2656

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LANDSCAPE STRUCTURE AND DIVERSITY IN RIPARIAN PLANT COMMUNITIES: A LONGITUDINAL COMPARATIVE STUDY

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ABSTRACT

Patterns of plant species richness and community composition were studied in diverse riparian zones. Eight rivers in south-western France, one river in north-western USA and four rivers in south-eastern Spain were compared. A brief review is presented of factors that have been singled out as controlling diversity along rivers. The proportions of plant group classified according to life-span, morphology, ruderality and location along the rivers were analysed. Both proportions of plant traits and total species richness differed considerably between rivers. Semi-arid rivers were more influenced by local patterns than the other rivers. The patterns exhibited by true riparian species and invading, essentially non-riparian species, showed the importance of the relationships between the river and its close surroundings. The mean proportion of ruderals remained roughly the same in all rivers, suggesting some regulatory mechanisms independent of the general environmental settings. The longitudinal patterns of species richness in riparian plant communities of the oceanic rivers could be related to the intermediate disturbance hypothesis, whereas semi-arid rivers showed very irregular patterns of species richness along their courses, as a consequence of the irregular water availability. Exotic and ruderal species were more sensitive than other groups to the longitudinal zonation of the rivers and to environmental factors influenced by humans. Also, the permanency of superficial water appeared as a major factor in the control of riparian community structure in semi-arid regions.

KEY WORDS: exotic plants; invasion; plant community; riparian; ruderals; species richness

INTRODUCTION

The unique characteristics of riparian systems result from their spatial location and configuration. Gregory *et al.* (1991) defined those systems as 'the interface(s) between terrestrial and aquatic ecosystems', linking the systems by exchange of materials and energy. Plant communities in these systems are likely to be affected by both longitudinal [i.e. upstream–downstream (Vannote *et al.*, 1980; Noss, 1983)] and transversal [i.e. stream–floodplain or floodplain–basin (Newbold *et al.*, 1981)] linkages for species recruitment and species diversity. They have also been defined as potentially important biotic sinks (Marks, 1983). In landscapes under human influences, riparian communities are influenced both by natural (hydrological, geomorphological) and human-made disturbance regimes. Therefore, natural upstream–downstream continuity or between-system linkages are modified in various ways, and river ecologists are confronted with a wide range of factors.

Riparian zones have been reported as some of the most species rich and most productive systems of temperature regions (Malanson, 1993; Naiman *et al.*, 1993). They are also some of the most sensitive to human influences and potentially most threatened ecosystems (cf. Malanson, 1993). Moreover, they appear as valuable models for understanding the role of diversity in ecosystems.

Even though riparian systems are frequently studied, little is known about spatial patterns in the diversity

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of plant communities along rivers and about their causal factors (Décamps and Tabacchi, 1993), especially landscape-related ones. The scope of this paper is to examine differences in the influence of landscape features on the diversity of riparian plant communities. These differences were studied from a longitudinal point of view, by comparing rivers located in south-western France, south-eastern Spain and north-western USA. The results of the study may be of potential importance to the managers of catchment areas, especially along regulated rivers where landscape linkages have been broken and are the subject of rehabilitation.

A REVIEW OF FACTORS AFFECTING PLANT DIVERSITY IN RIPARIAN SYSTEMS

Despite the wide range of factors that influence species richness in plant communities (Tilman and Pacala, 1993), few authors have analysed in detail the patterns of species richness or of general community structure along rivers. Instead, most of the literature tends to focus on strictly compositional patterns (Malanson, 1993).

Table I summarizes some important factors that might control the species richness of riparian and

Table I. Principal references in the literature concerning the factors possibly controlling plant species richness in riparian communities

Factor type	Environmental variable	Reference
Biotic factors	Anemochory	Nilsson *et al.*, 1993
		Planty-Tabacchi, 1993
	Hydrochory	Nilsson *et al.*, 1991b
		Johansson and Nilsson, 1993
		Nilsson *et al.*, 1993
		Planty-Tabacchi, 1993
	Invasions	Fox and Fox, 1986
		McIntyre *et al.*, 1988
		Planty-Tabacchi, 1993
	Leaf litter mass gradients	Nilsson and Grelsson, 1990
	Litter mass gradients	Nilsson and Grelsson, 1990
	Standing crop	Day *et al.*, 1988
Geomorphology and landscape patterns	Fluvial–geomorphic landforms	Nanson and Beach, 1977
		Hupp, 1982
		Hupp and Osterkamp, 1985
		Hupp, 1990
		Baker, 1988
		Tabacchi, 1992
	Fragmentation	Hanson *et al.*, 1990
	Height of the river margin	Nilsson *et al.*, 1991a
	Lateral erosion and channel changes	Salo *et al.*, 1986
		Harris, 1987
		McBride and Strahan, 1984a
		McBride and Strahan, 1984b
		Baker, 1988
		Tabacchi, 1992
	Substrate fineness	Robertson *et al.*, 1978
		Dunn and Scott, 1987
		Nilsson *et al.*, 1989
		Nilsson *et al.*, 1991a
	Substrate heterogeneity	Nilsson, 1987
		Kalliola and Puhakka, 1988
		Nilsson *et al.*, 1989
		Nilsson *et al.*, 1991a
	River size	Planty-Tabacchi, 1993
		Nilsson *et al.*, 1994

Table I. Continued

Factor type	Environmental variable	Reference
Hydrology	Current velocity	Nilsson, 1987
		Roberts and Ludwig, 1991
	Exposure gradients	Johnson *et al.*, 1976
		Keddy, 1983
		Wilson and Keddy, 1986
		Shipley *et al.*, 1991
		Tabacchi, 1995
	Instream flow volume	Taylor, 1982
		Stromberg and Patten, 1990
		Stromberg, 1993
	Flood	Hack and Goodlett, 1960
		Honser and Minckler, 1963
		Bell, 1974
		Johnson *et al.*, 1976
		Smith, 1980
		Conner *et al.*, 1981
		Hupp, 1982
		Reichembacher, 1984
		Frangi and Lugo, 1985
		Hupp and Osterkamp, 1985
		Pearlstine *et al.*, 1985
		Walker and Chaplin, 1986
		Harris, 1987
		Hugues, 1988
		Kalliola and Puhakka, 1988
		Nilsson and Keddy, 1988
		Baker, 1989
		Lisle, 1989
		Baker, 1990
		Hughes, 1990
		Stromberg *et al.*, 1991
		Medley, 1992
	Flood frequency	Sigafoos, 1961
		Teversham and Slaymaker, 1976
		Adams and Anderson, 1980
		Denslow, 1980
		Malanson, 1984
		Salo *et al.*, 1986
		Swanson *et al.*, 1988
		Baker, 1989
		Dollar *et al.*, 1992
		Duncan, 1993
	Flow regulation	Ward, 1976
		Holmes and Whitton, 1981
		Casado *et al.*, 1989
		Camargo and García de Jalón, 1990
		Nilsson *et al.*, 1991a
		García de Jalón *et al.*, 1994
		Hey *et al.*, 1994
		Maheshwari *et al.*, 1995
	Mean anual discharge	Nilsson *et al.*, 1991a
	Water level regime	Franz and Bazzaz, 1977
		Walker and Chapin, 1986
		Nilsson *et al.*, 1991a
		Décamps *et al.*, 1995
	Water pH	McClelland and Ungar, 1970

floodplain plant communities. Multi-scale studies could identify the differential expression of micro- and macroenvironmental variables on community structure in the different river zones (e.g. Baker, 1989), but these are still very scarce. At the scale of an entire river or hydrological network, geomorphology or hydrology are the driving factors. The observed floristic patterns are often explained by an intermediate disturbance regime. The spatial heterogeneity resulting from geomorphological processes is viewed as one of the major causes of high species richness. However, few studies are devoted to the role of heterogeneity itself, within or around the riparian zone, in explaining these patterns. The effect of the landscape structure within the riparian corridor and in the surrounding matrix has not been studied as thoroughly for riparian plant communities as it has for animal communities (Forman and Godron, 1986; Turner and Gardner, 1991). At the scale of an entire reach, studies have often been carried out without knowledge about the magnitude of floods. However, current velocity, flood magnitude and frequency, and mean discharge have been found to influence the species richness in riparian vegetation (Teversham and Slaymaker, 1976; Nilsson, 1987; Roberts and Ludwig, 1991; Stromberg *et al.*, 1991). At the local scale, little is known about the microclimatic effects on community structure (see Corillion, 1985; Tabacchi, 1995).

Direct or indirect human influences, such as the dramatic effects of big dams, have become the object of many studies, but most of these studies focus on aquatic macrophytes. Some studies, however, deal with the effects of moderate regulation on species richness in riparian communities (e.g. Nilsson *et al.*, 1991a).

Biotic factors and processes directly related to species diversity are rarely presented as major topics in riparian plant ecology (see Malanson, 1993, for a synthesis). Conclusions often result from an individualistic, population-oriented approach. Biological invasions have recently been given some attention as a phenomenon very sensitive to disturbance and to landscape patterns (Drake *et al.*, 1989; Di Castri *et al.*, 1990).

