

Comparison of landscape diversity in forests of the upper Rhine and the middle Loire floodplains (France)

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Traditional measures of biotic indices (α , β , δ) from phytosociological relevés are used to compare diversity at three scale-levels in the upper Rhine valley (Alsace, northeastern region) and the middle Loire (Bourgogne, central region), France. Both study areas include a tributary. The Ill, which is the Rhine tributary in this sector, has no forest communities in common with the main river because of opposite hydrological and edaphic characteristics. This is not the case in the Loire valley, in which the fluvial characteristics are close to those of its tributary, the Allier.

Nearly all forest communities (12/14) were shown to be species-rich, due to the role of natural disturbances. Species richness peaks in late-successional forests of the Rhine valley (for example, up to 50 woody species in *Quercus-Ulmetum*). Sixty per cent of the forest-communities are common to the two floodplains, which explains why 85% of the families, 65% of the genera and 55% of the species are in common. Compared to the Loire valley, the Rhine valleys shows higher biotic diversity. This was related first to its geographical situation, and second to higher landscape heterogeneity. Human disturbance through river management is responsible for changes in species composition as shown by floristic comparison of flooded and unflooded sites. Insularity of natural forests among man-made landscapes is involved in species diversity. In order to preserve the natural diversity of such rich landscapes, floodable areas should be recreated and the attitudes of foresters should evolve accordingly.

Keywords: species richness; alluvial forest; Rhine and Loire landscape; fluvial dynamics; conservation

Introduction

Temperate alluvial landscapes of extensive river plains are natural non-steady state systems characterized by short-term cyclic changes in landscape composition and diversity, due to continuous reworking by river erosion, deposition and channel migration. Such cyclical patterns, together with a wide range of soil conditions, regular fluctuations in propagule immigration during flooding, aerated substrates, high nutrient and water reserves, and relative climatic mildness in extended valleys, account for the species richness, forest-types and successional stages which have been recorded along the Danube, the Rhine, the Rhône, the Loire and the Oder (Wendelberger, 1952; Karpati and Toth, 1961; Walter, 1979; White, 1979; Carbiener, 1983, 1984; Passarge, 1985; Grubb, 1987; Schnitzler, 1988; Pautou and Wuillot, 1989; Schnitzler, 1995a, b; Loiseau, in press).

This study presents a synthesis of floristic and phytosociological researches carried out from 1980 to 1995 in two big floodplains in France, the upper Rhine valley (Alsace, north

eastern region) and the middle Loire (Bourgogne, central region), about 500 km apart. Both areas include a tributary: the Ill in the Rhine valley and the Allier in the Loire valley. Detailed descriptions of the forest-communities and habitat type (soil gradient of texture, drainage, geochemistry) as well as interpretations of the sylvigenetic processes and plant migrations has been published previously (Corillion, 1957, 1989; Schnitzler, 1988; Schnitzler *et al.*, 1991, 1992; Schnitzler, 1995a, b; in press a and b).

The aim of this paper is to compare regional biotic diversity in the two landscapes, which are characterized by natural strong fluvial dynamics but which differ in regional climate, soil gradients and human influence. I use traditional non-spatial diversity measures α , β , δ (Whittaker, 1972; Wilson and Shmida, 1984) within forest diversity and range of species variation among forest communities of the two floodplains.

Study area

The Rhine and the Loire plains are geologically young areas which have been subjected to climatic and tectonic change during the Holocene (Delance *et al.*, 1988; Striedter, 1988; Vogt, 1992). The natural dynamics of the Loire and the Rhine were defined as a series of braids and anastomoses (Maire and Cloots, 1982; Carbiener, 1984). During the Holocene and historic periods, the Rhine and the Loire morphogeneses have resulted in complex morphological and sedimentological patterns (terraces, backwater depressions, ridges), all laid down either over gravelly deposits rich in carbonates (Rhine), or over sandy acidic deposits (Loire), which retains an ample water table. In the Rhine valley, the deposits can locally reach a depth of 140 m, whereas they do not exceed 6 m along the Loire. Details of the climatic, hydrologic and sedimentological environments are presented in Table 1.

