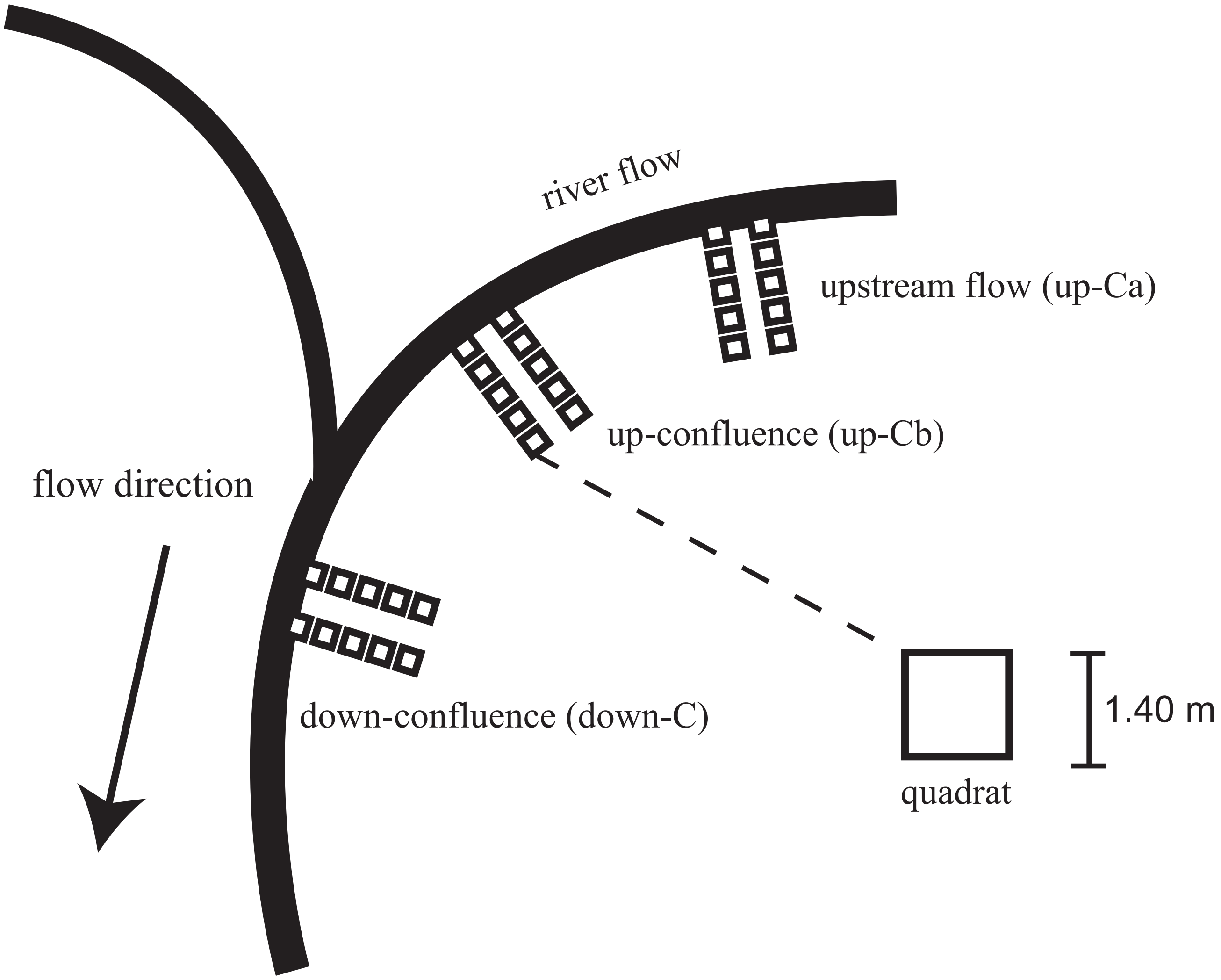


Fig. 5-2. Study areas and quadrats within a confluence. We established upside-stream flow (up-F), upside-confluence (up-C), and downside-confluence (down-C) sites at each confluence. Each belt transects consisting of ten quadrats (1.4 x 1.4 m) each were laid out at right angles to the flow direction at each site.

Community structure and bare ground area

I investigated community structure (species component and abundance) in the summer (from late August to late September 2007) and spring (from early May to early June 2008) for each quadrat. In the Mukogawa River basin system, peaks of flow volume occur in early spring (ca. March-April) and early summer (ca. July-August) almost every year. Sampling was conducted immediately following these periods to examine the effect of floodings as ecological conditions on community structures. I listed all plant species found in each quadrat and recorded the proportion of quadrat area covered by each species. I categorized listed species into 8 functional groups based on life form and morphology (annual forb, grass and vine, perennial ferm, forb, grass and vine and woody species) (Appendix 5-1). My categories followed the "Wild flowers of Japan" series (Satake *et al.* 1981, 1982a, b; Satake *et al.* 1989a, b). I identified two perennial ferm species, I included data of perennial ferns in analyses of whole communities, but did not examine a similarity of this functional group solely. I did not examine a similarity of annual vines solely in spring because less than 3 species were found in all confluences. Although I could not identify several Poaceae and Cyperaceae and small seedlings (approximately 14 species in the spring and 12 in the summer) to the species level, I included these individuals in analyses of whole of communities when I were able to determine morphospecies. These un-identified species were not dominant species. I totalized plant data of five guadrats as each belt transects data.

I recorded the areas of natural bare ground in each belt. Because direct measurement of the degree of disturbance is often difficult (Pollock *et al.* 1998), I used the proportion of bare ground area as an index of flood disturbance, i.e., I assume that a large bare ground area indicates the occurrence of strong flood disturbance.

Similarity index

I calculated Bray-Curtis dissimilarity index (BCDI) of plant species composition between four up-Ca and up-Cb belt transect pairs (up-up pairs) and between four up-Cb and down-C transect pairs (up-down pairs) from each confluence data set. I then calculated similarity index as 1 – BCDI.

Statistical analysis

I used generalized linear mixed effect models (GLMMs) with Gaussian error distribution (identity link) and a likelihood ratio test to examine the difference in similarity index of whole community and each functional group between up-up and up-down pairs. In the models, the similarity index of whole community or each functional group was considered as a response variable. The exploratory variables were the type of pairs (up-up or up-down, fixed effect). Additionally I incorporated confluence identity into the models as a random term to account for differences among confluences in non-measured environmental factors such as tributary size and the number of artificial constructions around the confluence. The neutral theory predicts no difference in the similarity index between up-up and up-down pairs, whereas the niche theory predicts a significant decrease in the similarity index in up-down pairs compared to up-up pairs.

I also applied GLMMs with Gaussian error distribution (identity link) and a likelihood ratio test to examine the effects of site position (up-Ca, up-Cb or down-C) and season (summer or supring) on the proportion of natural bare ground area.

All analyses were done with the statistical package R ver. 2.7.1 (R Development Team, 2008).

Results

Plant species composition and natural bare ground

I identified 127 and 130 plant species in summer and spring, respectively and total species number was 185 (Table 5-1). The numbers of summer-unique and spring-unique species were 58 and 55, respectively. The species-rich functional groups were annual and perennial forbs (Table 5-1). There was no large difference in the number of species for each functional group between summer and spring (Table 5-1). In summer the most abundant functional group was annual forb and perennial grass and forb followed (Fig. 5-3a). On the other hand, perennial grass was most abundant and followed by annual and perennial forbs in spring (Fig 5-3b).

Natural bare ground areas was significantly lower in summer than that in spring (chi-squared value: 24.98, $p < 0.001$) and significantly differ in site position (chi-squared value: 54.195, $p < 0.001$) (Fig. 5-4).

Similarity index

There was no difference in the similarity index of whole community between up-up and up-down pairs in summer, whereas a significant decrease in the index was found in summer (Fig. 5-5). I also found the same trends for annual grasses, perennial forbs, grasses and vines (Figs. 5-6c, d, 5-7). For annual forbs, there were difference in the similarity index in both seasons, but significantly increase in summer whereas significantly decrease in spring (Fig. 5-6a, b). For woody plants, no difference in the similarity index was found both in summer and spring (Fig. 5-8).

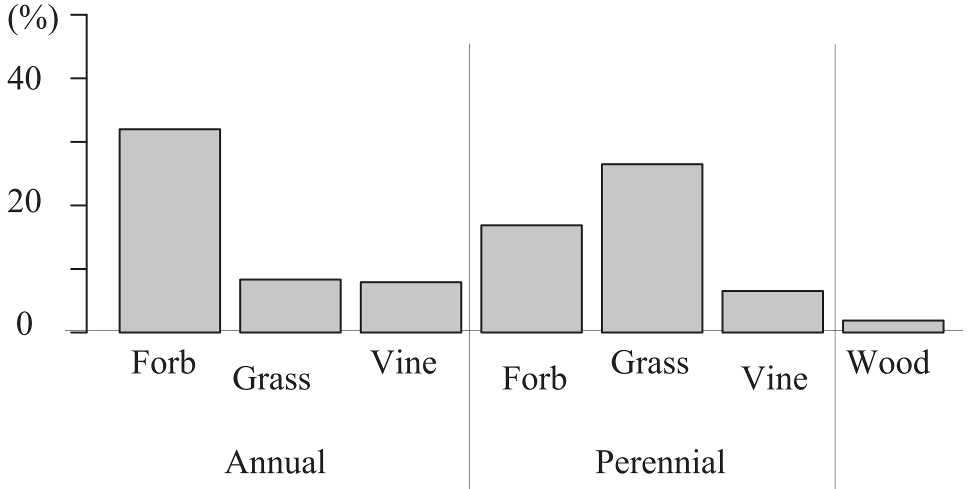
Table 5-1. The number of species for seven functional groups.