The effects of the relationships between riparian zones and their surroundings on riparian plant community structure, illustrated by the invasion of 'external' species, have not been much studied. As shown in Table I, most studies are devoted to abiotic regimes and disturbances. Few consider biotic processes such as invasion or competition. Moreover, the competition between 'external' and true riparian species is only the subject of a few case-studies; such as the invasion of salt cedar along the Colorado River (e.g. Harris, 1966).

THE COMPOSITE NATURE OF RIPARIAN PLANT ASSEMBLAGES

As a consequence of the shifting mosaic of landforms and communities resulting from natural disturbance (Whittaker and Levin, 1977), high levels of species richness are usually found along rivers. For example, one of us (Tabacchi, 1992) found that plant species richness in a riparian zone of the Adour (SW France) was 47% higher than in the surrounding hillslopes. Moreover, we found 1396 species along the entire corridor of this river (335 km), accounting for about one fifth of the flora of France.

The invasion of new species along a river mainly results from stochastic local recruitment during early colonization. The riparian corridor constitutes the main vector of this process. However, as the floodplain develops or as the corridor structure becomes altered, the transversal links between the river and its basin may become more important for recruitment of external species. The suitability of many habitats for non-riparian, specialized species, and the empty space made available by the partial or complete destruction of habitats locally enhance species richness through recruitment of non-riparian species. Species-rich communities are frequently found at earlier stages and in highly or moderately disturbed locations. They are most often dominated by annual, ruderal plant populations, with a high resilience. Some of these species are riverside specific, but many of them can also be found in non-riparian habitats, such as wasteland, fields, coastal sand dunes or urban areas.

It is likely that many non-riparian species have colonized the riparian zones following the increase of human influences on the landscapes. We address three main causes: (1) the increased fragmentation of riparian corridors, which modifies the permeability of the river–floodplain ecotone; (2) the diversification of land use in the floodplain and in the riparian zone itself, which modifies the spatial distribution of disturbance and landscape connectivity; (3) the flow regulation, which has similar effects as in (1) and also reduces habitat diversity. As a result, the importance of plants that are not riverside specific increases all over the world.

Considering Keddy's (1989) hypotheses: (1) the observed species have adapted in the past so that their present niche fits the fundamental niche, or (2) the realized niche is smaller than the fundamental one following pre-existing hierarchical competitiveness. This implies that allochthonous species should have a fundamental importance within riparian systems.

Many studies have pointed out the importance of allochthonous plant species in riparian communities (Ashton and Mitchell, 1989; Nilsson *et al.*, 1989; Ferreira, 1992; Planty-Tabacchi, 1993; Planty-Tabacchi *et al.*, 1996). Nilsson *et al.* (1991a) used the concept of 'naturalness' as a way to discriminate between riparian and non-riparian (in that study, ruderals) components of riverside communities. However, some confusion between ecological behaviour and geographical or ecological origin may occur when considering the different components of the riparian flora. We do not pretend to give a formal solution to the problem in this paper. The following definitions were used.

1. *Exotic species* (E) were defined as foreign species to a given region, intentionally or unintentionally introduced following human activities, and able to sustain and reproduce in the absence of human care (see Planty-Tabacchi, 1993, for an exhaustive review of the concept). The *native species* (N) are the opposite.
2. *Riparian species* (RI) were defined as any species that are specific to riversides, wetlands or swamp zones. We widened the common definition by including phreatophytes as well as riparian species *sensu stricto*, helophytes and aquatic macrophytes.
3. *Ruderal species* (RU) were defined in accordance with Thellung (1911–1912), Harper (1944), Frenkel (1977) and Grime (1979). Most of the ruderal plants are pioneer species, mainly short-lived, with high reproductive effort. They are likely to colonize habitats subjected to human-induced disturbance. Many species can be classified as both ruderal and riparian (ruderal and exotic) because they are also favoured by natural disturbance.

Thus, among the many ways to split riverside communities into different components, we will consider that riparian communities can be viewed as an assemblage of exotic and native species, as well as of riparian and non-riparian and ruderal and non-ruderal species.

SITES AND METHODS

Rivers sampled

The species richness of riparian plant communities was sampled in three countries (Figure 1) during three surveys. The characteristics of the sampled river systems are given in Table II.

The Andarax, Carboneras, Aguas and Almanzora rivers (Figure 1A) were studied between 1991 and 1993 in south-eastern Spain (Salinas, 1994). The Andarax River flows from the Sierra Nevada mountains (2000 m a.s.l.) to the Mediterranean Sea. Its middle course is located between the Sierra de los Filabres and the Sierra de Gador. The Carboneras River results from the confluence of several diffuse temporary streams that originate in the Sierras de Cabrera and de Alhamilla. It is fed by groundwater in its middle course. The Aguas River and the Almonzora River originate in the Sierra de los Filabres (900 m a.s.l.). The main climate encountered there is a typical Mediterranean, semi-arid climate (Le Houérou, 1982; Capel, 1990). The annual precipitation ranges from 690 mm (Upper Andarax) to 210 mm (Lower Andarax). Superficial water is likely to disappear locally during several months in most of the rivers. Moreover, gypsum occurs here and there along the lower Andarax, and in the middle and lower courses of the Carboneras and Aguals rivers (Martin-Vivaldi, 1991), disrupting the riparian corridor with halophylic vegetation. In the cultivated areas of the lower courses, riparian vegetation is usually constrained by severe cutting (essentially of salt ceder and *Arundo donax*). Cultivation along the lower and middle courses of the Andarax and Almanzora rivers includes mostly orange orchards and vegetables. The Upper Andarax is lined by vineyards and poplar plantations. More or less abandoned pastures, orchards and matorrals cover the rest of the land. The upper and middle courses of the Carboneras and Aguas rivers are planted with almond trees, and their lower plains are used for vegetable cultivation.

Eight rivers were studied in south-western France (Figure 1B) from 1988 to 1994 to survey their exotic communities (Planty-Tabacchi, 1993). Two of them were main rivers: the Garonne River and the Adour River. The Adour River was also studied from 1987 to 1992 in a separate survey of both exotic and native plants (Tabacchi and Planty-Tabacchi, 1990; Tabacchi *et al.*, 1990; Tabacchi, 1992, 1995; Planty-Tabacchi *et al.*, 1996). The six other rivers studied for exotics are the main tributaries of the Adour River (Arros, Luy, Midouze, Gave de Pau, Gave d'Oloron, and Nive rivers). All these rivers, except the Midouze River and the Luy River, originate in the higher Central Pyrenees (more than 2500 m a.s.l., where the annual precipitation approximates 2500 mm). The Midouze and Luy rivers originate in the foothills of the mountains, and as a consequence, they appear as relatively sluggish streams, mostly crossing agricultural areas. In contrast, the Gave de Pau, Gave d'Oloron and Nive rivers flow through the mountains. The Adour and the Garonne rivers exhibit a wide range of hydrological regimes, from nival to pluvial. Estuaries were included in the sampling of these two rivers. Most of the Adour drainage basin is under Atlantic (oceanic) climatic influence. However, the Arros River receives some Mediterranean influence due to its proximity to the Garonne

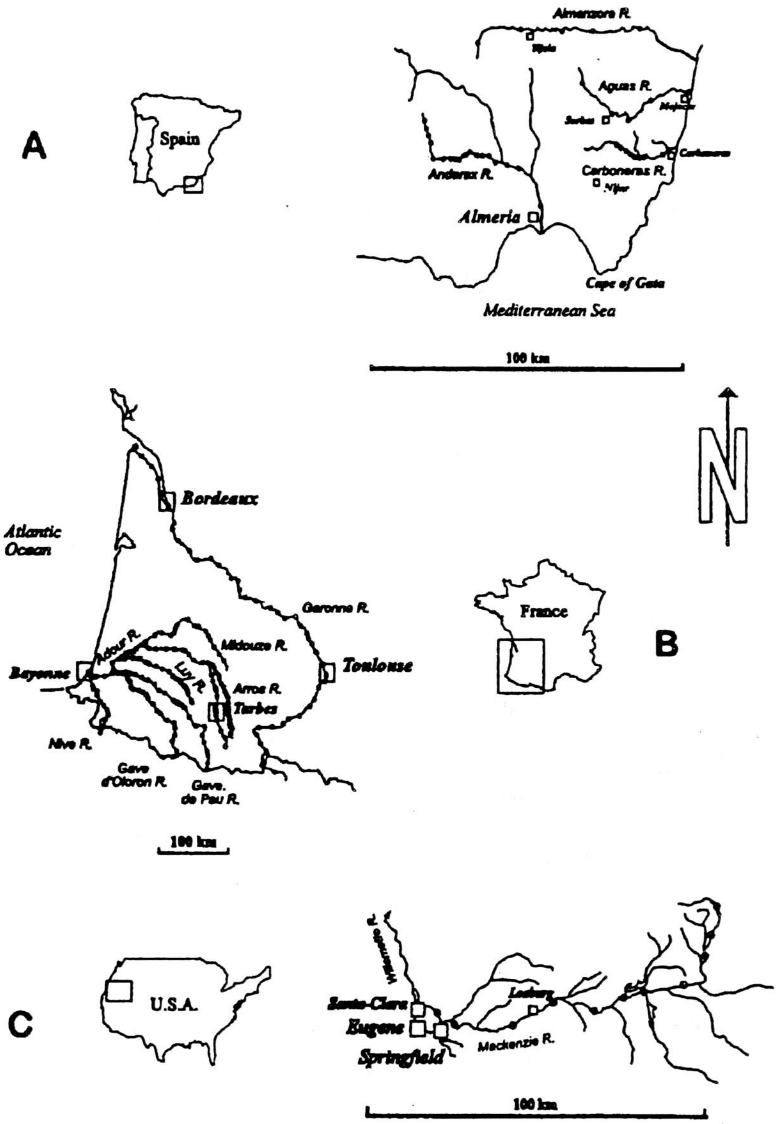

Figure 1. Location of the sampling sites (black dots) along the studied rivers. Major towns are shown by empty sqaures. A: Spanish streams. B: French streams. C: North American stream