In the upper Rhine rift valley, the study area is located between Colmar and Strasbourg. The area mainly concerns two alluvial units: the eastern annual Rhine high-water bed and the western Ill floodplain. The Rhine rises in the Alps and the Ill in the Jura. The Rhine high-water bed is a well-drained area, characterized by summer floods and calcareous, light-textured deposits. Embankments 2–3 km distant from the main channel were built in the middle of the 19th century. The Rhine was then canalized from 1950 to 1970; this has eliminated morphogenesis and links between the river and the adjacent forest ecosystems. The Ill floodplain, which runs through a western Rhine tectonic depression, is poorly drained with neutral, even-textured deposits laid down during spring and winter floods. Fluvial activity is still present despite local embankments, and all the forests are under the influence of the present floodplain.

In the Loire valley, the study area is located between Villeneuve/Allier and Charité/Loire. This area corresponds to the confluence zone between the Allier and the Loire, locally called 'Le Bec d'Allier'. Both rivers rise in the Massif Central and flooding periods can occur from winter to the beginning of summer. The Loire and the Allier are not canalized, but they were embanked during the 19th century at a distance of 100–200 m from the main bed. The Loire and Allier are characterized by a great irregularity of fluvial dynamics (see Table 1), as well as a great abundance of sand. This landscape is therefore particularly unstable, due to rapid changes in relief.

Upstream of the Rhine and the Allier barrages have been constructed, which constitute another limit to natural fluvial dynamics. Following all this river management, the general level of the water has decreased in both alluvial landscapes. In the Loire valley, lowering of

Table 1. Climatic, hydrologic and sedimentological characteristics of the upper Rhine and the middle Loire valleys

	Rhine	Loire
Floodplain		
Situation		
Region	Alsace	Bourgogne
Latitude	48°N	46°N
General orientation of the valley	South/north	South/north
Borders of the study area	Colmar to Strasbourg	Villeneuve/Allier to Charité/Loire
Mean altitude (m)	140	160
Floodplain length (km)	60	62
Floodplain width (km)	2–10	0.3–2
Floodplain area (km ²)	201	112.3
Remnant forested area (km ²)	82	34.2
Climatic characteristics		
Climatic tendency	Suboceanic	Suboceanic
Annual precipitation (mm)	500–600	700
Annual temperature (°C)	10	10
Hydrologic regime		
Main period of flooding		
For the main river	May–June	May–June; winter
For the tributary	Winter, spring	May–June; winter
Extreme floodings (m ³ .s)	202 ^a /5700 ^b	10 ^c /6000 ^d
Present-day amplitudes of the water table	2 m	2–3 m
River management		
Main river		
Tributary	Canalization from 1950 to 1970	Embankments during the 19th century
Sedimentology, pedology		
Underground deposits	Local embankments	Natural course
Depth of the deposits (m)	Calcareous gravels	Acidic sands
Soil characteristics along the main river	Up to 65 m	6–8 m
Soil characteristics along the tributary	Calcareous silt; pH = 8–8.5	Acidic silt and sand; pH = 4–6
	Neutral clay and silt; pH = 6–7	Acidic silt and sand; pH = 4–6

^aObserved at Basel; ^bObserved at Basel in June 1876. Data from Sanchez (1992); ^c, ^ddata from Braque (1982).

water levels, coupled with absence of major floods for over a century, have favoured the extension of natural sandy islands (Bomer, 1971).

In the two valleys, loss of natural forest cover (estimated through the total surface of the floodplain, which was naturally forested) is considerable. In the Rhine valley, 40% of the surface had disappeared by the end of the 18th century, followed by the loss of another 50 000 ha in the middle of the 19th century (Schnitzler, 1994). The remnant forests now cover about 82 km². In the Loire valley, loss of forest has reached 80% (Schnitzler, 1995b), and the present-day area is only about 35 km². However the forests are now spreading from abandoned pastures and from the extension of the natural islands. Natural forests of the two landscapes are in the minority, split into forest mosaic with different degrees of human intervention. Sixty-five per cent of the 30 km² along the Rhine floodplain are plantations (Asael, 1991). Along the Loire, I estimate forests with a quite natural state at less than 5000 ha.