Functional groups	Summer	Spring	Total
Annual forb	49	53	74
Annual grass	9	8	15
Annual vine	6	1	6
Perennial forb	39	43	56
Perennial grass	8	13	15
Perennial vine	8	5	8
Wood	8	7	11
Total	127	130	185

Note: function group categolization was referred to "The wilf flower of Japan" series.

Fig. 5-3

(a) Summer



(b) Spring

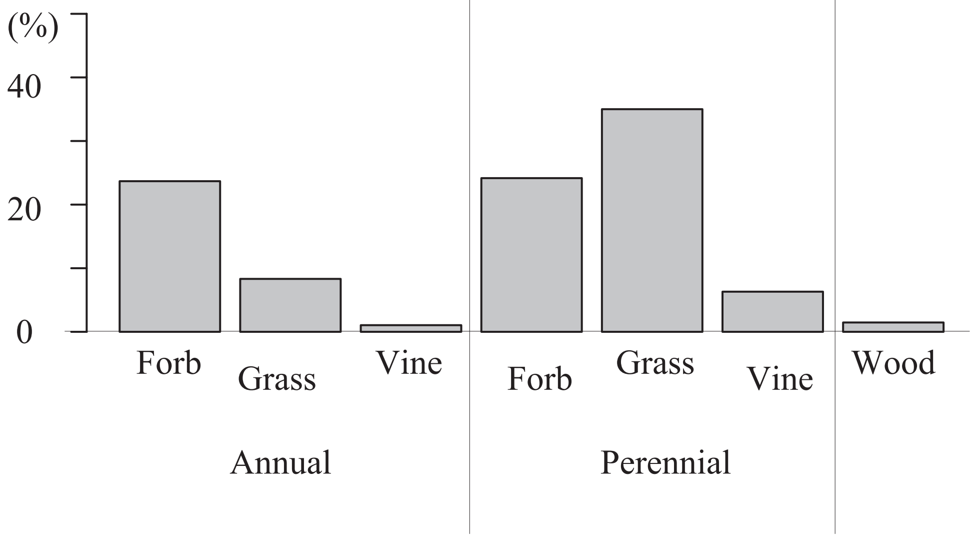


Fig. 5-3. Total percentages of each functional group.

Fig.5-4

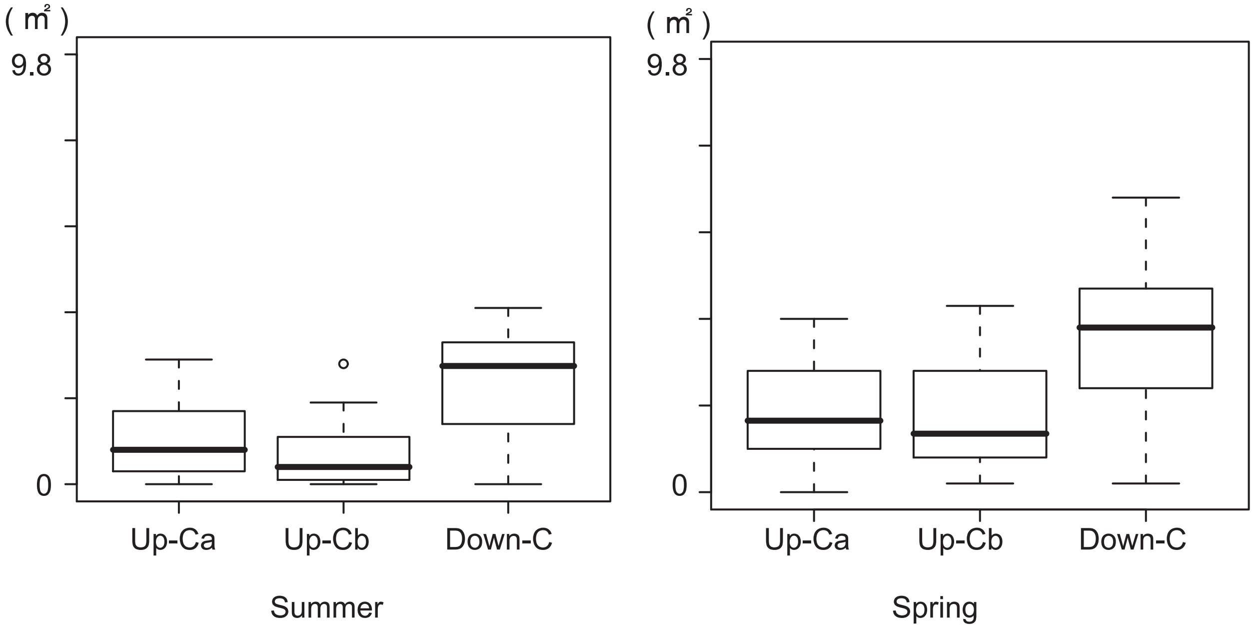


Fig. 5-4. Percentages of bare ground area in each quadrat.

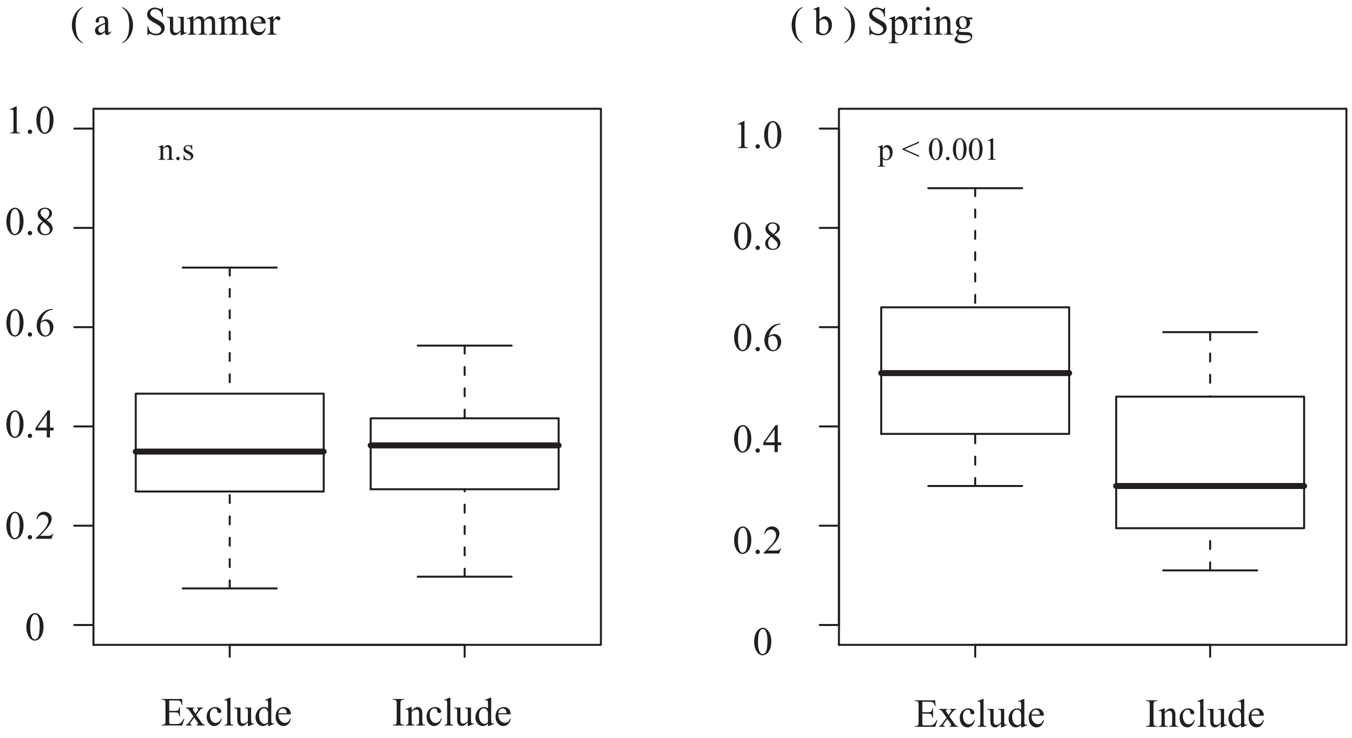
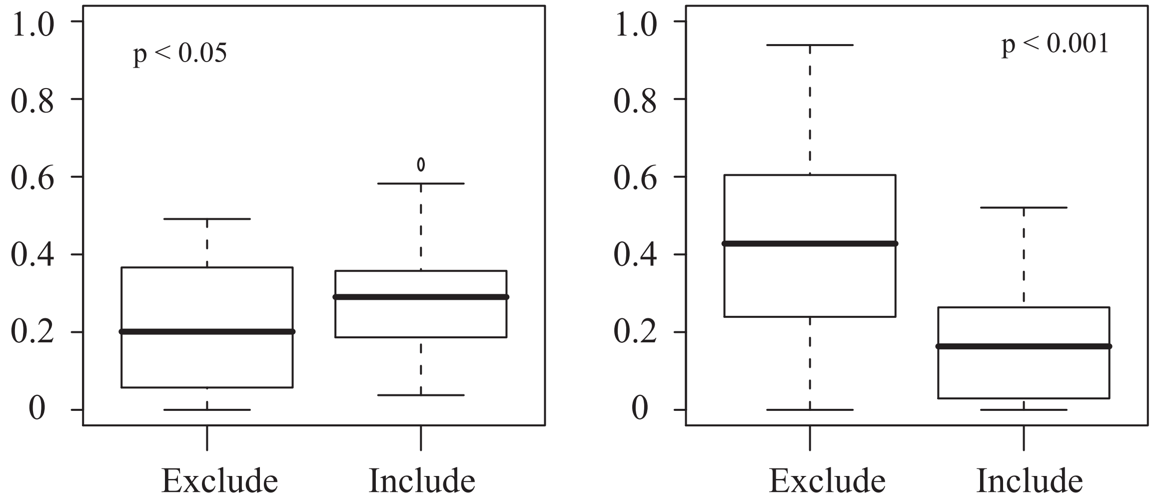
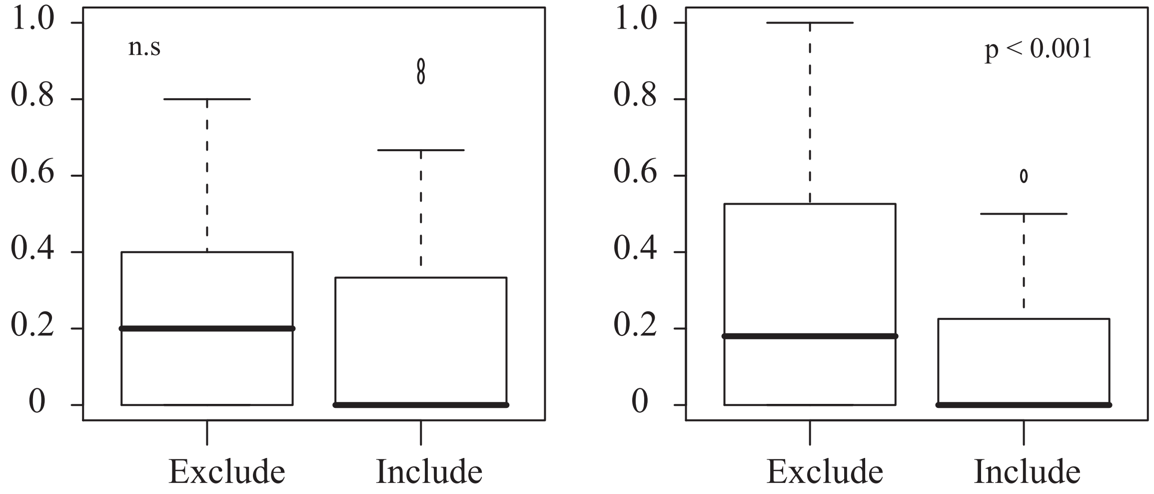