Table II. Main characteristics of the studied systems

River	Location	Length (km)	Mean annual discharge ($m^3 s^{-1}$)	No. of study sites	Plant communities studied
Aguas	SE Spain	70	< 0·5	5	natives + exotics
Almanzora	SE Spain	125	2	5	natives + exotics
Andarax	SE Spain	70	1	19	natives + exotics
Carboneras	SE Spain	50	< 0·5	8	natives + exotics
Adour[a]	SE France	335	350	32	natives + exotics
Mackenzie	NW USA	150	170	11 (15)[b]	natives + exotics
Garonne	SW France	650	650	43	exotics
Adour[a]	SW France	335	350	70	exotics
Arros	SW France	120	20	25	exotics
Gave d'Oloron	SW France	135	110	21	exotics
Gave de Pau	SW France	210	190	34	exotics
Luy	SW France	155	20	22	exotics
Midouze	SW France	145	20	17	exotics
Nive	SW France	85	40	13	exotics

[a] The Adour River has been studied for both 'native + exotics' and 'exotics'.
[b] 15 sites were studied along the MacKenzie system (Table IV) of which 11 were used in the longitudinal survey.

catchment area. The lower mean annual precipitation is found in the course of the middle Garonne (600 mm). All these rivers cross a variety of landscapes, dominated by corn and wheat fields. Forested lands are common in the mountain and the piedmont. The Gave de Pau and the Adour are the most dynamic rivers from a geomorphological point of view. Riparian corridors are little affected by humans along the Adour, Gave de Pau, Gave d'Oloron and Luy rivers. The corridor of the Luy contrasts greatly with the surrounding intensive agricultural land use. The lower Adour floodplain includes extensive marshes with large forests. This 'Barthes' region has been managed, but only the estuarine zone can be considered as altered by this management. In this stretch the Atlantic oak replaces black poplar in plantations. The upper course of the Arros River can be considered as natural. It contrasts sharply with the middle and lower courses, which are included in an intensively cultivated plain. At this point, the vegetal corridor of the river is almost absent. The Garonne River is the more regulated, with dams and high weirs. Most riparian forests in the middle course are poplar plantations. The other rivers can be considered as little regulated with only small weirs along their courses.

The Mackenzie River, in Central Oregon, USA (Figure 1C) has also been studied in 1992 in a comparative study of native and exotic communities here and in the Adour River (Planty-Tabacchi, 1993; Planty-Tabacchi *et al.*, 1996). This river originates in the Western Cascade Range (at about 1500 m a.s.l.). It is a tributary of the Willamette River, which flows into the Columbia River. The Mackenzie is torrential in its upper two-thirds, where some high falls are found. The river originates in pristine north-western forest. The upper valley is constrained and widens sharply at the piedmont where it crosses a few coniferous plantations. In its lowest course it meets urban and agricultural landscapes. The climate is influenced by the Pacific Ocean, with moist landscapes in the upper reaches (Central), and drier landscapes in the lowlands (Willamette Valley). The transition along the Mackenzie Valley is followed by sharp temperature and precipitation gradients. Annual mean precipitation ranges from 2500 mm (Cascades) to 1000 mm (Willamette Valley).

Riparian vegetation

The riparian vegetation of the Spanish semi-arid rivers is dominated by *Tamarix africana* and *Tamarix canariensis*. In the upper reaches, riparian zones are colonized by *Alnus glutinosa*, *Ulmus minor*, *Populus alba*, *P. nigra* and *Salix atrocinerea*. *Nerium oleander* occurs where the substrate is rocky. The dominant surrounding vegetation is a shrubland (matorral) which usually comes directly into contact with the stream edge. At the middle and lower courses, the invading *Nicotiana glauca* and *Arundo donax* dominate.

The riparian vegetation of the Mackenzie River is dominated by coniferous species, such as *Pseudotsuga menziesii*, *Libocedrus decurrens*, *Tsuga heterophylla* and *Thuja plicata*. Deciduous trees (*Salix* spp., *Acer macrophyllum*, *Alnus rubra*, *Populus trichocarpa* and *Fraxinus latifolia*) become dominant as the elevation decreases. The understorey is diversified with mostly *Sambucus coerulea*, *Acer circinatum*, *Vaccinium* spp., *Ribes* spp. and *Castanopsis chrysophylla*. The herbaceous stratum is also very diversified with many ferns. Numerous exotics (26% of the total), 60% of which have come from Europe, were found along this river (Planty-Tabacchi *et al.*, 1996).

The riparian vegetation of the French rivers is dominated by *Salix alba*, *Fraxinus angustifolia*, *F. excelsior*, *Alnus glutinosa*, *Ulmus minor*, *Populus nigra* and *Acer* spp. Communities other than forests are also very well represented. The Atlantic oak (*Quercus robur*) is common within the Adour basin; this species constitutes the dominant tree of floodplain forests of the lower Adour River. It is rarer along the Garonne River, where *Quercus pubescens* dominates instead. *Populus alba* is also present on the Garonne River. Coniferous species only occur in the mountainous zone, except along the lower Midouze River, which comes into contact with the Landes Forest (*Pinus maritima*). Four hundred and twenty exotic species were found along these rivers (Planty-Tabacchi, 1993). Some of the exotics, such as *Robinia pseudoacacia*, *Impatiens glandulifera*, *Acer negundo*, *Reynoutria japonica* and *Oenothera* spp., can dominate the riparian communities locally.

Sampling design and data analysis

Each study site corresponds to a stretch of the river that was considered to be representative for both botanical and geomorphological diversity. It corresponds to the frequently flooded zone (10-year floodplain for the French and American rivers, and the boundary between riparian vegetation and matorral for the Spanish ones). The species of higher vascular plants were counted during random walks within each site until no new species were found. Data were simultaneously collected by two scientists. The two resulting species lists were later compared. Since the area of the sampling zone may have varied, we used transformed species richness (TSR = number of species/$\log_{10}$ of the sampled area) as defined by Gleason (1922) and Whittaker (1972).

We classified the first observed species into groups according to (1) their life-span and (2) their physiognomy. First, we distinguished between annuals (A), biennials (B) and perennials (P, including herbaceous and woody species). Secondly, we distinguished between herbaceous species (H), vines (V, woody lianas), trees (T, height > 4·5 m), tall shrubs (TS, 1 m < height < 4·5 m) and small shrubs (SS, 1 m > height). All groups were processed as percentages of the total species richness in the data analysis. Moreover, we derived the following groups from the definitions of ruderal and riparian species given above. Species classified in the first two of these four groups may be called 'external' species.

1. *Non-riparian, non-ruderal species* (NRUNRI), which include all species even from non-riparian habitats, that do not exhibit ruderality as defined above.
2. *Non-riparian, ruderal species* (RUNRI), which are found occasionally or regularly in riparian zones, but that are normally very common in other habitats.
3. *Riparian, non-ruderal species* (NRURI), which are strictly confined to riparian systems.
4. *Riparian, ruderal species* (RURI), which do not live outside the riparian zone or other wetlands.

Species groups are the nomenclature for vascular plants follow Hitchcock *et al.* (1955–1969), Tutin *et al.* (1964–1980), Guinochet and De Vilmorin (1973–1984), García-Rollán (1974) and Valdés *et al.* (1987). Data on species groups were expressed as percentages of total species richness (i.e. relative species richness). Overall aspects of the composition of the flora of each river system were analysed considering (1) the total number of species found in all sites and (2) the average number of species found for the entire flora (mean transformed species richness) or for each studied species group.

Data describing physical attributes of the local structure of the riparian corridor and of the riverside landscape were collected from field observations and maps, GISs or aerial photographs. Qualitative variables were categorized in order to describe the environmental factors of interest (Table III). The purpose of the statistical analysis was to test for significant effects between categories of a given factor on the relative species richness for each plant group. Since some of the factors may be interdependent, but not completely redundant, a one-way ANOVA was performed for each factor. Analyses were performed for each of the sampling sets, i.e. for a given river or for pooled rivers (Spanish rivers under mediterranean semi-arid climate and French rivers studied only for exotic species).