Method

I defined the vegetation types of the two study areas by the phytosociological method of Braun-Blanquet (1964). Stand plot (40 × 40 m) was selected in the most natural forests of the two floodplains. For each stand plot ($N' = 614$ in the Rhine valley, $N' \times 168$ in the Loire valley) a species list of the vegetation stratum was compiled and the cover of each species was estimated.

In order to assess biotic diversity, three scale levels were employed, which included landscapes, communities and species level patterns. This choice follows the proposal of Whittaker (1972). The first scale level (35–85 km²) involved a comparison of biotic diversity among the two floodplains of the Rhine and the Loire. Community richness, which is a count of the number of vegetation types present in the two landscapes, was calculated, as well as the number of common communities. Family and genera richness were calculated as the total number of families and genera present in the two landscapes. Species richness (γ diversity) was calculated as the total number of species present in the cumulative samples. I added the total number of woody elements as significant of 'hospitality'. Beta diversity was determined for a transverse transect from the main river to the edges. Two measures were used following the conclusions of Wilson and Shmida (1984): $\beta_1 = S/\alpha - 1$ where S is the total number of species and α an average sample richness; and $\beta_2 = g + 1/2\alpha$. β_2 combines the idea of species turnover reflected by the gain (g) and loss (l) of species along the geographical gradient.

At the second scale-level (20–50 km²), non-spatial measures of biotic diversity (i.e. community, family, genera and species richness) were determined within each floodplain, among the main two rivers (Rhine and Loire) and their respective tributaries (Ill and Allier). β diversity was determined following the same geographical gradient (from each river to the edges of its floodplain).

At the third scale-level (5–2000 ha), four measures of species richness (mean and total number of woody plants and grasses; mean and total number of woody plants) were calculated for each forest community in the two landscapes.

Results

Fourteen forest communities divided into ten phytosociological associations were described in the Loire and the Rhine (Table 2). Their ecological characteristics are summed up in Table 3. Early and mid-successional associations are *Salici-Populetum nigrae*, *Fraxino-Populetum albae* and *Ligustro-Populetum nigrae*. Along the Rhine and the Loire, the late-successional stage is represented by four main sub-associations of *Quercu-Ulmetum*. The Rhine forests also include *Pruno-Quercetum*, which occupies ancient alluvial terraces situated at the edges of the highwater bed. The Rhine and Ill forests have no common community. The Ill forests were divided into four associations, *Carici-Alnetum glutinosae*, *Pruno-Fraxinetum*, *Alno-Carpinetum* and *Stellario-Carpinetum*, which are distributed along a hydromorphy gradient. In the Loire valley, *Carici-Fraxinetum* can be considered as a variant of *Pruno-Fraxinetum*.

Most forest communities are common to the Rhine and Loire landscapes, which explains the fact that 85% of the families, 65% of the genera and 55% of the species are common to the two valleys, despite the geographical distance and the differences in climate, substrates and hydrology (Table 4). Compared to the Loire valley, the Rhine valley shows higher community richness, as well as a higher family, genera and species richness (Table 5). β diversity is higher in the Rhine landscape.

All forest communities of the study areas are species-rich (Table 6) except in swamps (*Carici elongatae-Alnetum*) and gravelly, dry terraces (*Stellario-Carpinetum*). Richness peaks in *Quercu-Ulmetum* in the Rhine floodplain, with a total of 51 woody species. This total falls to 37 in the Loire valley, in which many species are lacking (for details, see Table 2). Noteworthy are the differences in species richness for *Fraxino-Populetum albae* between the two valleys: a total of 111 species along the Rhine, and only 25 along the Loire. The number of woody species is two-thirds less along the Loire and likewise for the comparison between *Pruno-Fraxinetum* and *Carici remotae Fraxinetum*.

Salici-Populetum nigrae on the contrary has a higher species richness along the Loire and the Allier. The differences between mean woody richness is particularly striking: 4.1 along the Rhine, 10.3 along the Loire.