Fig. 5-5. Bray-Cutis similarity index between exclude- and include confluence on all species communities.

Fig. 5-6


(a) Annual forb in summer

(b) Annual forb in spring


(c) Annual grass in summer

(d) Annual grass in spring

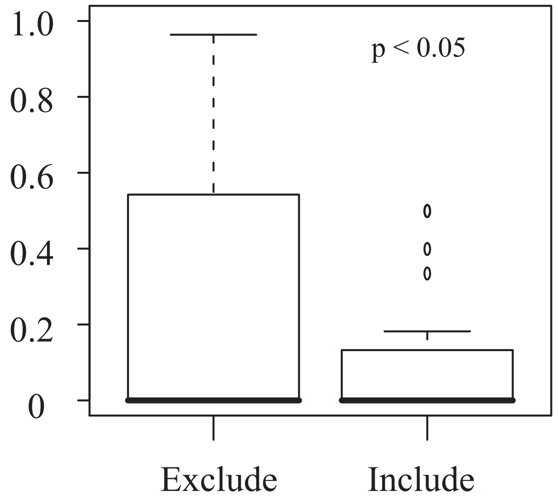
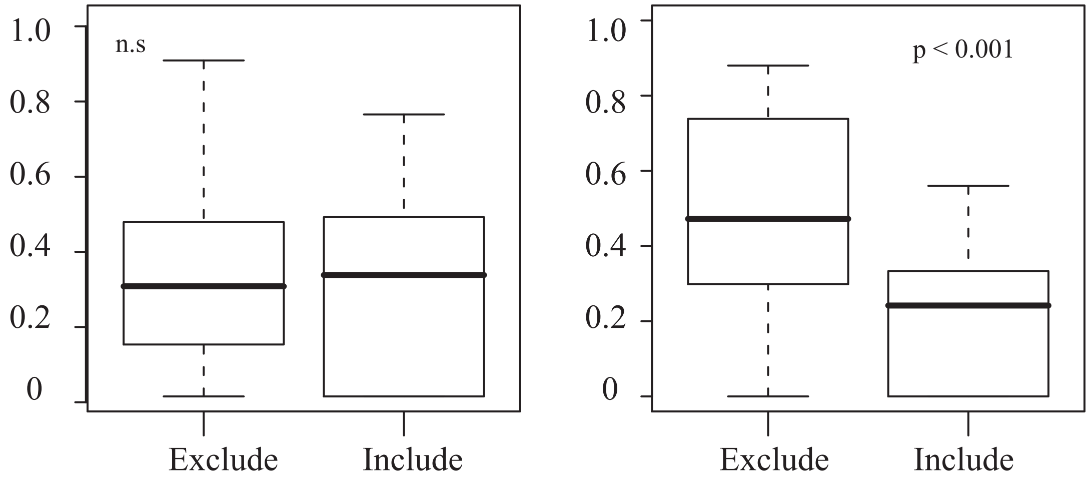
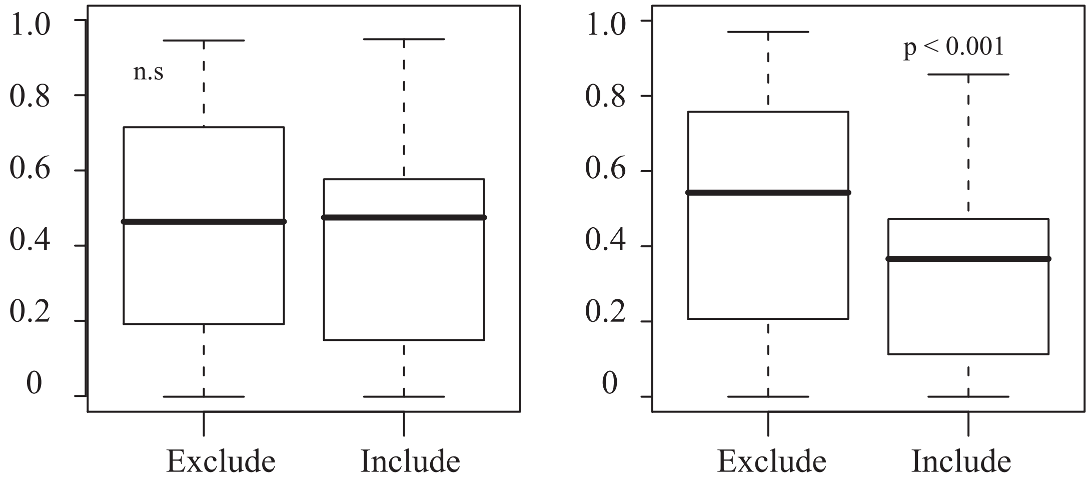

(e) Annual vine in summer

Fig. 5-6. Bray-Cutis similarity index between exclude- and include confluence on annual species communities.

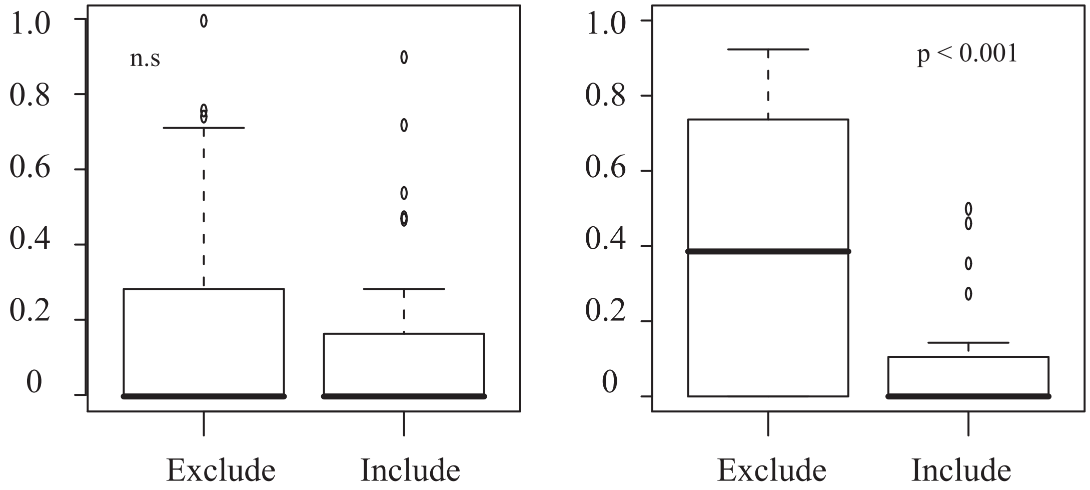
Fig. 5-7


(a) Perennial forb in summer

(b) Perennial forb in spring


(c) Perennial grass in summer

(d) Perennial grass in spring


(e) Perennial vine in summer

(f) Perennial vine in spring

Fig. 5-7. Bray-Cutis similarity index between exclude- and include confluence on perennial species communities.