Besides the factors described in Table III, we studied the permanency of superficial water for temporary streams, using three classes: (1) no water (dry streambed for more than a year), (2) intermittent drying (dry streambed during low-water periods) and (3) permanently wet streambed. This variable could not be tested for streams where superficial drying out of the main channel is not a regular event (Adour River), or only concerns one site (Mackenzie, site 1).

Table III. Definition of the categories used in ANOVAs in order to analyse the effect of the categorical factors studied (see text for sampling design)

Factor	Categories	Definition
Intensity of human influence	1. None	Natural areas, with no physical effects of human activities on the main channel
	2. Very weak	Sparsely affected by natural resources exploitation; no effect on the main channel but the riparian vegetation may be modified
	3. Weak	The structure of the riparian vegetation and of the river channel is slightly affected by human activities
	4. High	The river may be regulated and the natural vegetation partially destroyed
	5. Very high	Corresponds to urban or intensively cultivated zones; the main channel is highly managed and the vegetation often anthropogenic
Main land use	1. Natural	No crop fields or urbanization in the surroundings of the river
	2. Pastures	Landscape dominated by artificial or managed pastures
	3. Cultivated (crops and orchards)	Landscape essentially agricultural, dominated by non-forested areas
	4. Forestry	Landscape dominated by forested areas including artificial riverine forests
	5. Moderate urbanization	Sparse urbanization or small towns (< 50 000) not located on the riverside itself
	6. Intense urbanization	Study site included in an urban area (town with population higher than 50 000)
River zonation	1. Upper course	Generally constrained (V-shaped valley), mountainous reaches with torrential hydrological regime (high slope, high frequency and low duration floods, coarse sediments)
	2. Middle course	Intermediate zone, typically with high degrees of spatial heterogeneity
	3. Lower course	Potamon, usually with low flood frequency but with long-duration floods. Fine sediments deposited. Includes estuaries if they exist
Intense urbanization	1. Present	Study site included in urban city (with population exceeding 50 000, except in southern Spain where cities with populations of more than 1000 were taken into account)
	2. Absent	Study site without any city as described above
Presence of weirs	1. Present	The river is regulated by a weir at the study site
	2. Absent	No weir on the studied reach

Longitudinal patterns were analysed using double-weighted least-square local smoothing (DWLS, McLain, 1974, not shown in Figures). Only the main rivers sampled for both natives and exotics (Andarax, Adour and Garonne rivers) were analysed.

RESULTS

General characteristics of the studied communities

The major purpose of this study was to examine the overall ('mean') community structure in each sampled river to discover possible links with regional characteristics.

The Adour as well as the Mackenzie were very species rich compared to the Spanish rivers (Table IV). Concerning the exotics, the Adour River was also more species rich that the other rivers. The Arros and Midouze rivers had least species, and also the lowest values of transformed species richness (TSR).

Percentages of annual species (A) were lower in the Mediterranean rivers than in the oceanic ones. However, the Mackenzie showed a low proportion of annual species (13% of the total). The riparian flora of the Carboneras River was almost entirely composed of perennials (97%). Annuals were well represented in the exotic communities of the Adour and Garonne basins. They represented about 40% in the riparian corridors of the Arros and Luy rivers. The lowest percentages were found for the torrential rivers (Nive, Gave de Pau and Gave d'Oloron).

Percentages of herbaceous species (H) were higher in the oceanic than in the Mediterranean rivers. Except for the Gave d'Oloron, which has a rocky bed along most of its course, exotic communities showed similar patterns. Trees (T) were completely absent in the riparian corridor of the Carboneras River. The per cent of trees varied from one river to another, even under similar climates. The Andarax River exhibited the highest percentage of trees (12%). High percentages (> 13%) were always found with exotics. Shrubs clearly dominated the Mediterranean region. However, the understorey in the riparian corridor of the Mackenzie River was species rich. Tall shrubs (TS) and small shrubs (SS) where almost always present along the Mediterranean streams, except for the Andarax which showed the lowest percentage of shrubs.

The percentage of exotics (E) was lowest in the Mediterranean streams. The Aguas River had most exotic species in this data set. The Adour and the Mackenzie had the highest percentage of exotics, amounting to 26% on average for the American river.

All riparian communities included similar percentages of ruderals (RU). The lowest proportion was found in the Andarax River, with only 20% ruderals. The Mackenzie showed the highest proportions of exotic (26%) and ruderal species (27%). In contrast, the Andarax had the highest percentage of riparian species (60%).

Table IV shows that non-ruderal, 'external' species (NRUNRI) represented more than 20% of the flora along most rivers. The higher values were found in the most constrained river under oceanic climate, the Mackenzie. No significant difference was found between Mediterranean and oceanic rivers. The extreme values found for the exotic sets were 17% (Arros River) and 38% (Adour River). Most of the riparian species (RI) were non-ruderals (see NRURI). The highest representation of riparian ruderals (RURI) was found within the Adour River corridor (7%). Non-ruderal, riparian species (NRURI) were the major components of the flora, comprising nearly 60% of the flora in the Andarax River.

Longitudinal trends in species richness

The longitudinal trends of transformed, total species richness (TSR, Figure 2) were rather regular in the Adour and the Mackenzie rivers, whereas the Andarax River showed a high variability between sites. Along the Adour River, TSR increased from source to piedmont, as the valley widens and bottomland species become more numerous. The more heterogeneous and disturbed middle course showed high values of TSR. Very complex and dynamic sites such as site 13 (Tabacchi, 1992) showed the highest values. The TSR decreased in the lower course, except for at the very end of the stream. Similar trends were found for the Mackenzie River. There, the increase of TSR in the upper course was less than for the Adour River, as the channel remained constrained by the valley until site 5. This site was analogous to site 13 of the Adour

Table IV. Mean values for species richness and proportions of plant groups for the different rivers

	Aguas*	Almanzora*	Andarax*	Carboneras*	Mackenzie*	Adour*	Adour†	Garonne†	Arros†	Gave d'Oloron†	Gave de Pau†	Luy†	Midouze†	Nive†
Species richness	59	109	168	61	851	1396	369	176	53	91	168	71	55	81
Transformed species richness	8·1	11·5	9·5	6·9	45·5	71·6	9·5	6·3	2	3·3	5·2	2·5	2·6	4·2
Annuals (%)	10·1	11·60	5·9	3	12·8	28·1	38	32·6	41	24·9	26·8	39·7	28·9	21·1
Biennials (%)	–	4·1	3·2	–	3·8	6·2	6·1	4·8	5·9	6·1	8·9	4·5	2·7	4·3
Perenials (%)	89·9	84·3	90·9	97	83·5	65·7	55·9	62·6	49·2	59·5	58·5	55·8	62·5	66·9
Herbaceous (%)	63·1	58·1	59·3	57·3	80·4	86·6	80·2	71·8	76·6	59·2	68·2	82·3	70·3	62·2
Vines (%)	1·7	4·3	8·2	1·3	0·7	2·5	1·9	2·5	–	0·8	0·7	–	1·2	1·9
Trees (%)	2·2	5·2	12	–	4·5	4·7	9·8	15	14·4	19·9	14·6	13·6	14·8	15·2
Tall shrubs (%)	23·2	22·6	17·9	26·6	10·2	4·2	7·7	9·3	5	9·7	8·3	4·1	6·4	12·6
Small shrubs (%)	9·8	9·8	2·6	14·9	4·3	1·9	0·5	1·5	–	0·9	2·3	–	1·5	0·5
Natives (%)	91·7	94·4	94·1	94·5	73·6	82·1								
Exotics (%)	8·3	5·6	5·9	5·6	26·4	17·9								
Ruderals (%)	43·3	32	20	32·5	27·4	45·2	40·4	34·9	48·1	43·5	45·9	44·4	28·8	36·7
Riparians (%)	38	39·8	60·1	32·3	33·1	26·2	23·5	29·9	32·2	19·1	18·6	31	29	28·7
Non-riparians, non-ruderals (%)	18·8	29·9	21·5	35·2	43·1	35·8	38·3	37·6	17	28·5	30	26	37	27·6
Riparians, non-ruderals (%)	38	31·1	58·5	32·3	29·6	19·1	21·5	27·6	30·9	18·5	18·3	29·7	28·4	28
Non-riparians, ruderals (%)	43·3	30·3	18·4	32·5	23·8	38·1	38·3	32·6	46·8	42·9	45·6	43·1	28·1	36
Riparians, ruderals (%)	–	1·7	1·6	–	3·6	7·1	2	2·3	1·3	0·6	0·3	1·3	0·7	0·7
Halophytes (%)	15·7	8·6	5	20·9	–	0·7	1	1	–	–	–	0·3	–	0·4

* Native and exotic species
† Only exotic species

River (Planty-Tabacchi, 1993). The Andarax River showed higher values of TSR in the upper than in the lower course. However, no clear pattern appeared here.