Human influence can be quantified by comparing measures of species richness between the flooded sub-associations of *Quercu-Ulmetum* (*populetosum* and *typicum*) and their equivalent outside the dykes, in which flooding was eliminated 150 years ago (*carpinetosum* along the Rhine, *loniceretum* along the Loire). The decreasing number of species is particularly high in the Loire valley (Table 6) where the fluvial dynamics is more active than along the Rhine.

Discussion

Differences in biotic diversity between the Rhine and the Loire has several explanations. Firstly, the geographical position is responsible for the absence or limitation of many plants. The particular position of the Rhine rift valley between two parallel mountains (Vosges and Schwarzwald) explains the presence of both continental and alpine species such as *Alnus incana*, *Prunus padus*, *Tilia cordata*, *Cornus mas*, *Daphne mezereum*, *R. nigrum*, *Ribes rubrum*, *Salix daphnoides*, *S. eleagnons*, *Anemone ranunculoides*, *Asarum europaeum*, *Carex alba*, *C. ornithopoda*, *Corydalis cava*, *Equisetum hyemale*, *Pulmonaria obscura* (Carbiener, 1970; Schnitzler, 1988; Schnitzler *et al.*, 1992). The geographical

Table 2. (Continued)

Family	Association	RHINE										ILL					LOIRE/ALLIER					ALLIER	
		SALIC POPULETUM	LIGUSTRO POPULETUM	FRAXINO POPULETUM	QUERCO	ULMETUM	carpinetum	PRUNO QUERCETUM	CARIGI ALNETUM	PRUNO FRAXINETUM	ALNO CARPINETUM	SAPTARIO CARPINETUM	SALIC POPULETUM	LIGUSTRO POPULETUM	POPULETUM	QUERCO	ULMETUM	montecetum	CARIGI FRAXINETUM	FRAXINO POPULETUM			
sub-association		21	7	250	48	54	19	48	13	34	82	8	57	24	19	46	4	5	10	3			
Gramineae	Brachypodium sylvaticum	IV 2	V 3	V 2	IV 1	V 2	IV 2	V 2	.	IV 1	V 2	.	II 2	II 2	IV 2	III 2	III 2	III 2	III 2	V 3			
	Bromus ramosus	.	I 1	.	I +	II	.	I +	.	.	.	III +			
	Dactylis glomerata	II +	III +	II +	II 1	II 1	I 1	I 1	IV 1	IV 1	III 1	I +	III +	II 1	III 2	III 2	III 2	III 2	III 2	III 2			
	Deschampsia caespitosa	IV +	II +	II +	III +	II +	I +	I +	IV 1	III 1	III 1	III 1	III +	III 1	II 2	II 1	II 2	II 2	II 2	II 2			
	Festuca gigantea	.	III 1	II +	.	.	.	III +	.	.	.	I +	III +	I +			
	Fragaria vesicaria	.	II 1	II +	.	.	.	II +	.	.	.	I +	III +	I +			
	Melica uniflora	.	.	II +	.	.	.	II +	.	.	.	I +	III +	I +			
	Melica nutans	.	.	II +	.	.	.	II +	.	.	.	III +	III +	III 2	III 2	III 2	III 2	III 2	III 2	III 2			
	Milium effusum	III 2	.	.	I +	.	.	.	III 2	III 2	III 2	III 2	III +	III 2	III 2	III 2	III 2	III 2	III 2	III 2			
	Phalaris arundinacea	.	.	.	I +	.	.	.	III 2	III 2	III 2	III 2	III +	III 2	III 2	III 2	III 2	III 2	III 2	III 2			