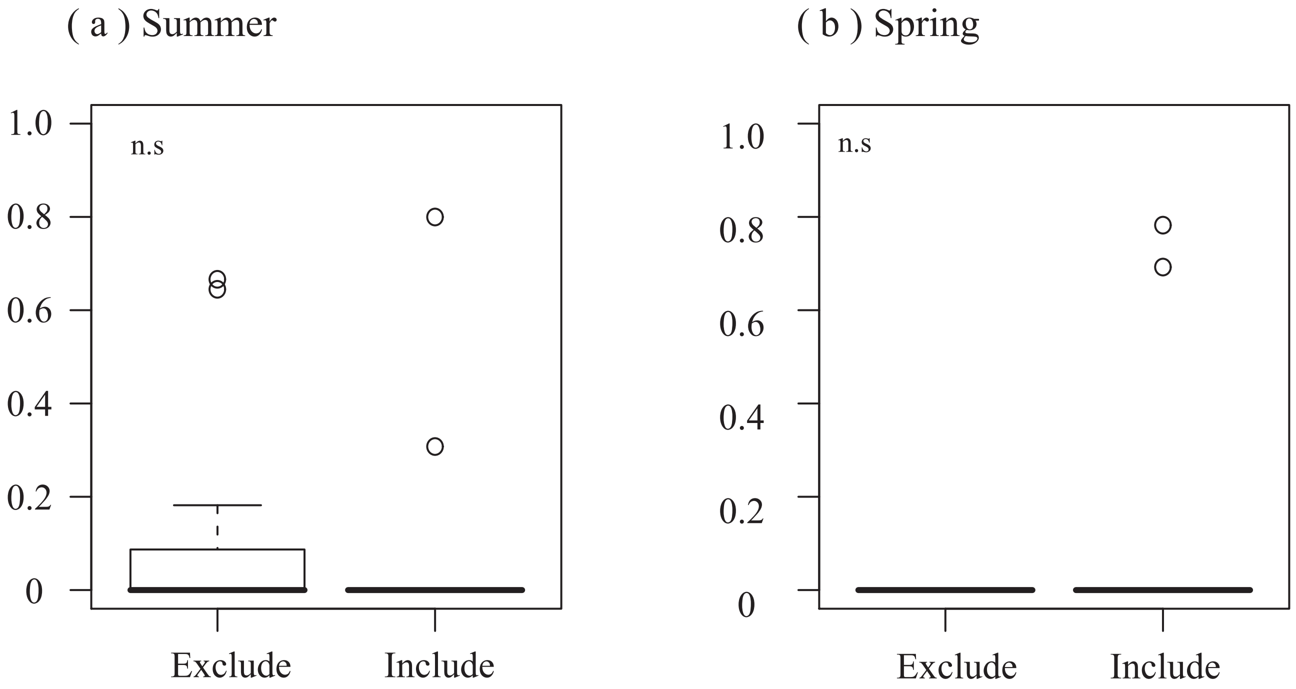


Fig. 5-8. Bray-Cutis similarity index between exclude- and include confluence on woody species.

Discussion

I examined riparian plant species compositions around 11 confluences to test the neutral and niche theories on riparian community structuring in two different seasons, and found the relative importance of neutral and niche processes was different between summer and spring. I found that the community similarity was not different between two up-confluence area pairs and up- and down-confluence area pairs in summer, supporting the neutral theory. On the other hand, the community similarity significantly decreased in up- and down-confluence areas in spring, supporting the niche theory. Natural bare grounds were more widely distributed at down-confluence areas than up-confluence areas, and more widely in spring than in summer, suggesting that there was a difference in disturbance regime between these areas and seasons. Below, I discuss this seasonal change in the mechanisms structuring plant community around river confluences.

My results suggest that in summer, communities were structured in the neutral way whereas niche process became prominent in spring (Fig. 5-5a). Paine & Herms (2009) suggested that neutral and niche assembly processes may vary among the components of an ecological community and dynamically through time (Paine & Harms

2009). In the data set, community compositions (i.e. the relative abundance of functional groups and members of each function groups) differed between seasons (Appendix). The difference in community composition may be responsible to the difference in dominant ecological process between seasons, although I found no large difference in similarity patterns among different functional groups. Moreover, I suggest that differences in plant colonizing and/or growing activities could explain the difference in community structuring between seasons. Generally, flooding during the growing season most strongly affects plant survival (Ferreira & Stohlgren 1999; Vervuren *et al.* 2003; van Eck *et al.* 2004), thus summer floodings would change abundance of established species and create large open space (bare grounds). Strong colonization to open spaces in summer might make neutral process obvious in summer. Annual forb community, which was the most dominant group in summer, had high similarity of up-down pairs compared to up-up pairs (Fig. 6a). These results implicated that anuual forbs dispersal according to neutral process strongly contributed community assemble in summer. On the other hand, plant distribution might be more limited by their competitive ability in spring because plant distribution patterns could be also affected by severe environmental conditions in the previous winter (van Eck *et al.* 2004). This idea should be examined further to control these plant activities experimentally.

Also I ignored seasonal differences in factors other than natural bare ground area, whose effects should be examined in future research.

The similarity patterns of woody plant community were consistent with the prediction of neutral process in both summer and spring. This result might be caused by insufficient data set for abundance of woody species (Fig. 5-3). Further study should be conducted to evaluate this finding.

Many studies (Hubbell 2001; Condit *et al.* 2002; Gilbert & Lechowicz 2004; Harpole & Tilman 2006; Thompson & Townsend 2006; Paine & Harms 2009; Rominger *et al.* 2009) suggested that both neutral and niche processes affect local community structure. My results were consistent with the suggestion. Some of these studies found that the relative importance of neutral and niche processes differs among functional groups within communities (Thompson & Townsend 2006); Rominger et al 2009). However, I found no evidence supporting these findings, although colonizing and growing ability can be different among functional groups. Difference in dispersal limitation among functional groups would be smaller than the difference between seasons. Recent studies of plant community structures have reported no or limited support for neutrality, although plants may be satisfying the requirements of the neutral theory (Thompson & Townsend 2006) and references therein). Those studied communities are established relatively stable (infrequently disturbed) areas, such as rain and boreal forests. My results showed that neutral process becomes obvious in plant growing season and in frequently disturbed riparian areas, suggesting that spatial and seasonal matching between open space creation and dispersal activity is the key to promote neutrality.

Appendix5-1. List of plants species occurring in the studied transects.
All scientific names were based on ylist(http://bean.bio.chiba-u.jp/bgplants/ylist_main.html).

Name	Life form	Function	Identify
Achyranthes bidentata Blume var. *fauriei* (H.L?v. et Vaniot)	perennial	forb	both
Actinostemma tenerum Griff.	annual	vine	summer
Aeschynomene indica L.	annual	forb	both
Agrimonia pilosa Ledeb. var. *japonica* (Miq.) kai	perennial	forb	summer
Albizia julibrissin Durazz.	wood	tree	both
Amaranthus blitum L.	annual	forb	summer
Amaranthus retroflexus L.	annual	forb	summer
Ambrosia artemisiifolia L.	annual	forb	summer
Ambrosia trifida L.	annual	forb	spring
Ampelopsis glandulosa (Wall.) Momiy. var. *heterophylla* (Thunb.) Momiy.	wood	vine	both
Aristolochia debilis Siebold et Zucc.	perennial	forb	summer
Artemisia annua L.	annual	forb	spring
Artemisia capillaris Thunb.	perennial	forb	summer
Artemisia indica Willd. var. *maximowiczii* (kai) H.Hara	perennial	forb	both
Arthraxon hispidus (Thunb.) Makino	annual	grass	summer
Aster ageratoides Turcz. var. *ageratoides*	perennial	forb	summer
Aster subulatus Michx. var. *subulatus*	annual	forb	summer
Astragalus sinicus L.	annual	forb	spring
Ave fatua L.	annual	grass	spring
Ave fatua L. var. *glabrata* Peterm.	annual	grass	spring
Bidens biterta (Lour.) Merr. et Sherff	annual	forb	both
Bidens frondosa L.	annual	forb	both
Boehmeria silvestrii (Pamp.) W.T.Wang	perennial	forb	spring
Boehmeria spicata (Thunb.) Thunb.	wood	shrub	summer
Brassica juncea (L.) Czern.	annual	forb	both
Briza maxima L.	annual	grass	spring
Calystegia hederacea Wall.	perennial	vine	summer
Calystegia pubescens Lindl.	perennial	vine	summer
Cardamine scutata Thunb.	annual	forb	both
Carex dimorpholepis Steud.	perennial	grass	spring
Carex kobomugi Ohwi	perennial	grass	spring
Cayratia japonica (Thunb.) Gagnep.	perennial	forb	both
Cerastium fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter et Burdet var. *angustifoli*	annual	forb	spring

Appendix5-1. Continued

Name	Life form	Function	Identify
Chamaesyce maculata (L.) Small	annual	forb	both
Chamaesyce nutans (Lag.) Small	annual	forb	summer
Chenopodium album L.	annual	forb	both
Chenopodium album L. var. *centrorubrum* Makino	annual	forb	summer
Chenopodium ambrosioides L.	annual	forb	both
Cicuta virosa L.	perennial	forb	spring
Clematis apiifolia DC.	perennial	vine	summer
Clinopodium gracile (Benth.) Kuntze	perennial	forb	summer
Coix lacryma-jobi L.	annual	grass	summer
Commeli communis L.	annual	forb	both
Conyza cadensis (L.) Cronquist	annual	forb	both
Conyza sumatrensis (Retz.) E.Walker	annual	forb	both
Coreopsis lanceolata L.	perennial	forb	summer
Cosmos sulphureus Cav.	annual	forb	summer
Crassocephalum crepidioides (Benth.) S.Moore	annual	forb	summer
Cuscuta campestris Yuncker	annual	vine	summer
Cyperaceae sp	annual	grass	summer
Desmodium paniculatum (L.) DC.	annual	forb	summer
Desmodium podocarpum DC. subsp. *oxyphyllum* (DC.) H.Ohashi	perennial	forb	summer
Deutzia creta Siebold et Zucc.	wood	shrub	summer
Digitaria ciliaris (Retz.) Koeler	annual	grass	both
Dioscorea japonica Thunb.	perennial	vine	both
Draba nemorosa L.	annual	forb	both
Duchesnea chrysantha (Zoll. et Moritzi) Miq.	perennial	forb	spring
Dunbaria villosa (Thunb.) Makino	perennial	vine	both
Eclipta thermalis Bunge	annual	forb	both
Eleusine indica (L.) Gaertn.	annual	grass	summer
Elymus tsukushiensis Honda var. *transiens* (Hack.) Osada	perennial	grass	spring
Epilobium pyrricholophum Franch. et Sav.	perennial	forb	spring
Eragrostis ferruginea (Thunb.) P.Beauv.	perennial	grass	spring
Eragrostis multicaulis Steud.	annual	grass	spring
Erigeron annuus (L.) Pers.	annual	forb	both
Erigeron philadelphicus L.	perennial	forb	both
Fallopia japonica (Houtt.) Ronse Decr.	perennial	forb	spring
Festuca ovi L.	perennial	grass	spring
Galium japonicum Makino	perennial	forb	both
Galium spurium L. var. *echinospermon* (Wallr.) Hayek	annual	forb	both