Longitudinal changes in percentages of the plant groups

The percentage of exotic species (E, Figure 3) increased regularly from the source to the piedmont for the Adour and for the Mackenzie rivers. This trend continued beyond the piedmont but with a lower slope. Maximum values (39·5% for the Adour River and 53% for the Mackenzie River) were found in the lowest part of the courses. The Andarax River showed a more irregular pattern, with a minimum value in the middle course (18·2%).

A similar longitudinal pattern was found for ruderals (RU, Figure 3). The Andarax River showed a contrasting pattern, with low percentages in the upper part and higher values in the lower part. The contribution of ruderals varied from 0 to 45·5% (Andarax), from 12 to 58% (Adour) and from 6·6 to 50% (Mackenzie).

The even proportion of riparian species (RI, Figure 3) along most rivers contrasted with strong variability in the Andarax River. The percentage of riparian species decreased for all streams in the lower course.

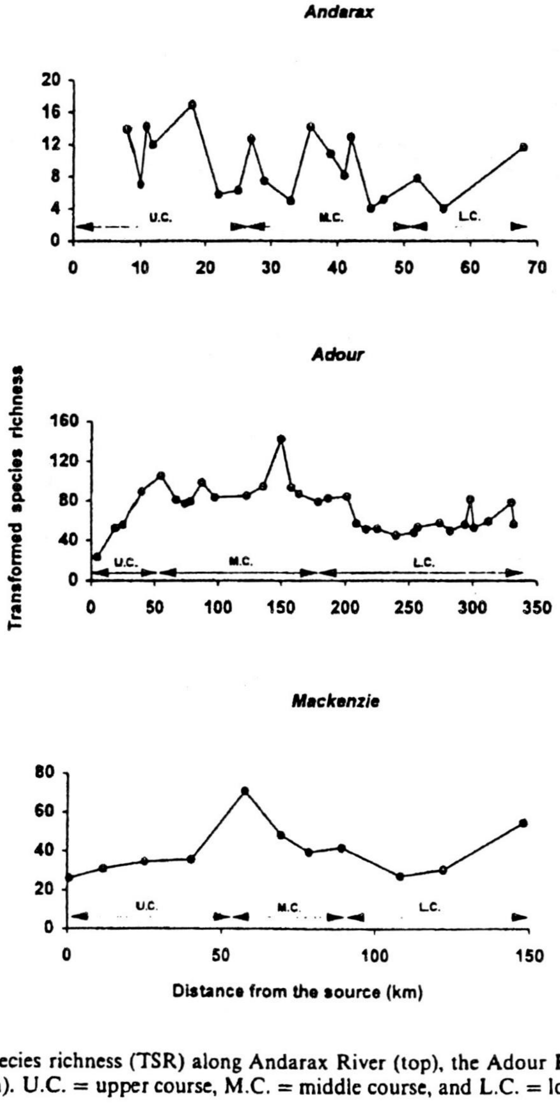

Figure 2. Changes in transformed species richness (TSR) along Andarax River (top), the Adour River (middle), and the Mackenzie River (bottom). U.C. = upper course, M.C. = middle course, and L.C. = lower course

However, a clear peak appeared in the marshy 'Barthes' region on the Adour River, just before the final decrease. The riparian species varied between 3–88% for the Andarax River, 12–51% for the Adour River and 24–44% for the Mackenzie River.

Non-ruderal, riparian species showed low values (< 10%) only in the lower courses (NRURI, Figure 4). A low contribution of these species was also found in site 17 of the Adour River, which exhibited cliff-like river banks. The Andarax River showed high spatial variability without any clear trends. In contrast, the Mackenzie River showed a regular pattern, with two maxima, one at the uppermost course (site 2) and one at the lowermost course (sites 8 and 9). The Adour River showed an intermediate pattern, with percentages increasing downstream up to the estuary, and a clear peak in the Barthes stretch.

Ruderal, but non-riparian species (RUNRI, Figure 4) along the Andarax River were rare along the uppermost 40 km, but more common further downstream. This pattern is similar to that observed for RU in the other rivers studied.

Non-ruderal, non-riparian species (NRUNRI, Figure 5) showed a U-shaped pattern in the Andarax River, with a clear central peak at sites 9 and 10. An asymmetric U-shaped pattern was also observed for the Adour River, indicating a strong decrease of proportions from the source to the piedmont, and then a stabilization of the decrease with a high spatial variability. The Mackenzie River showed a more regular pattern with a rather constant decrease of the percentages of NRUNRI. However, the sites of the constrained channel (sites 1 to 4) clearly exhibited higher values than those of the unconstrained channel.

The proportion of ruderal riparian species (RURI, Figure 5) alternated between zero and relatively higher values along the Andarax River. The contribution of this group to the total species richness was more regular in the Adour River, where it was intermediate between that of the non-riparian ruderal species (RUNRI) in

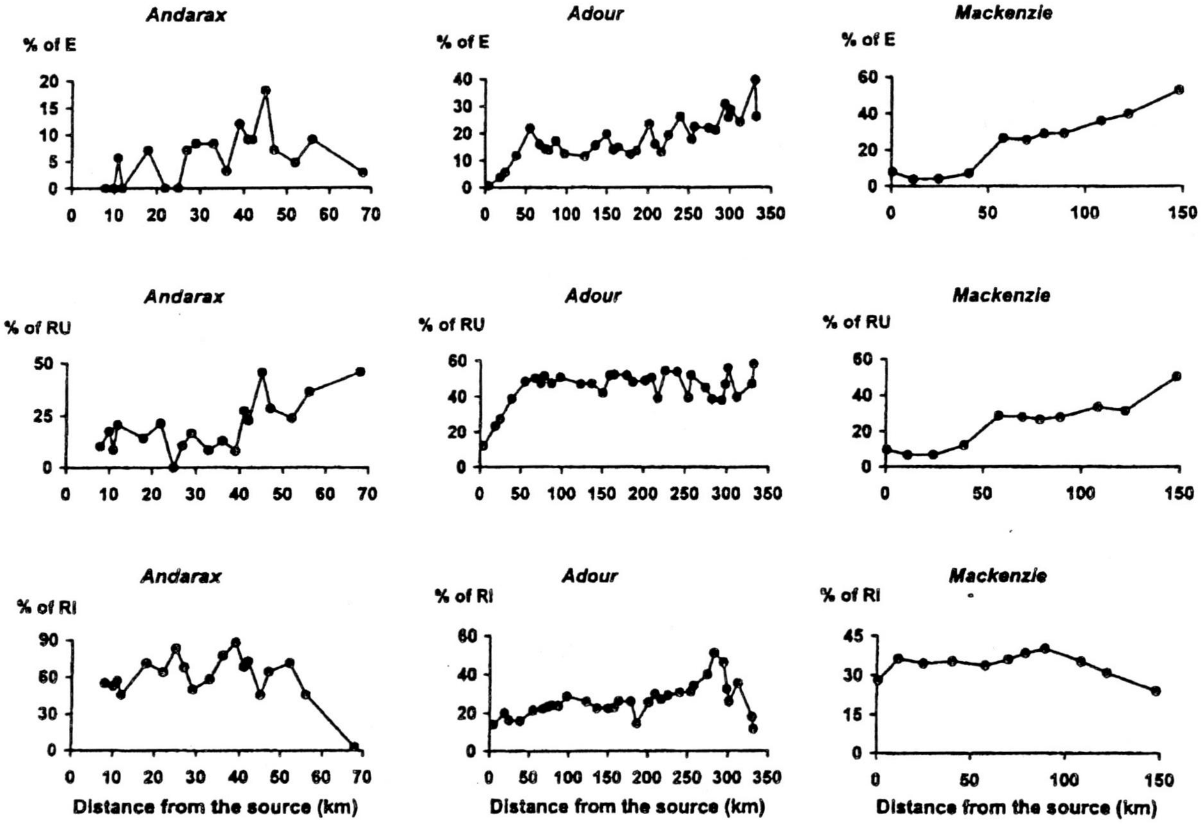

Figure 3. Changes in percentages of exotics (E), ruderals (RU) and riparian species (RI) along the three rivers studied

the upper part of the course, and that of the non-ruderal, riparian species (NRURI) in the middle and lower courses. The RURI group in the Mackenzie River showed a slight increase downstream.

Factors affecting the community structure

Between-stream differences. Table V synthesizes the results found in ANOVAs when analysing the effect of various environmental factors on species richness distribution. Variables that have shown significant differences for a given sampling set (single river or pool of rivers) are shown in Table V (vertically reading).

The intensity of human influence (HI), the dominant land-use type (LU) and the presence of intense urbanization (U) were the only three factors significantly affecting some groups in the four Spanish rivers pooled. When the Andarax River was analysed by itself, the number of groups that appeared to be sensitive to land use increased from one to six. Also, the river zonation was significant for six plant groups.