Poa palustris	III 2	.	.	II 2	III 2	III 2	III 2	III 1	III 1	III 2	III 2	III 2	III 2	III 2	III 2				
Poa nemoralis	.	.	II +	II 2	III 2	III 2	III 2	III 1	III 1	III 2	III 2	III 2	III 2	III 2	III 2				
Luzula pilosa	.	.	I +	I +	I +	I +	I +	II +	II +	II +	II +	II +	II +	II +	II +	II +	II +	II +	II +				
Galeopsis tetrahit	V 2	III 1	III 2	II 1	IV 1	V 2	III +	IV 1	II +	II +	III +	IV +	IV 4	IV 3	IV 3	IV 3	III 2	III 2	III 2				
Glechoma hederacea	.	.	I +	II 1	IV 1	V 2	III +	IV 1	II +	II +	III +	IV +	IV 4	IV 3	IV 3	IV 3	III 2	III 2	III 2				
Lamium galeobdolon	I +	.	I +	II 1	II +	III +	III +	IV 1	III 2	III 2	III 2	IV 1	IV 1	IV 3	IV 3	III 2	III 2	III 2	III 2				
Lamium maculatum	IV 1	III 1	IV 1	IV 1	III 1	IV 1	IV 1	IV 1	I +	I +	I +	IV 1	IV 1	IV 2	IV 2	IV 2	IV 2	IV 2	IV 2				
Stachys sylvatica	II +	I +	III 1	III 1	III 1	III 1	III 1	V 2	IV 1	IV 1	IV 4	I +	IV 4	IV 2	IV 2	IV 2	IV 2	IV 2	IV 2				
Allium ursinum	III 1	III 1	III 1	III 1	III 1	III 1	III 1	V 2	III 1	III 1	III 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1				
Arum maculatum	I +	III +	III +	III 1	III 1	III 1	V 2	V 2	III 1	III 1	III 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1	IV 1				
Convallaria maialis	.	.	III +	III 1	III 1	III 1	V 2	V 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2				
Ficaria verna	.	.	I +	II +	II +	II +	II +	II +	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2				
Iris pseudoacorus	II 1	.	II 1	I +	IV 1	V 2	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1				
Paris quadrifolia	I +	I +	V 2	IV 1	IV 1	IV 1	IV 1	IV 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1	III 1				
Polygonatum multiflorum	I 2	II 2	II 2	IV 1	IV 1	IV 1	IV 1	V 2	.	.	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2				
Scilla bifolia	.	.	II 2	IV 1	IV 1	IV 1	IV 1	IV 2	.	.	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2	III 2				
Lythrum salicaria	I +	.	I +	I +	.	.	.	III 1	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +				
Cannabaceae	Humulus lupulus	II 1	.	III +	IV 2	III 1	I +	III 1	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +				
Oenotheraceae	Circaea lutetiana	IV +	I +	III +	IV 2	III 1	I +	III 1	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +	I +				
Orchidaceae	Epipactis helleborine	I +	I +	I +	I +	I +	I +	I +			
	Listera ovata	I +	I +	I +	I +	I +	I +	I +			
Papaveraceae	Orchis purpurea	.	.	I +	I +	I +	I +	I +			
	Platanthera bifolia	.	.	I +	I +	I +	I +	I +			
	Corydalis cava	.	.	I +	I +	I +	I +	I +			
	Polygonum persicaria	.	.	I +	I +	I +	I +	I +			
Polygonaceae	Polygonum persicaria	.	.	I +	I +	I +	I +	I +			
	Rumex sanguineus	I +	.	I +	III +	II +	.	.	I +	III +	II +	.	.	I +	II +	.	.	III 1	III 1				