Appendix5-1. Continued

Name	Life form	Function	Identify
Galium verum L. subsp. *asiaticum* (kai) T.Yamaz. var. *asiaticum* kai f. lacteum (Maxin	perennial	forb	spring
Geranium thunbergii Siebold ex Lindl. et Paxton	perennial	forb	both
Geum japonicum Thunb.	perennial	forb	spring
Glycine max (L.) Merr. subsp. *soja* (Siebold et Zucc.) H.Ohashi	annual	forb	both
Gphalium affine D.Don	annual	forb	both
Helianthus tuberosus L.	perennial	forb	both
Hemistepta lyrata Bunge	annual	forb	spring
Houttuynia cordata Thunb.	perennial	forb	both
Humulus scandens (Lour.) Merr.	annual	vine	both
Hydrocotyle sibthorpioides Lam.	perennial	forb	both
Indigofera pseudotinctoria Matsum.	wood	shrub	summer
Ipomoea triloba L.	annual	vine	summer
Iris pseudacorus L.	perennial	forb	spring
Ixeridium dentatum (Thunb.) Tzvelev	perennial	forb	spring
Juncus decipiens (Bucheu) kai	perennial	grass	both
Justicia procumbens L. var. *procumbens*	annual	forb	summer
Kummerowia striata (Thunb.) Schindl.	annual	forb	summer
Lactuca indica L.	annual	forb	summer
Lamium amplexicaule L.	annual	forb	spring
Lamium purpureum L.	annual	forb	spring
Leersia japonica (Honda) Makino ex Honda	perennial	grass	spring
Lespedeza cuneata (Dum.Cours.) G.Don	perennial	forb	both
Lindernia procumbens (Krock.) Borb?s	annual	forb	both
Lobelia chinensis Lour.	perennial	forb	summer
Lobelia chinensis Lour.	perennial	forb	spring
Lolium multiflorum Lam.	annual	grass	spring
Ludwigia epilobioides Maxim.	annual	forb	both
Luzula kjellmannia Miyabe et Kud?	perennial	grass	both
Lycopus lucidus Turcz. ex Benth.	perennial	forb	both
Lythrum anceps (Koehne) Makino	perennial	forb	summer
Macleaya cordata (Willd.) R.Br.	perennial	forb	summer
Mallotus japonicus (L.f.) M?ll.Arg.	wood	tree	summer
Mazus pumilus (Burm.f.) Steenis	annual	forb	spring
Mentha arvensis L. subsp. *arvensis*	perennial	forb	both
Metaplexis japonica (Thunb.) Makino	perennial	vine	both
Miscanthus sinensis Andersson	perennial	grass	both

Appendix5-1. Continued

Name	Life form	Function	Identify
Monochoria vagilis (Burm.f.) C.Presl	annual	forb	summer
Mosla scabra (Thunb.) C.Y.Wu et H.W.Li	annual	forb	summer
Murdannia keisak (Hassk.) Hand.-Mazz.	annual	forb	summer
Myosotis scorpioides L.	annual	forb	both
Equisetum arvense L.	perennial	ferm	both
Equisetum hyemale L.	perennial	ferm	summer
Oenothera biennis L.	annual	forb	both
Oenothera glaziovia Micheli	annual	forb	both
Oenothera speciosa Nutt.	perennial	forb	spring
Oenthe javanica (Blume) DC.	perennial	forb	both
Oplismenus undulatifolius (Ard.) Roem. et Schult.	annual	grass	spring
Oxalis corniculata L.	perennial	forb	both
Oxalis dillenii Jacq.	perennial	forb	both
Paederia scandens (Lour.) Merr.	perennial	vine	both
Panicum bisulcatum Thunb.	annual	grass	summer
Papaver dubium L.	annual	forb	spring
Paspalum distichum L.	perennial	grass	both
Pennisetum alopecuroides (L.) Spreng.	perennial	grass	summer
Perilla frutescens (L.) Britton var. *crispa* (Thunb.) H.Deane	annual	forb	both
Persicaria lapathifolia (L.) Delarbre	annual	forb	both
Persicaria longiseta (Bruijn) Kitag.	annual	forb	both
Persicaria sagittata (L.) H.Gross var. *sibirica* (Meisn.) Miyabe	annual	forb	summer
Persicaria senticosa (Meisn.) H.Gross	annual	forb	summer
Persicaria thunbergii (Siebold et Zucc.) H.Gross	annual	forb	both
Phragmites australis (Cav.) Trin. ex Steud.	perennial	grass	both
Phragmites japonica Steud.	perennial	grass	both
Phytolacca america L.	perennial	forb	both
Picris hieracioides L. subsp. *japonica* (Thunb.) Krylov	annual	forb	summer
Plantago asiatica L.	perennial	forb	both
Plantago lanceolata L.	perennial	forb	both
Poa annua L.	annual	grass	both
Portulaca oleracea L.	annual	forb	summer
Potentilla freynia Bornm.	perennial	forb	both
Potentilla sprengelia Lehm.	perennial	forb	spring
Pueraria lobata (Willd.) Ohwi	perennial	vine	both
Quercus serrata Murray	wood	tree	spring
Ranunculus sceleratus L.	annual	forb	spring

Appendix5-1. Continued

Name	Life form	Function	Identify
Ranunculus silerifolius H.L?v. var. *glaber* (H.Boissieu) Tamura	perennial	forb	spring
Robinia pseudoacacia L.	wood	tree	spring
Rorippa indica (L.) Hiern	perennial	forb	spring
Rosa multiflora Thunb.	wood	shrub	both
Rubia argyi (H.L?v. et Vaniot) H.Hara ex Lauener	perennial	forb	both
Rumex acetosa L.	perennial	forb	both
Rumex japonicus Houtt.	perennial	forb	both
Sagi japonica (Sw.) Ohwi	annual	forb	spring
Sagittaria pygmaea Miq.	perennial	forb	summer
Salix chaenomeloides Kimura	wood	shrub	spring
Salix miyabea Seemen subsp. g*ymnolepis* (H.L?v. et Vaniot) H.Ohashi et Yonek.	wood	shrub	both
Salsola komarovii Iljin	annual	forb	both
Sanicula chinensis Bunge	perennial	forb	summer
Schoenoplectus triqueter (L.) Palla	perennial	grass	spring
Sedum sarmentosum Bunge	perennial	forb	spring
Senecio vulgaris L.	annual	forb	spring
Setaria pumila (Poir.) Roem. et Schult.	annual	grass	summer
Setaria viridis (L.) P.Beauv.	annual	grass	summer
Sicyos angulatus L.	annual	vine	summer
Sisyrinchium rosulatum E.P.Bicknell	annual	forb	spring
Solanum ptychanthum Dul	annual	forb	summer
Solidago altissima L.	perennial	forb	both
Sonchus asper (L.) Hill	annual	forb	spring
Sonchus oleraceus L.	annual	forb	spring
Stellaria media (L.) Vill.	annual	forb	spring
Stellaria uliginosa Murray var. *undulata* (Thunb.) Fenzl	annual	forb	spring
Taraxacum officile Weber ex F.H.Wigg.	perennial	forb	both
Torilis japonica (Houtt.) DC.	annual	forb	spring
Trapa japonica Flerow	annual	forb	spring
Trifolium dubium Sibth.	annual	forb	spring
Trifolium pratense L.	perennial	forb	both
Trifolium repens L.	perennial	forb	both
Trigonotis peduncularis (Trevir.) Benth. ex Hemsl.	annual	forb	spring
Typha latifolia L.	perennial	grass	summer
Verbe boriensis L.	perennial	forb	summer
Verbe brasiliensis Vell.	perennial	forb	spring

Appendix5-1. Continued

Name	Life form	Function	Identify
Veronica agallis-aquatica L.	perennial	forb	spring
Veronica arvensis L.	annual	forb	spring
Veronica persica Poir.	annual	forb	spring
Vicia hirsuta (L.) Gray	annual	forb	spring
Vicia sativa L. subsp. *nigra* (L.) Ehrh.	annual	forb	spring
Vicia tetrasperma (L.) Schreb.	annual	forb	summer
Xanthium occidentale Bertol.	annual	forb	both
Zehneria japonica (Thunb.) H.Y.Liu	annual	vine	summer

Chapter VI

Conservation idea: Locating local hotspots in riparian ecosystems: the convergence of threatened plant species and human activity at river confluences and meanderings.

Abstract

The ability to quickly locate biodiversity hotspots in a given broad area is critical for effective conservation planning. In riparian ecosystems, flooding provides diverse habitats for plants and animals but is a nuisance to human settlement. Thus, frequently disturbed areas in riparian ecosystems that harbor high biodiversity are more likely to experience strong artificial-control measures. I tested this hypothesis and determined how to easily find these areas using river maps. I examined the effect of two terrain components (the number of confluences and the degree of meandering per unit area) that could potentially influence flooding frequency on both the distribution of threatened species and the degree of artificial modification at three different grain sizes using two riparian data sources. I found that the numbers of both threatened species and artificial constructions increased with the number of confluences and the degree of meandering per unit area. Additionally, my results demonstrated that confluences and meanderings provide different habitat conditions for threatened plant species. I proposed that a per-unit-area confluence density and river length map would be a useful tool for locating local biodiversity hotspots, thus improving conservation and management planning.