The vegetation of the Adour and Mackenzie rivers appeared to be sensitive to the land-use dominant type, to river zonation, to urbanization and, to a lesser degree, to a moderate regulation of the flow. The effect of the intensity of human influence was apparent for the Adour River, but not for the Mackenzie River.

Overall, only the exotic communities (Table V, columns 6–14) were sensitive to all the environmental variables tested. However, a significant effect of weirs was only expressed by a few groups. When each river was considered individually, only the communities of the Adour and Nive rivers were highly dependent on the intensity of human influence in the riparian zone. The Arros, the Gave de Pau and the Gave d'Oloron rivers were those most influenced by the dominant land-use type in their surroundings. No significant effect was found for the Midouze and Luy rivers. Exotics of the Garonne, the Nive, and the Gaves rivers were the

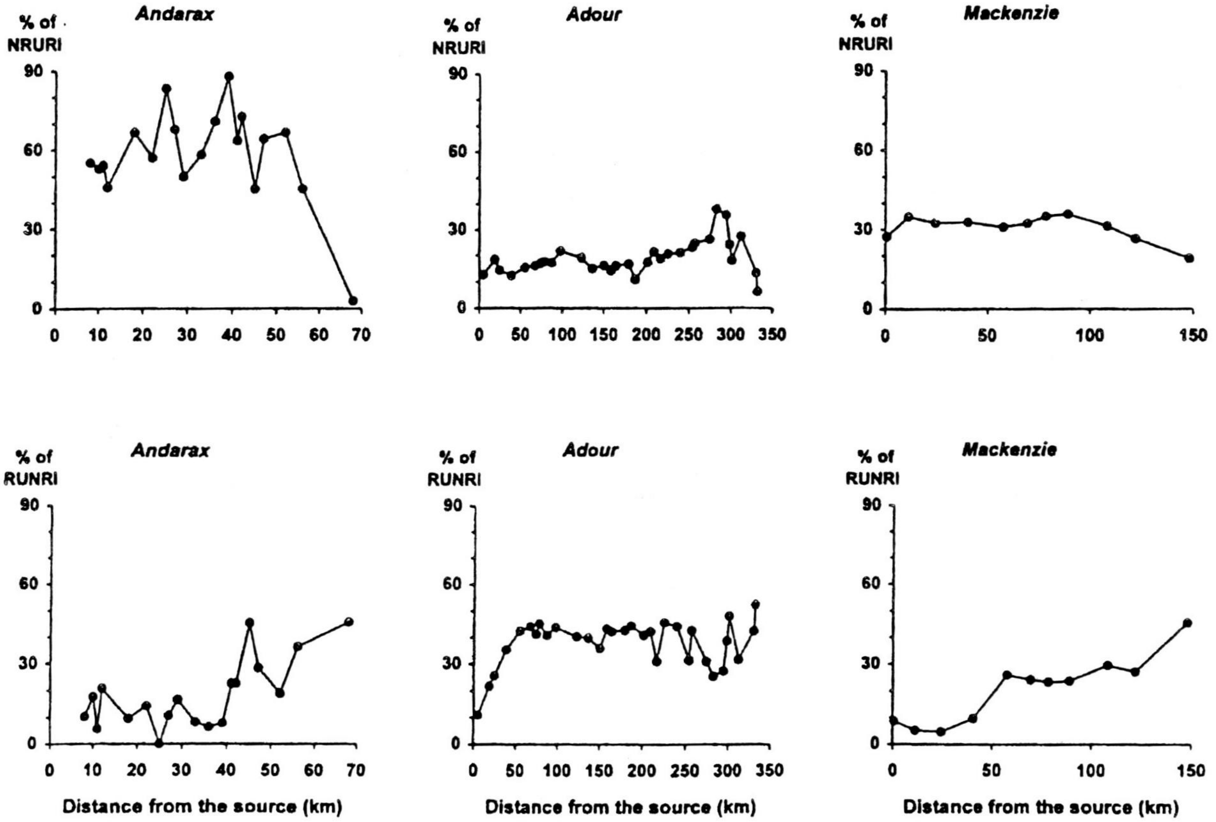

Figure 4. Changes in percentages of non-ruderal riparian species (NRURI) and non-riparian ruderals (RUNRI) along the three rivers studied

most sensitive communities to the river zonation. Exotic communities of the Adour River were influenced by intense urbanization. The moderate regulation of the rivers by weirs appeared to modify the distribution of exotic species richness for the Adour, Arros and Luy rivers.

Species groups as indicators of spatial changes. Table V (horizontal reading) indicates what species groups were the most sensitive to the environmental factors studied. The intensity of human influence (HI), land-use (LU) and river zonation (RZ) were the most important factors in affecting the patterns of total species richness. This was also the cause for annuals, perennials, herbaceous species, ruderals and non-riparian ruderals. The proportions of tall shrubs (TS) varied between sites according to the presence of weirs (W) only for the exotic community of the Adour. The percentage of trees (T) seemed to depend mostly on river zonation (RZ), but only for exotics. Strictly riparian species (RI) were sensitive to the land use, their location along the river and to the presence of large urban areas. However, relatively few rivers responded that way. Non-riparian, non-ruderal species were very sensitive to land use and river zonation. Riparian ruderals appeared to be more sensitive to the river zonation than to other human-induced factors. They were the group that was most affected by weirs.

Additional analyses showed that no significant differences in the permanence level of superficial water can be found for the Andarax River. Significant responses (ANOVA, $P < 0{\cdot}02$) between all categories were shown by the small percentages of small shrubs, halophytes, ruderals, riparians, non-ruderal riparians, non-riparian ruderals and riparian ruderals. Results for the four Spanish rivers pooled were very similar. TSR expressed a sensitivity of the communities to the permanence level of superficial water (ANOVA, $P = 0{\cdot}008$). However, significant differences were only found between annual drying out and permanent

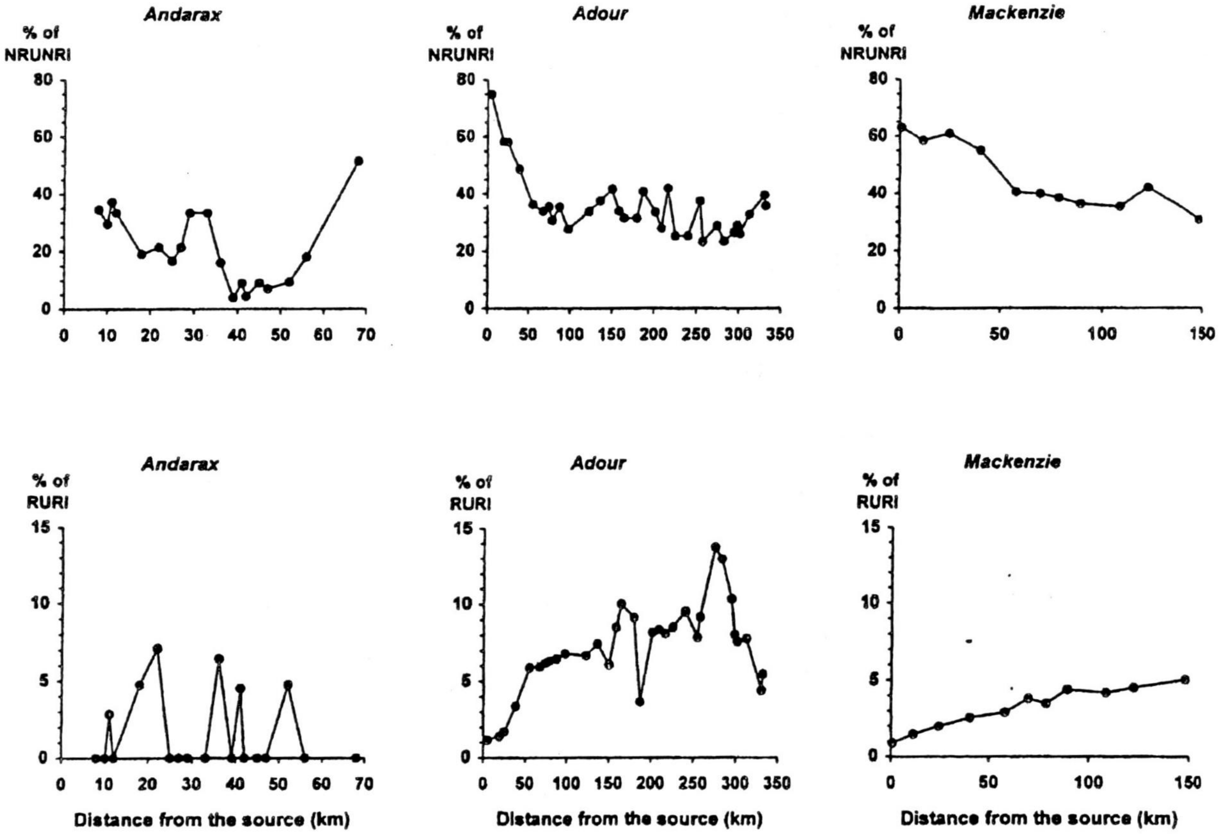

Figure 5. Changes in percentages of non-riparian, non-ruderal species (NRUNRI) and riprian ruderals (RURI) along the three rivers studied