Table 3. Ecology (physiography and hydrology) and area (ha) per vegetation type in the Rhine and Loire valleys

Name of association	Physiography	Flooding regime
Rhine valley		
Rhine		
<i>Salici-Populetum nigrae</i>	River banks of low elevation	3–8 days several times a year in summer
<i>Ligustro-Populetum nigrae</i>	Gravelly terraces of high elevation	1–2 days every 3–5 years in May–June
<i>Fraxino-Populetum albae</i>	Silty terraces	1–3 days every 3–5 years in May–June
<i>Quercu-Ulmetum populetosum</i>	Silty-sandy low terraces	1–3 days every 3–5 years in May–June
<i>Quercu-Ulmetum typicum</i>	Silty-sandy low terraces	Unflooded for 30 years
<i>Quercu-Ulmetum tilietosum</i>	Sandy high terraces	Every 10 years in May–June
<i>Quercu-Ulmetum carpinetosum</i>	Sandy low terraces	Unflooded for 150 years
<i>Pruno-Quercetum</i>	Silty Holocene terraces	Major floods in summer
Ill		
<i>Carici elongatae Alnetum</i>	Clayey swamps	5–6 months every year in spring/winter
<i>Pruno-Fraxinetum</i>	Old channels	1–2 weeks in spring/winter
<i>Alno-Carpinetum</i>	Clayey-silty low terraces	3–8 days in spring/winter
<i>Stellario-Carpinetum</i>	Gravelly Würmian terraces	Major floods in summer
Loire valley		
Loire		
<i>Salici-Populetum nigrae</i>	Sandy river banks of low elevation	3–8 days several times a year in spring/winter
<i>Ligustro-Populetum nigrae</i>	Gravelly high river banks and islands	1–2 days every 3–5 years in spring/winter
<i>Quercu-Ulmetum populetosum</i>	Sandy islands	3–5 days every 1–2 years in spring/winter
<i>Quercu-Ulmetum typicum</i>	Sandy low terraces	3–5 days every 3–5 years in spring/winter
<i>Quercu-Ulmetum tilietosum</i>	Sandy high terraces	Every 10 years in spring/winter
<i>Quercu-Ulmetum loniceretum</i>	Sandy low terraces	Unflooded for 150 years
<i>Carici elongatae-Fraxinetum</i>	Old channels	1–2 weeks every year in spring/winter
Allier		
<i>Salici-Populetum nigrae</i>	Sandy river banks of low elevation	3–8 days several times a year in spring/winter
<i>Ligustro-Populetum nigrae</i>	Gravelly high river banks and islands	1–2 days every 3–5 years in spring/winter
<i>Fraxino-Populetum albae</i>	Silty low terraces	1–3 days every 3–5 years in winter/spring
<i>Quercu-Ulmetum populetosum</i>	Sandy islands	3–5 days every 1–2 years in spring/winter
<i>Quercu-Ulmetum typicum</i>	Sandy low terraces	3–5 days every 3–5 years in spring/winter
<i>Quercu-Ulmetum tilietosum</i>	Sandy high terraces	Every 10 years in spring/winter
<i>Carici elongatae-Fraxinetum</i>	Old channels	1–2 weeks every year in spring/winter

Table 4. Common biotic diversity among and within Rhine and Loire landscapes; values are expressed in per cent

	Rhine/Loire	Rhine/Ill	Loire/Allier
Family	85	77	100
Genera	65	69	1.1
Species	55	59	1
Community	60	0	75

position of the Loire valley in Central France, open to Mediterranean influences, explains the presence of *Fraxinus angustifolia*, *Tilia plathyphyllos*, *Pulmonaria longifolia* (Loiseau, in press).

Secondly, the results are consistent with the physiographic, hydrological and edaphic descriptions (see Tables 1 and 2). The Rhine valley has higher spatial heterogeneity and a finer-grained mosaic of elements, which is due to the great differences in environmental conditions between the main river and its tributary, the Ill. This increases the number of vegetation units and their degree of contrast among edge habitats. There is no community common to the Rhine and the Ill forests, even if 77% of families, 65% of genera and 59% of species are common to both. High β diversity in the Ill forests reflects a high partitioning of species between habitats, due to contrasted gradients (from swamps to very dry terraces). The Allier and the Loire on the contrary are rivers of similar fluvial dynamics and sediment characteristics, which explains the high similarities in biotic diversity. β diversity of the Loire and the Allier is intermediate between Rhine and Ill floodplains, which suggests an intermediate contrasted landscape. Among the edaphic factors, limestone and texture are very selective. The absence of limestone prevents or limits the growth of calcareous plants such as *Populus alba*, *Berberis vulgaris*, *Corylus avellana*, *Lonicera xylosteum*, *Euphorbia amygdaloides*, *Helleborus foetidus* in the Loire landscape. But the presence of acidic soils in the latter valley favours growth of *Acer negundo*, *Evonymus europaeus* (often of giant dimensions), *Lonicera periclymenum*, *Salix triandra*, *S. viminalis*. Abundance of clay, coupled with moist soils, favours the eutrophic geophyte synusia (*Allium ursinum*,