要約

生物多様性ホットスポットを見つけることは、保全計画を立案する上で、極めて重要な項目である。河川生態系では、洪水によって多様な生息場が創出され、生物多様性が高まっている。しかし反面、洪水は人間活動を脅かす要因でもある。すなわち、頻繁に洪水が発生する場所は生物多様性が高いと同時に、強い人為改変圧にさらされている可能性がある。本章は、単位面積あたりの合流点数と河川延長という２つの地形要因を用いて仮説を検証し、簡単に河川生態系におけるホットスポットを見つけ出すことを試みた。検討は２つのデータソースを利用し、２つのスケール（メッシュサイズ）で行った。その結果、単位面積あたりの合流点および河川延長が大きい地域は多くの絶滅危惧種が生育し、同時に多くの人工工作物が存在していた。さらに単位面積あたりの合流点の数、河川延長はそれぞれ別のハビタットを創出し、異なった絶滅危惧種の生育に貢献していることが示唆された。単位面積あたりの合流点の数、蛇行度は河川生態系におけるホットスポット探索の手がかりとして有効である可能性が示された。

Introduction

Riparian zones (the fringes of rivers or streams) are among the most biologically diverse and productive ecosystems worldwide (Naiman *et al.* 1993; Burkart 2001; Whited *et al.* 2007). Habitat distribution and turnover within riparian zones are strongly influenced by the flooding regime (Whited et al. 2007). Flooding-induced disturbances provide dynamic and complex biophysical habitats in riparian zones (Naiman *et al.* 1993; Burkart 2001), which in turn maintain biological diversity across space and time (Tockner & Stanford 2002; Stanford *et al.* 2005). Thus, the flooding disturbance would be one of the key factors affecting biodiversity in riparian zones(Benda *et al.* 2004).

On the other hand, flooding is a globally crucial, nuisance factor to human settlement and activity near rivers. Therefore, many riparian zones have been heavily modified to control the impact of flooding on human lives (Poff et al. 1997; Rinaldi & Johnson 1997; Washitani 2001). For example, many fluvial systems are compromised by flow regulation via dams, diversions, and revetments (Nilsson & Berggren 2000; Richter & Richter 2000; Tockner & Stanford 2002; Whited et al. 2007). Moreover, some river lines have been straightened or lined (Rinaldi & Johnson 1997). As a result, the magnitude of flooding has been reduced, and diverse riparian habitats and ecological processes have been lost in modified regions (Rinaldi & Johnson 1997).

Here, I hypothesize that those riparian areas with the potential to harbor the highest biodiversity due to frequent disturbances are coincident with those exposed to high artificial-control pressures. I predict that areas with many confluences and/or a high degree of river meandering will harbor high biodiversity due to frequent disturbances. Because both around confluences (Benda *et al.* 2004) and abundant meanderings area (Rinaldi & Johnson 1997) expected to more frequently flooding occur in riverine areas. If my predictions are supported, these areas of river ecosystems may be threatened and vulnerable biodiversity hotspots. My results may yield important insights into easily locating local biodiversity hotspots and may provide a new polestar for river management planning.

In this chapter, I examined the hypothesis that areas with many confluences and/or meanderings harbor high biodiversity and have been heavily modified. Using existing data sets for the distributions of river channels, threatened species, and artificial modifications for the rivers in Hyogo Prefecture, Japan, I examined whether the number of confluences and total river length (an indicator of the degree of meandering) per unit area were positively related to the number of either threatened floodplain species (an indicator of biodiversity) or artificial constructions (an indicator of artificial modification) per area at different grain sizes (10 × 10, 5 × 5, and 1 × 1 km). I also examined the relationship between the presence of three flooding-sensitive threatened plant species (*Actinostemma lobatum*, *Penthorum chinense*, and *Sparganium erectum* ssp. *stoloniferum*) and both the number of confluences and total river length per unit area. Finally, I discuss the validity of the hypothesis and how to apply my results to identifying local hotspots of riparian plant species diversity.

Methods

Study area and data sources

The study was conducted in Hyogo Prefecture, Japan (34°41' N, 135°12' E, 8395.61 km^2; Fig. 6-1). The mean annual precipitation is 1264.7 mm, and the mean annual temperature is 16.9°C (Japan Meteorological Agency).

I used data from two existing sources to extract information on the locations of rivers, confluences, artificial constructions, and threatened species distribution. Data were derived from the Research for the Natural Environment of Rivers in Hyogo Prefecture (RNER) and the Census for River and Riparian Areas (CRR). The RNER was conducted from 2002 to 2006 by the Hyogo Prefecture government (HyogoPrefecture 2007) and used previous chapters, whereas the CRR has been conducted every year since 1993 by the Japanese governmental agency, the Ministry of Land, Infrastructure, Transport, and Tourism.

Data sets

I examined three grain sizes in my analyses: the Japanese Standard Second Mesh (10 × 10 km; hereafter, 10-km grain), the Standard Third Mesh (1 × 1 km; 1-km grain), and a medium mesh (5 × 5 km; 5-km grain). The locations of the 10- and 1-km grains were arbitrarily determined by the Japanese government (Ministry of Internal Affairs and Communications, Japan). Four 5-km grains were superimposed into each Standard Second Mesh. The numbers of confluences and the total river length per unit area, as well as the numbers of threatened species and artificial constructions (e.g., dams and revetments) per unit area, were calculated using the RNER data set. In this study, I did not distinguish between types and sizes of artificial constructions. I defined threatened species as those listed on the national Red List and in local Red Data Books (Appendix 3). To examine species-specific responses to river confluences and meanderings, I also created presence-point distribution data for three threatened riparian species, *A. lobatum*, *P. chinense*, and *S. erectum*, using both the RNER and CRR data sets. A presence-point number was calculated for each species at each grain size. These three species were selected because the numbers of presence-points were higher than those of other species studied in the rivers of Hyogo Prefecture, they each exhibit ecological traits related to flooding (i.e., require some sort of water regime), and they are well known endangered riparian species in Japan (Yonemura *et al.* 2000; Ishii *et al.* 2005; Takakuwa *et al.* 2006). During data collection, I excluded overlapping species records from 2 data sources. All calculations were conducted using GIS software (ArcView 3.3 ESRI Japan).

Fig.6-1

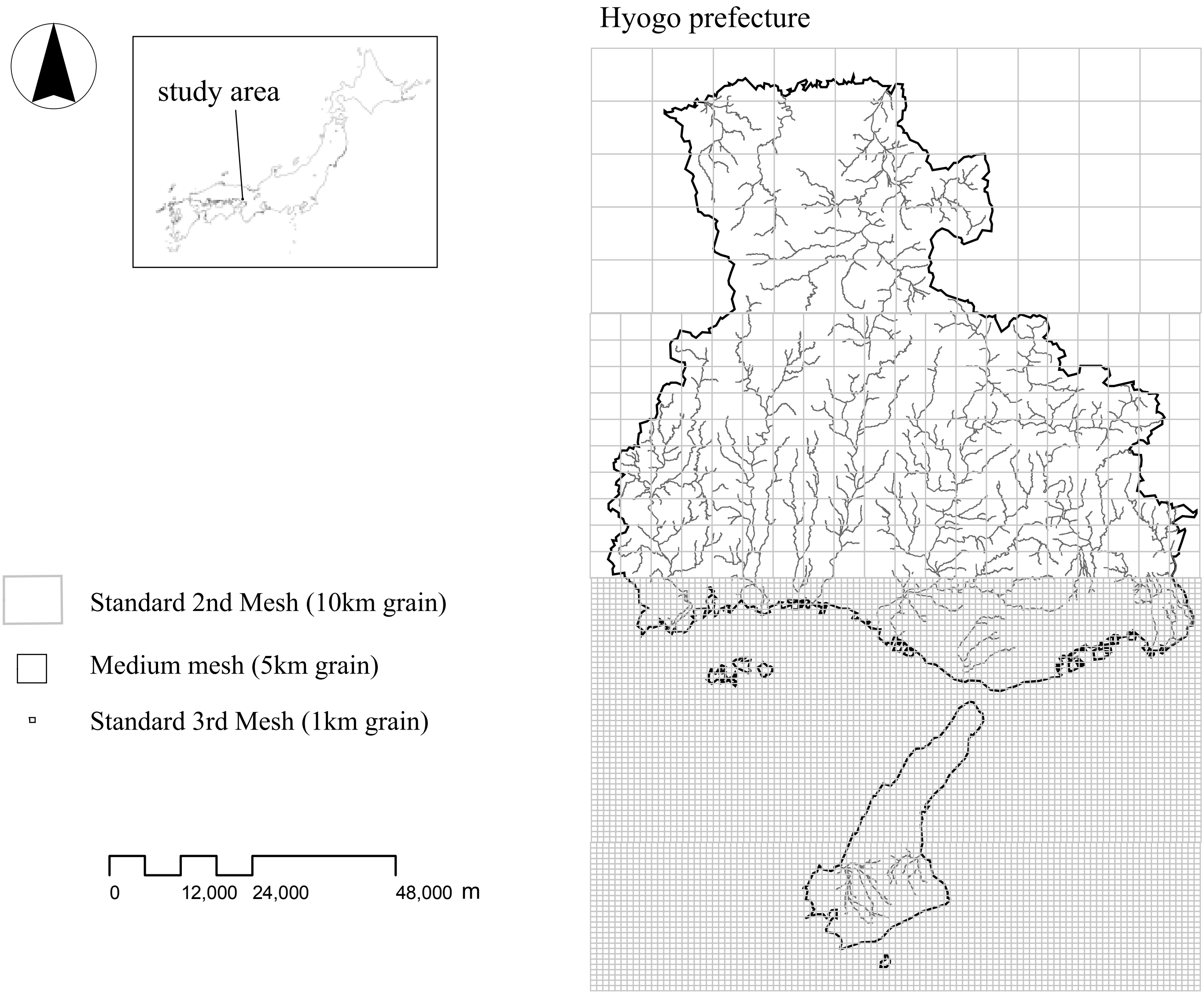


Fig. 6-1. The location of study rivers in Hyogo prefecture, Japan and three types of grains used in the present study.