Table V. Factors inducing a significant response ($P < 0{\cdot}05$) in one-way ANOVAs for a given sample set (columns) and a given plant group (rows)

Plant group	Four rivers pooled*	Andarax*	Adour*	Adour†	Mackenzie*	Eight rivers pooled†	Garonne†	Arros†	Gave d'Oloron†	Gave de Pau†	Luy†	Midouze†	Nive†
Transformed species richness				HI,LU,U		HI,LU,RZ,U	HI,LU,RZ	HI,LU,RZ	HI,LU,RZ	LU,RZ	HI	RZ	HI,RZ
Annuals (%)		HI,LU,RZ	HI,LU,RZ	HI	LU,RZ,U	HI,LU			LU,RZ	HI,LU,RZ			HI,RZ
Biennials (%)			W	RZ,U	LU,RZ	U	LU	RZ	RZ				
Perenials (%)		RZ	HI,LU	HI	LU,RZ,U	LU,RZ		W,LU					HI
Tall shrubs (%)				W									HI
Herbaceous (%)	HI			W,HI,RZ		HI,LU,RZ,U	LU,RZ		LU,RZ	HI,LU,RZ			HI,LU,RZ
Vines (%)			HI,RZ			LU		-		RZ	-		
Small shrubs (%)			HI,LU	LU		W		-		RZ,U	-		
Trees (%)				HI		HI,RZ,U	LU,RZ	LU,RZ		LU,RZ	RZ	RZ	HI
Exotics (%)	U	LU,RZ,U	HI,RZ,U	-	W,LU,RZ,U	-	-	-	-	-	-	-	-
Ruderals (%)		RZ	HI,LU,RZ	HI,U	LU,RZ,U	HI,LU,RZ,U		LU	HI	HI,LU			HI,RZ
Riparians (%)		LU	W,RZ	HI,LU	U	LU,U	RZ		LU		W,RZ		HI
Non-riparians, non-ruderals (%)	LU,U	LU,RZ,U	HI,LU,RZ	HI	LU,RZ	HI,LU,RZ	RZ	LU,RZ	LU,RZ	LU,RZ		RZ	
Riparians, non-ruderals (%)		LU	RZ,U	HI,LU	LU,U	LU,U			LU		W		HI
Non-riparians, ruderals (%)		LU,RZ	W,HI,LU	HI,U	LU,RZ,U	HI,RZ,U		LU	HI	HI,LU			HI,RZ
Riparians, ruderals (%)			HI,RZ	W,RZ	LU,RZ	W,HI,LU,RZ	LU,RZ			RZ	HI,RZ	RZ	RZ

* Exotics and natives

† Exotics only

Abbreviations for the factors are: HI = intensity of human influence; W = presence of weirs; LU = main land use; RZ = river zonation; U = intense urbanization

Unrepresented groups are denoted by (–)

superficial water for the TSR. Other groups with highly significant responses ($P < 0{\cdot}006$) were percentages of small shrubs, ruderals, riparians, non-ruderal riparians, non-riparian ruderals and riparian ruderals.

DISCUSSION

Species richness and landscape structure

This section refers to rows 1 and 2 of Table IV. The higher species richness of the riparian corridors of the Mackenzie and the French rivers than the Spanish rivers is the consequence of a milder climate which favours mesic and hydric communities. It may also be due to the habitat diversity and smooth transversal gradients found under oceanic influences. We (Planty-Tabacchi *et al.*, 1996) suggested that the high species richness of the Adour and Mackenzie rivers might result from (1) the presence of non-altered sources of riparian and non-riparian species at the regional scale and (2) a relatively high level of spatial heterogeneity within the riparian corridor following river dynamics. This last point is probably more important for the very dynamic Adour River (Tabacchi, 1992) than for the Mackenzie River, whose intense natural dynamics have been recently modified in some parts of the course (EA, 1991). The hypothesis that the river dynamics are likely to favour 'external' species is supported by findings about exotics, which are most species rich in the most dynamic streams. In contrast, bottomland rivers (Luy, Midouze, Aguas and Carboneras) tend to exhibit low TSR. The length of the river does not appear to be a discriminant factor for the recruitment of 'external' species. However, the relatively high values of exotics found in the riparian corridor of the highly managed Garonne River suggest an accumulation of species as the river crosses new areas and successively recruits new species. In semi-arid climates, riparian vegetation is more isolated from the surroundings by sharp ecological gradients. Moreover, the temporary character of superficial water availability induces a high selection pressure on riparian plants (low values for the more arid Aguas and Carboneras). Similarly, low values of species richness have been observed by Szaro (1990) in semi-arid riparian communities in south-western USA.

Importance of species traits to community and landscape structures

This section refers to rows 3–19 of Table IV. The mean community composition in terms of life span (A, B, P, Table IV) also seems to be dependent on climate and stream dynamics. High percentages of short-lived species were found mostly along the Adour River. Because of their dominant ruderal-type strategy, exotics also included high percentages of annuals. The low values found for the Mackenzie River may be explained by the low extent of bare sediment along most of its course. The rapid colonization of stream banks by shrubs or even coniferous species does not favour the establishment of short-lived, light-demanding species. For the riparian corridors of the Spanish rivers, the hydrological regime may explain the low percentages of annuals. These plants cannot rapidly develop deep roots to reach groundwater. Olsvig-Whittaker *et al.* (1983) drew the same conclusions in their study in the Negev Desert.

The morphologies of plants (TS, H, V, SS, T, Table IV) varied according to the dominant regional vegetation pattern. High percentages of shrubby species were found in the riparian zone of the Spanish rivers and the Mackenzie River. Along the Spanish rivers, the riparian zone was dominated by tall shrubs, reflecting the matorral pattern of the surroundings. The riparian forests of the Mackenzie River were also rich in shrubby vegetation, for example in the areas surrounded by old-growth pristine, or younger planted, Pacific coniferous forests (Dyrness *et al.*, 1974). However, on average, patterns of the Mackenzie River communities were more similar to those found along Atlantic river than to those found along Mediterranean semi-arid rivers. The low percentage of herbaceous (exotic) species found along the Gave d'Oloron River is mainly due to the importance of the rocky bed of this river.

Communities under mediterranean climatic influences have been pointed out as some of the areas most sensitive to biological invasions (Di Castri *et al.*, 1990; Groves and Di Castri, 1991). However, the percentages of exotics found along Spanish streams (E, Table IV) were significantly lower than those found along the Adour and Mackenzie rivers. This may be due to a low level of recent human influence along the semi-arid rivers. The hydrological regime in this region has favoured strong competitors among native species. Most exotics in the mediterranean semi-arid climate are adapted to semi-arid non-riparian environment (cf. Groves and Di Castri, 1991). As a consequence, unspecialized exotics are not favoured in the riparian environments studied. The wide range of climatic and soil characteristics, and water availability of the oceanic corridors enhance the establishment of exotics (Planty-Tabacchi, 1993). Moreover, the increasing fragmentation of the landscape, and the increasing connectivity between terrestrial and river networks also facilitate invasions (Planty-Tabacchi, 1993). Surprisingly, we found higher percentages of exotics in the riparian corridor of the Mackenzie River than in that of the Adour, although the latter has been managed for a much longer time (several centuries). The fact that the Mackenzie valley has been used as a main travelling route for a long time may explain this.

The relatively constant proportions of ruderals among all the streams is surprising. The ruderals found in this study were mostly non-riparian. Very few, except along the Adour, were specific to riverine environments. Higher percentages of ruderals were found in very dynamic, open streams. The presence of ruderals generally reflects the level of disturbance within the riparian corridor, but also in the near uplands. The relatively high abundance of ruderals along the Arros River can be viewed as a consequence of the close contact between the riparian vegetation and the adjacent cultivated soil. The Andarax showed a lower percentage than the other rivers. This may result from the little space available for non-riparian vegetation within the narrow riparian corridor. Also, the regularly cut edge of mixed salt cedars and *Arundo donax* along the Middle Andarax constitutes a barrier to invasion of the narrow streambed by species from adjacent crop fields. When the channel suddenly widens in its lower course, the matorral invades the non-inundated habitats of the channel, excluding other species from the riparian habitats.

Strictly riparian species also showed a relatively constant proportion, ranging from 20 to 40%. However, the highest percentage (60%) was found along the Andarax River. The other semi-arid rivers also showed high values, clearly indicating the sharp gradient between the matorral and the riparian zone. This gradient does not allow unspecialized species to enter the corridor easily and to compete more efficiently with true riparian species. This is confirmed by the low percentages in non-riparian groups (NRUNRI, RUNRI). The percentage of non-riparian, non-ruderals may be an indicator of how much the riparian corridor can integrate 'external' species. The high values of NRUNRI found along the Mackenzie River confirm that the riparian zone is not nearly dissociated from external forests along most of its course. Conversely, the very low values found for the Arros River indicate that few other 'external' species than ruderals can occupy the riparian corridor, because of its isolation from non-cultivated areas.