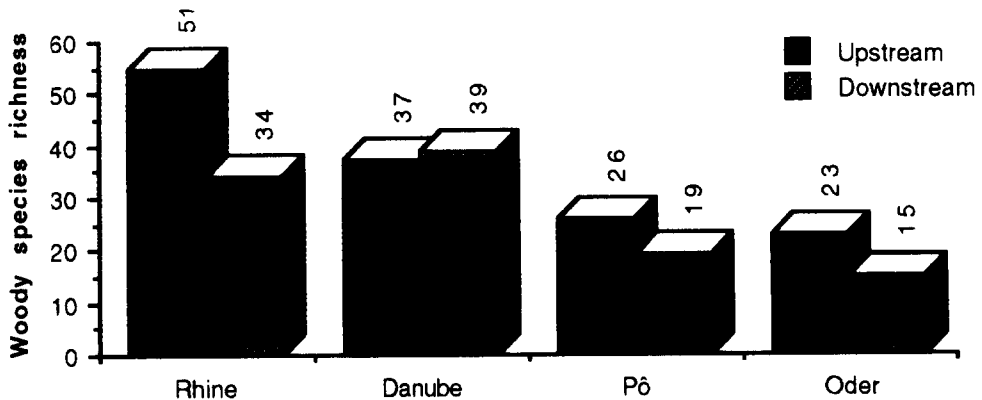
Table 5. Patterns of landscape diversity and community richness in the Rhine and Loire valleys

	Community richness	Family richness	Genera richness	Total species richness	Total woody species richness	β_1 diversity	β_2 diversity
Rhine valley	12	56	113	157	56	1.07	0.66
Rhine floodplain	8	53	107	143	52	0.26	0.26
Ill floodplain	4	29	83	106	37	0.98	0.98
Loire valley	8	47	98	110	46	0.49	0.41
Loire floodplain	7	47	98	110	46	0.48	0.41
Allier floodplain	7	47	98	110	46	0.47	0.41

(1): $\beta_1 = S/\alpha - 1$ where S = total number of species and α = number of species in each of the samples. (2): $\beta_2 = g + l/2\alpha$ where g is the gain of species and l is loss.

Table 6. Biotic diversity in the different forest communities of the Rhine and Loire valleys

	Species richness St	Mean species richness St	Woody species richness Sw	Mean woody species richness Sw
Rhine floodplain				
Salici-Populetum nigrae	81	18.4	31	4.1
Ligustro-Populetum nigrae	63	28.6	35	10.6
Fraxino-Populetum albae	111	28.9	47	15.9
Querco-Ulmetum populetosum	99	31.2	44	17.8
Querco-Ulmetum typicum	92	33.7	43	15.7
Querco-Ulmetum tilietosum	90	34.4	44	17.6
Querco-Ulmetum carpinetosum	84	34.8	41	16.7
Pruno-Quercetum	77	37.1	39	16.1
III floodplain				
Carici elongatae-Alnetum	51	18	14	4.1
Pruno-Fraxinetum typicum	85	27.1	32	10
Alno-Carpinetum	87	35	32	13.7
Stellario-Carpinetum	41	16.6	12	4.3
Loire/Allier floodplain				
Salici-Populetum nigrae	89	23.1	37	10.3
Ligustro-Populetum nigrae	78	23.7	32	9.8
Fraxino-Populetum albae	25	10	16	9
Querco-Ulmetum populetosum	65	24.6	30	13.4
Querco-Ulmetum typicum	71	24	28	12.3
Querco-Ulmetum tilietosum	41	24.5	22	13.1
Querco-Ulmetum loniceretum	44	25.5	25	16
Carici remotae-Fraxinetum	42	16	21	10



Rhine: from Strasbourg (France) to Mainz (Germany)

Danube: from Wien (Austria) to Gemenc (Hungary)

Pô: from Novare to Messolla (Italy)

Oder: from Breslau to Frankfurt (Germany)

Figure 1. Decreasing species diversity from upstream to downstream in the hardwood forests of European big rivers.

Scilla bifolia, *Anemone ranunculoides* (Schnitzler *et al.*, 1991) and explains their low abundance or absence in the Rhine, the Loire and Allier forests.