Statistical analyses

I examined the effects of river confluence and meandering on the distributions of threatened species, artificial constructions, and presence-point numbers of *A. lobatum*, *P. chinense*, and *S. erectum* ssp. *stoloniferum* using generalized linear models (GLMs) with Poisson error distribution and Wald tests. In these models, I treated the number of confluences, total river length, and their interaction as explanatory variables and the number of threatened species, artificial constructions, or species' presence-points as response variables. In the model for artificial constructions, I included total river length as an offset term (Agresti 2002), because artificial constructions are likely to be established at un equal distance within a given river line. I constructed models for the 10- and 5-km grain data sets. I did not analyze the 1-km grain data set, because at this grain size, the threatened species data set contained too many zeroes (7329 of 7419 meshes had zero records) and there were too few confluences per mesh (0.07 ± 0.28, mean ± s.d.).

All statistical analyses were conducted using the statistical package R ver. 2.6.1 (R Core Development Team 2008).

Results

For the 10-km grain data set, the mean number of confluences was 3.35 and total river length was 32.87 km, and the mean numbers of threatened species and artificial constructions were 0.86 and 91.78, respectively. The mean numbers of presence-points of the three focal threatened species were 1.24 (*A. lobatum*), 0.48 (*P. chinense*), and 0.072 (*S. erectum* ssp. *stoloniferum*).

For the 5-km grain data set, the mean number of confluences was 0.83 and total river length was 8.49 km, and the mean numbers of threatened species and artificial constructions were 0.54 and 28.57, respectively. The numbers of presence -points of the three threatened species were 0.38 (*A. lobatum*), 0.15 (*P. chinense*), and 0.015 (*S. erectum* ssp. *stoloniferum*).

The GLM results for threatened species and artificial constructions for the 10- and 5-km grain data sets exhibited similar trends (Table 6-1). The number of confluences and total river length were significantly positively related to the number of threatened species at these grain sizes, with the exception of the number of threatened species at the 10-km grain. The number of confluences and total river length were significantly positively related to the number of artificial constructions at both the 10-

and 5-km grains. The interaction between the number of confluences and total river length was significantly negatively related to both the number of threatened species and artificial constructions at both grain sizes, excluding the case of the number of threatened species at the 10-km grain. The number of threatened species was not correlated with the number of artificial constructions at either grains (10-km grain: adjusted *r*-squared = -0.010, *p* = 0.87; 5-km grain: adjusted *r*-squared = 0.0015, *p* = 0.23).

The effects of the number of confluences and total river length on the number of presence -points of the three threatened species differed among species and between grain sizes (Table 6-2). For *A. lobatum*, total river length had a significant positive effect at both the 10- and 5-km grain, whereas the number of confluences had a significant negative effect at only the 10-km grain (Table 6-2). The interaction between confluence number and total river length did not have a consistent effect on the three species. For *P. chinense*, the number of confluences had a significant positive effect at both grain sizes, whereas total river length had a significant positive effect on the number of presence -points only at the 5-km grain (Table 6-2). The effect of the interaction was significantly negative at both grain sizes. For *S. erectum* ssp. *stoloniferum*, the effects of total river length and the number of confluences were significantly positive only at the 5-km grain

(Table 6-2). The interaction negatively affected this threatened species only at the 10-km grain size.

Table6-1. Results of GLMs for the numbers of threatened species and artificial constructions. Estimated coefficients (SE are shown with the results of Wald tests. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$

Grain size	Variables	Threatened species	*z* value		Constructions	*z* value	
10km	Confluence	-0.05901 (0.1044)	-0.565	n.s	0.1723 (0.003044)	56.6	***
	Total river length	0.00001687 (0.000008457)	1.995	*	0.00004299 (0.0000003189)	134.79	***
	Interaction	-0.0000001343 (0.000001983)	-0.068	n.s	-0.00000336 (0.00000005782)	-58.11	***
	Intercept	-0.5226 (0.2865)	-1.824		2.804 (0.01368)	205.05	
5km	Confluence	0.4016 (0.1941)	2.069	*	0.3206 (0.02629)	12.2	***
	Total river length	0.0001332 (0.00001996)	6.674	***	0.0001284 (0.000002738)	46.91	***
	Interaction	-0.00003434 (0.00001437)	-2.389	*	-0.00002709 (0.000001908)	-14.2	***
	Intercept	-1.874 (0.2213)	-8.469		2.122 (0.03032)	69.97	

Table6-2. Results of GLMs for the numbers of presence -points of Actinostemma lobatum, Penthorum chinense, and Sparganium erectum ssp. stoloniferum. Estimated coefficients (SEs) are shown with the results of Wald tests. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$.

Grain size	Variables	*Actinostemma lobatum*	*z* value		*Penthorum chinense*	*z* value		*Sparganium erectum* ssp. *stoloniferum*	*z* value	
10km	Confluence	-0.3909 (0.1141)	0.1141	***	0.3437 (0.1028)	3.342	***	1.239 (0.4373)	2.832	**
	Total river length	0.00003333 (0.000006722)	4.958	***	0.000005548 (0.00001333)	0.416	n.s	0.0001872 (0.00006448)	2.904	**
	Interaction	0.000004085 (0.000001943)	2.102	*	-0.000007879 0.000000992	-2.634	**	-0.00002819 (0.000009426)	-2.991	**
	Intercept	-0.4096 (0.2545)	-1.609		-1.001 (0.3809)	-2.628		-10.65 (3.288)	-3.238	
5km	Confluence	0.4003 (0.2664)	1.502	n.s	0.8727 (0.3496)	2.496	*	0.9449 (0.8831)	1.07	n.s
	Total river length	0.0001998 (0.00002281)	8.76	***	0.0001231 (0.00004045)	3.043	**	0.00006231 (0.0001352)	0.461	n.s
	Interaction	-0.00004569 (0.00001916)	-2.385	*	-0.00006776 (0.00002882)	-2.351	*	-0.00005082 (0.00007221)	-0.704	n.s
	Intercept	2.839 (0.2834)	-10.019		-3.114 (0.4282)	-7.273		-5.106 (1.338)	-3.816	

Discussion

I found that threatened species diversity and/or the number of artificial constructions were significantly higher in riverine areas with many confluences and/or with more meanderings at two different grain sizes. Thus, my results suggest that increased disturbances at confluences and meanderings provide habitats for threatened species, but are also very likely to experience strong artificial control. Washitani (2001) suggested that many threatened riparian plants have become vulnerable because of recent drastic changes in river environments caused by intensive modern river management for flooding control and water utilization (Washitani 2001). Additionally, Ward et al. (1999) proposed that river regulation has been particularly extensive in species-rich river-floodplain environments (Ward et al. 1999). My results strongly support these predictions and further indicate that recent river management especially destroys habitats created by flooding.

My analyses also demonstrated that the effects of the confluences and meanderings on the numbers of species presence-points differed among the three focal threatened species. These results suggest that river confluences and meanderings provide different habitat conditions for individual plant species. *A. lobatum* consistently preferred areas with more meanderings at both grain sizes, whereas *P. chinense* occurred in areas with many confluences. Previous studies have shown that *A. lobatum* prefers wet and relatively stable habitats (Takakuwa et al. 2006), whereas *P. chinense* prefers wet and disturbed habitats (Yonemura et al. 2000). Thus, confluences may provide more frequently disturbed habitats compared to meanderings, as reflected by the varying distribution of these two threatened species along the disturbance regime. The distribution of *S. erectum* ssp. *stoloniferum*, which also prefers wet and disturbed habitats (Ishii et al. 2005), was significantly positively affected by the number of confluences and total river length at a 10-km but not a 5-km grain size. One possible explanation for this difference between the two grains is that *S. erectum* ssp. *Stoloniferum,* may have a wider minimum area requirement (MAR) than the other species (Lambeck 1997). This supposition should be further examined in future studies. Overall, my findings suggest that both confluences and meanderings were important for maintaining the diverse habitats of threatened species. Although my results only highlight general patterns, further research is warranted to examine the ecological processes by which confluences and meanderings create a diversity of habitats for threatened species.

Conclusions and Implications

My results indicated that riverine areas with many confluences and meanderings harbor an abundance of threatened species but are also currently under threat by strong artificial control measures. Additionally, my findings suggested that confluences and meanderings provide different disturbance regimes that create diverse habitats in riparian ecosystems. Habitat conservation and management must be key elements in any program to minimize or reduce the expected diminution of the world’s biotic diversity (Smith et al. 1998). Thus, sound management plans must be implemented for threatened species, and to this end, it is crucial to understand and catalog the causes of habitat loss when formulating possible management strategies (Smith et al. 1998; Van Dyke 2008). My results strongly suggest that reductions in the frequency of disturbances such as those caused by revetments around confluences and straightened or lined rivers have led to declines of threatened species in riparian floodplains. Thus, in critical areas such as confluences and meanderings, the conflict between biodiversity and flooding control must be resolved for floodplain species conservation.

My findings also provide new insight for conservation and management planning. My approach demonstrated that local biodiversity hotspots in riparian floodplains can be easily found using river maps. Based on the locations of river lines, I were able to create per-unit-area confluence density and river length maps. I then identified at-risk areas rich in threatened species diversity. In addition, confluences harbored much more common vegetation compared to single flow areas (Chapter 3). These easily-drawn hotspot maps will strongly promote effective conservation and management planning in riparian zones.