Longitudinal gradients and local features

A striking contrast exists between the longitudinal patterns exhibited by the Andarax River and those occurring along the Adour and the Mackenzie. This contrast results mainly from a high spatial variability, and also from the absence of clear longitudinal patterns along the semi-arid Mediterranean river (see Figures 2–5). The patterns observed along the Adour and the Mackenzie may be related to the intermediate disturbance hypothesis (Connell, 1978; Malanson, 1984) with maximal species richness in the middle course (Tabacchi, 1992; Planty-Tabacchi, 1993; Planty-Tabacchi *et al.*, 1996). Similar patterns were found by Nilsson *et al.* (1989) for north European rivers. The irregularity of patterns for the Andarax suggests that discontinuities induced by the shifts between intermittent and permanent surface water during most of the year are directly reflected by the vegetation. Spanish sites pooled and tested for this factor gave a significant response for most sampled plant groups. However, no significant response was found in ANOVA for TSR for the Andarax alone. The lack of data for the uppermost Andarax does not allow us to test the altitudinal change for TSR found for the oceanic rivers from the source to the piedmont. However, the low values of TSR in the Middle Andarax, when the channel becomes more constrained by the surrounding mountains, are analogous to the low values of TSR in the constrained Upper Mackenzie. The channel constriction also results in the lower species richness of riparian species in site 17 of the Adour River, which showed cliff-like river banks (cf. Tabacchi and Planty-Tabacchi 1990; Tabacchi *et al.*, 1990). Nilsson *et al.* (1991a) made similar observations concerning the effect of high river margins. Lower courses use to exhibit low species richness (cf. Nilsson *et al.*, 1989). This can be viewed as a result of lower disturbance frequencies (Malanson, 1984) and of longer durations of inundation, which favour only specialized species (mostly helophytes). This hypothesis may be verified in values found for a long-flooded area of the 'Barthes', on the Adour River, where non-ruderal and ruderal riparian species have a great importance in the community. This group does not exhibit as clear a response in the Lower Mackenzie, where a less-developed floodplain only exists downstream from the confluence with the Willamette.

The downstream increase of exotic species along the Adour and the Mackenzie corroborates the results of Nilsson *et al.* (1989) for ruderals along Swedish rivers. In our study, ruderals responded very similarly to exotics. There are two alternative explanations for this pattern: (1) although all the invading exotics are not ruderals in our sampling area, many of them can belong to both categories (this is particularly the case for the Mackenzie); (2) both groups are known to be favoured by human influences that increase downstream (see the results of the ANOVA analyses). Most ruderal species are favoured by naturally high disturbances (Grime, 1979) but also by habitat fragmentation (Hanson *et al.*, 1990) and by the presence of cultivated fields. This group, as well as exotics, may be a good predictor of human influences along the stream. Despite their low percentages, riparian ruderals also showed regular responses along the oceanic streams. When flooding conditions were stressful for unspecialized ruderals (i.e. most of the ruderals), non-ruderal riparian species as well as riparian ruderals increased. This was very obvious for the Adour River ('Barthes' reach). The widening of the main channel slowed down the increase of non-riparian ruderals, whereas riparian ruderal continued to increase following a more suitable habitat supply. The increase of non-riparian ruderals in the Lower Andarax reflects the increase in human influences. Riparian ruderals were only present when the main channel provides permanent water. The competition with non-riparian species is likely to be too strong for the sustainability of riparian ruderals in stretches with temporary water. This is the case for the lowermost site of the Andarax, where almost only *Tamarix canariensis* was able to survive with a wide dried bed invaded by matorral species.

Non-ruderal riparian plants are logically the group most sensitive to the local configuration of the river. A widening of the channel reduced their proportions in the Lower Andarax and in the Lower Mackenzie. Also, they decreased in percentage in the Andarax when the strongly constrained channel favoured the invasion of species from the surrounding matorral. This was not the case on the Upper Mackenzie (except for site 1, which dried out temporarily), because the river banks remained suitable for specialized (hydrophilous) vegetation.

This edge effect, with invasion by 'external' species when the channel became constrained or wide, also appeared for the Andarax for non-riparian, non-ruderal plant species. However, this group appeared to decrease downstream along the Adour and the Mackenzie. Their strong decrease along the altitudinal gradient in the Upper Adour clearly corresponded to a change in riparian vegetation, which integrated successively fewer mountain species. This is also the case for the Mackenzie. However, although Hobbs and Hopkins (1991) suggested that riverine corridors are not likely to be useful for upland species, Tabacchi (1992) showed that upland species could colonize lower reaches of rivers after migration from mountains along the hills. Such local contacts with hills or very contrasting habitats can explain most of the little peaks observed along the Adour River.

Sensitivity of plant groups to various factors

The significant effects of various environmental factors on the community composition of the Andarax can be explained by the great variability in human influences and hydrology along its course. This variability was lower along the semi-arid streams (Table IV). The high number of significant responses to the intensity of human influences for the Adour River, which includes both managed and unmanaged corridor stretches, can be explained in a similar way. This is not true for the Mackenzie River which, except in its last two downstream study sites, shows little evidence of human effects.

As suggested by previous studies on wetlands (McIntyre *et al.*, 1988; Planty-Tabacchi, 1993; Tabacchi, 1995), and even in other systems (Mooney and Drake, 1986; Drake *et al.*, 1989; Groves and Di Castri, 1991), exotic communities are greatly sensitive to both natural and human-induced disturbances, for any tested factor except the presence of weirs. Surprisingly, riparian ruderal species appeared to be the group most sensitive to moderate regulation (weirs). Non-ruderal riparian species also showed sensitivity to the presence of weirs, indicating that moderate regulation may affect natural community patterns.

Results found using ANOVAs for permanency of superficial water in semi-arid rivers show that the only temporary continuity, induced by longitudinal changes in the natural water supply, is probably the most important factor to structure semi-arid riparian communities. Hughes (1990) came to similar conclusions from minimum food frequency and duration data. No doubt, this factor drives other environmental constraints, such as human effects on the riparian zone.

The sensitivity of many species groups to the river zonation indicates that, at least under temperate oceanic climates, longitudinal geomorphic patterns are predominant in governing community structure. Non-riparian, non-ruderal species appeared to show stronger differences than true riparian species, probably as a consequence of intense recruitment at high altitudes and close to hillslopes at lower elevations. Community structure may not be affected by the factors studied here but only by changes in landscape structure. These factors may directly or indirectly affect the competition balance between the true riparian species and 'external' invaders. This is suggested by the observed between-year changes in community structure related to changes in climate and hydrology in the riparian zones of the Adour River (Tabacchi, 1995; Décamps *et al.*, 1995).

CONCLUSIONS

This study showed that the control of species diversity and overall community composition of riparian vegetation does not depend only on river-related processes and structures, but rather on the simultaneous effect or regional (river-independent) and local factors. In this context, as stated by Kellman (1970), accessibility is a major factor in species dynamics and diversity. However, the external edges of the riparian corridor are often forgotten (Cargill, 1988), because they are likely to play a minor role to the interior ones, which are more exposed to the hydrological disturbance. The role of the external edges in controlling species richness seems to be fundamental. In semi-arid riparian communities this control is enhanced by changes in the flow permanency, which allow upland vegetation (matorral) to invade the riparian zone. In oceanic, temperate riparian communities the edge structure, primarily delineated by natural disturbance, is also controlled by human activities, which modify the permeability of this ecotone.

Various human effects, even of recent origin, have significant effects on riparian plant groups. Community structure is likely to have changed from pristine conditions, especially following the invasion of 'external' species. This suggest that riparian systems may be easily invaded by 'external' species following changes in landscape structure. However, as suggested by Church (1995), the time-scale related to structural changes in river ecosystems may be controlled by macro- and microscale factors that have not been identified in this study. In particular, spatial (longitudinal) patterns in the resilience of the system and detailed competitive processes deserve more study.

A reference to 'external' species such as ruderals and exotics may be a useful tool in investigating the relationships between the river and its catchment area. Indeed, exotics have been pointed out to be sensitive to both regional and local patterns. Surprising structures occurred when comparing the proportions of ruderals, which were almost constant whatever type of river was being considered. This suggests some control of this supposed 'external' component by the river itself, independent of the regional constraints. Also, when regional environmental constraints are low, regular longitudinal patterns, possibly related to the river disturbance regime, may be found for autochthonous as well as for allochthonous species.

Moreover, rivers can be viewed as permanent or temporary vectors of species dispersal through the riparian corridor towards downstream terrestrial systems (Planty-Tabacchi, 1993) or one may find some refugia within the riparian zone following regional or historical constraints (Meave *et al.*, 1991). Thus, understanding the internal (river-related) and external control of riparian communities may provide the basis for efficient management strategies for biodiversity conservation (Naiman *et al.*, 1993) at the local scale (riparian reaches) or at the regional scale (catchment area and hydrological network).

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