Thirdly, the scarcity of a community in one landscape and its abundance in the other can constitute an explanation for the lower species diversity of *Fraxino-Populetum albae* in the Loire (only 1 ha against nearly 100 along the Rhine) and of *Carici remotae-Fraxinetum* in the Loire valley (only a few hectares) compared to its variant *Pruno-Fraxinetum*, widespread along the Ill with about 1500 ha.

Fourthly, human influence is evident. Big floodplains were uninhabited early in history (for the Rhine valley, see Striedter, 1988). Loss or addition of species and changes under man's influence in the functional and structural attributes of forests are difficult to perceive and quantify. Nevertheless, we know enough to be able to say that the most likely response will be an increase in the fragility of ecosystems. Increasing insularity of forests among pastures, meadows, villages or towns has limited the gene pool of animal and plant species. In addition, the remnant, often fragmented forests were managed for timber productivity. Foresters fight natural structure and species composition by replacing natural states with plantations, destroying lianas and underlayers, introducing alien plants (*Acer negundo*, *Robinia pseudacacia*, *Solidago gigantea*, *Impatiens glandulifera*) and suppressing the sylvigenetic phases of forest senescence and death. Nowadays, all the forests of the industrialized countries have changed their species composition and structure to an unknown degree (see Jones, 1945; Harris, 1984; Carbiener, 1991a). River management has also changed natural states as observed in *Quercu-Ulmetum* (flooded and unflooded for 150 years) (Schnitzler, 1994). Outside the dykes, many species which avoid flooding are now abundant such as *Acer pseudoplatanus*, *Acer campestre*, *Carpinus betulus*, *Prunus avium*, *Berberis vulgaris*, *Viburnum lantana*. The lower number of species in *Salici-Populetum* along the Rhine than along the Loire is also due to elimination of flooding, which has interrupted migration of propagules along the longitudinal profile of the river. Along the Loire, which has kept a more natural course, circulation of species is still very active (Corillion, 1957, 1989; Loiseau and Braque, 1972; Loiseau, in press).

In spite of long-term negative human influence, nearly all forest communities of the two big valleys are characterized as woody species-rich, particularly late-successional hardwood forests (*Quercu-Ulmetum*). Such high woody species richness is well-known in all broad floodplain forests of the great temperate rivers such as the Mississippi, Missouri, Rhine, Danube and so on (Carbiener, 1970; Grubb, 1987; Brinson, 1990; Carbiener, 1991b). Among all *Quercu-Ulmetum* of Europe, the Rhine association is particularly rich in woody species, as shown in data from other alluvial forests of this association in north-western and central Europe (Fig. 1), due to favourable local conditions (Carbiener, 1970). This richness decreases downstream along the rift with the decrease of the slope, which induces a lower kinetic flood energy and an increase of hydromorphy in the meander sector (Dister, 1984; Carbiener and Schnitzler, 1990) (Fig. 1).

Conclusion: a controlled rational use of forest floodplains by man

Measurements of landscape diversity reported here suggest highly complex functioning in the alluvial system, synonymous with high diversification and competition avoidance. Preservation of these ecological features is dependent on the preservation of natural processes. In the valleys studied, this is far from being the case. Human interference has included disturbance decrease or suppression through flood management, coupled with

fragmentation of the forest pattern and inappropriate forestry. These processes have led to an unexpected decline in natural control mechanisms, new selection pressure and increasing ecosystem fragility. These considerations have led to an international convention, known as the Ramsar Convention (established in 1971 in Iran), which has adopted guidelines and standards on various aspects of wetland conservation and international co-operation (Lethier, 1992). In the reports of a IUBS-SCOPE UNESCO workshop (1991), which prepared the UN Conference on Environment and Development (Brazil, June 1992), the role of human activity in altering landscape structure was extensively debated, in relation to ethical and aesthetic considerations, loss of unique landscapes and species, and speculation on the management of human economies. Urgent practical steps are required to halt a process of insularization of alluvial community types. For this purpose, protected areas provide help in reflecting natural conditions, but they must not become small sanctuaries acting as traps and constantly endangered by surrounding human-dominated lands. Two complementary actions are widely known to be highly efficient: the re-creation of floodable areas and protection of ripisylves against felling and inappropriate sylviculture.

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