Appendix6-1. List of threatened plant species examined in this study. These species were listed in national and/or local (Hyogo, Osaka, Kyoto, and Okayama Prefectures) red data books (RDB). The RDB category was standardized based on the International Union for Conservation of Nature (IUCN) categories (EN: Endangered, VU: Vulnerable, LR: Lower risk, O: other). The species examined in the presence point analyses are indicated with asterisks.

Species	Family	National RDB	Hyogo Pref. RDB	Neighbor Prefecture RDB
Achyranthes longifolia	Amaranthaceae	-	VU	
Actinostemma lobatum *	Cucurbitaceae	-	**LR**	
Ammannia multiflora	Lythraceae	-	-	LR
Anaphalis margaritacea ssp. *yedoensis*	Compositae	-	VU	
Aster tripolium	Compositae	VU	LR	
Carex teiogyna	Cyperaceae	-	-	O
Chikusichloa aquatica	Poaceae	-	EN	
Corydalis raddeana	Papaveraceae	LR	LR	
Eupatorium japonicum	Compositae	LR	VU	
Ixeris repens	Compositae	-	LR	
Orobanche coerulescens	Orobanchaceae	VU	EN	
Osmunda lancea	Osmundaceae	-	VU	
Penthorum chinense *	Saxifragaceae	**LR**	**VU**	
Phacelurus latifolius	Poaceae	-	LR	
Potentilla chinensis	Rosaceae	-	LR	
Rorippa cantoniensis	Cruciferae	LR	-	
Rotala pusilla	Lythraceae	VU	-	
Schoenoplectus validus	Cyperaceae	-	LR	
Sedum japonicum	Crassulaceae	-	LR	
Solidago yokusaiana	Compositae	-	EN	
Sparganium erectum ssp. *Stoloniferum* *	Sparganiaceae	**LR**	**VU**	
Spiraea thunbergii	Rosaceae	-	-	LR
Suaeda maritima	Chenopodiaceae	-	LR	
Urtica angustifolia	Urticaceae	-	LR	

Chapter VII

General discussion

General discussion

In this thesis, I found positive effects of river confluences on vegetation and plant species diversity in river systems of Hyogo Prefecture. To the best of my knowledge, this is the first report that demonstrated confluence effects on riparian plant diversity. Flooding disturbances, which occur more frequently around river confluences, played important roles in maintaining biodiversity in riparian areas. Thus, my attempt to find out general patterns of confluence effects and underlying mechanisms maintaining plant diversity was basically achieved. In this Chapter, I once summarized my main findings in each chapter, and discuss the role of confluence effects and their conservational importance in maintaining biodiversity in river ecosystems.

In the Chapter 2, I tested the hypothesis that around river confluences, frequent disturbances create heterogeneous habitats and consequently increase a vegetation diversity using the data set from all river systems of Hyogo Prefecture. The results supported the hypothesis and suggest the generality of confluence effects on vegetation diversity in a broad scale.

In the Chapter 3, I further tested the confluence effects on 8 functional vegetation groups that were likely to be more influenced by flooding disturbances than other vegetation types. This test was conducted in the Kakogawa river basin system where is the largest basin systems in Hyogo Prefecture. I found that the patches of herbaceous vegetations (annual forb, grass, vine, and perennial forb, grass vegetations) were more frequently found around river confluences than single -flow areas, whereas woody vegetations avoided confluence areas. Regular and intermediate flooding disturbances around river confluences would facilitate the colonization of the two herbaceous vegetations, however woody plant vegetations preferred more strongly disturbed areas. These results demonstrate that river confluences provide regularly and intermediately disturbed habitats, and stably harbor herbaceous hydrophilic vegetations at landscape (river basin) scales.

In the Chapter 4, I tested confluence effects on plant species diversity in 11 river confluences within the Mukogawa river basin system. I compared plant species diversity and the extent of bare ground between up- and down-confluence areas in summer and spring. I found that species diversity, especially annual plant species was highest at down-confluence areas in summer. The extent of bare ground was significantly greater at down-confluence areas than at upside confluence areas in summer and spring. The recruitment of annual species was higher in the summer than in the spring, and rapid occupancy of bare grounds by them might occur in the summer. I suggest that within river systems, spatial and seasonal differences in patterns of flooding function together to regulate plant species diversity. This ecological process is likely to degrade in artificially concreted rivers, around which floodings infrequently occur.

In the Chapter 5, I tested validity of both neutral theory and niche theory as potential explanations for the assembly of plant communities to compare community similarities between up-confluence and up-confluence site pair and between up-confluence and down-confluence site pair within 11 river confluences in the Mukogawa river basin system. The pattern of similarity in summer was consistent with the prediction by neutral theory, whereas that in spring was consistent with that by niche theory. The result showed that the relative importance of neutral and niche processes on community structures changed seasonally.

It the Chapter 6, I found that the numbers of both threatened species and artificial constructions increased with the number of confluences and the degree of meandering per unit area. According to the results, I suggested that areas with many confluences and/or with more meanderings are local biodiversity hotspots in river ecosystems. Based on the locations of river lines, we are able to create per-unit-area confluence density and river length maps, with which we can easily identify local hotspots. These easily-drown hotspot maps will promote effective conservation and management planning in riparian areas.

According to these results, I suggest that frequent (regular) and intermediate flooding disturbances around confluences enhance plant diversity in different two ways: vegetation and species sorting among diverse habitats provided by flooding disturbances (Chapter 2, 3, 6) as well as facilitation of neutral process by creating large bare ground areas during the plant growing season (Chapter 4, 5). Both niche theory and neutral theory have been suggested as potential explanations for the assembly, dynamics, and structure of diversity patterns (Hubbell 2001; Silvertown 2004; Harpole & Tilman 2006; Thompson & Townsend 2006). However niche theory and neutral theory are not mutually exclusive when multiple species share a single niche within communities. Interestingly, my findings indicate that relative importance of niche and neutral processes on riparian plant community varied in time and space in riparian ecosystems. At broad scale, niche theory well explained vegetations and rare species diversity around confluences (chapter 2, 3, 6) whereas, at small scale, plant species diversity was well explained both by niche and neutral theories (chapter 4, 5). In particular, neutral processes strongly shown under the spatial and seasonal matching between open space creation and the terms when high dispersal activity (Chapter 5). Recent studies on scale effects suggested that shown ecological processes were often scale-dependent (Hobbs

2003). However, limited empirical evidences have demonstrated a temporal variation of community-structuring mechanisms. My findings might show the new perspective, namely, shown ecological processes is also timing-dependent. My findings are valuable both on basic science for biodiversity theory and applied science for conservation.

My findings that both α and β diversity was higher around confluences also provide very important concept of plant diversity conservation in river ecosystems. Frequent and intermediate disturbance was suggested to occur and create large natural bare grounds around confluence, which, in turn, promote plant diversity. Thus, in order to conserve both α and β plant diversity in river ecosystems, the disturbance regime should be conserved around confluences. Because floodings are globally crucial, nuisance factor to human settlement and activity near rivers, many riparian zones have been modified to control the impact of flooding on human lives (Poff *et al.* 1997; Rinaldi & Johnson 1997; Washitani 2001). Especially, areas around confluences were more heavily modified than other areas (Chapter 6). The artificial modifications should restrict a range of disturbance regime, leading to a decrease in the impact of infrequent but strong flooding around confluences, and to reduction in the frequency of small disturbances (Rinaldi & Johnson 1997). In Japan, the River Act (established in 1896) puts the first priorities of river managements on “flooding disaster prevention” and “water utilization”. Thus, ideally, we should establish river management plans which achieve flooding control and water utilization without destroying biological environments.

In order to conserve diversity through keeping neutral process, species diversity within regional species pools should be conserved. This means that a regional-level conservation planning is necessary. In this thesis, I showed the plant community assembly was consistent with neutral theory at least in summer (Chapter 5). Base on neutral theory, community assembly was decided by regional species pool, in other words, regional biodiversity potential. Thus, plant species diversity around river confluences reflects the biodiversity potential of the river ecosystems. Additionally, it is likely to reflect the whole of the biodiversity potentials because river ecosystems were connected along the lengths of rivers or streams. Thus, if the river ecosystems have poor biodiversity potentials, intact river confluence could not show high biodiversity. River confluences make apparent the biodiversity potentials. When we find the endangered species at the riparian area, we protect at the area in most cases. However, it is not always a sufficient strategy. We should protect wider areas around finding point and their disturbance regimes.

River confluences might provide several habitats for other animals at the river basin scale because diversity in vegetation also provides diverse habitats and foods for animals (Qian & Ricklefs 2008). In the future study, I should test the confluence effects on animal communities in riparian ecosystems.

In the following section, I would like to propose the practical ideas for managements and biodiversity conservation of river ecosystems based on my findings.

Principles:

- Preserve a wide range of floodings without causing disasters on human life and activity in river ecosystems.
- Areas around river confluence have higher conservation priority than single flow areas.

River management practices

1. We should not concrete low-flow channels. This is because concrete low-flow channels reduce flooding disturbances in riparian areas.
2. When we have to modify river conditions at a certain area, regional biodiversity as well as that in the target area should be preliminarily assessed. Modification should have minimum impacts on regional biodiversity in order to conserve the mechanism

maintaining biodiversity through neutral process.

Conservation practices

3. We put high conservation priority on river systems with high biodiversity potential. In these systems, conservation and restoration practices would effectively maintain and increase high biodiversity.
4. Per-unit-area confluence density and river length maps are recommended to use to identify high conservation priority areas within given river systems when available conservation resources are not enough to assess their biodiversity. Areas with high confluence density are likely to harbor many threatened species that prefer more frequently disturbed habitats and those with long river length harbor threatened species more stable wetland conditions.

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