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Continuity and discontinuity of the riparian vegetation along a fluvial corridor

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Abstract

The concept of continuity/discontinuity is applied to the riparian vegetation of the corridor of the River Adour (S.W. France), in order to precisely define longitudinal structure, and to test the degree of floristic continuity of the fluvial axis. The measure of floristic connectance along the river course is based on presence/absence data, and is applied to successive stretches of the river, at various resolution levels. This analysis shows that the River Adour corridor cannot be assumed to be floristically continuous. The observed discontinuities may correspond to two types of change in the riparian vegetation: zones of slow change (high level of floristic connectance) or zones of sharp change (low level of floristic connectance).

Introduction

Several authors have described the ecological changes one can observe along hydrographic networks in temperate climates (Vannote *et al.* 1980; Ward and Stanford 1983; Statzner and Higler 1985; Minshall *et al.* 1985; Naiman *et al.* 1987). Riparian vegetation has received little attention in this respect, despite its recognized importance in the functioning of river ecosystems (Cummins *et al.* 1984; Petersen *et al.* 1987; Pinay and Décamps 1988) or in its dynamics (Pautou and Décamps 1985; Décamps *et al.* 1988). Recent developments relate the richness of the riparian vegetation to the river continuum concept (Nilsson *et al.* 1989) or emphasize the need for a better characterization of land/inland water ecotones along fluvial systems (Naiman *et al.* 1988a, b; Pinay *et al.* 1990).

This paper proposes an approach to the perception of the longitudinal continuities and discontinuities of the riparian vegetation of the Adour River, France, at various levels of resolution. Three main questions were addressed: (1) How to relate the numbers of common species of consecutive sites to the degree of longitudinal continuity of the riparian vegetation? (2) Are the structures drawn up in such a way as to be in agreement with the analysis of environmental data? (3) How do those structures vary according to the spatial scale chosen? We used simple enumeration of species in order to answer these questions.

The river and its riparian vegetation

The River Adour stretches along 335 km from the Central Pyrenees (alt. 2200 m) to the Atlantic Ocean (Fig. 1). Its catchment area is 17 000 km². The Arros River (confluence from order 5 to 6) magnifies its geomorphological activity in the upper main tributary, the Gaves River (confluence from order 6 to 7), contributes two thirds of the

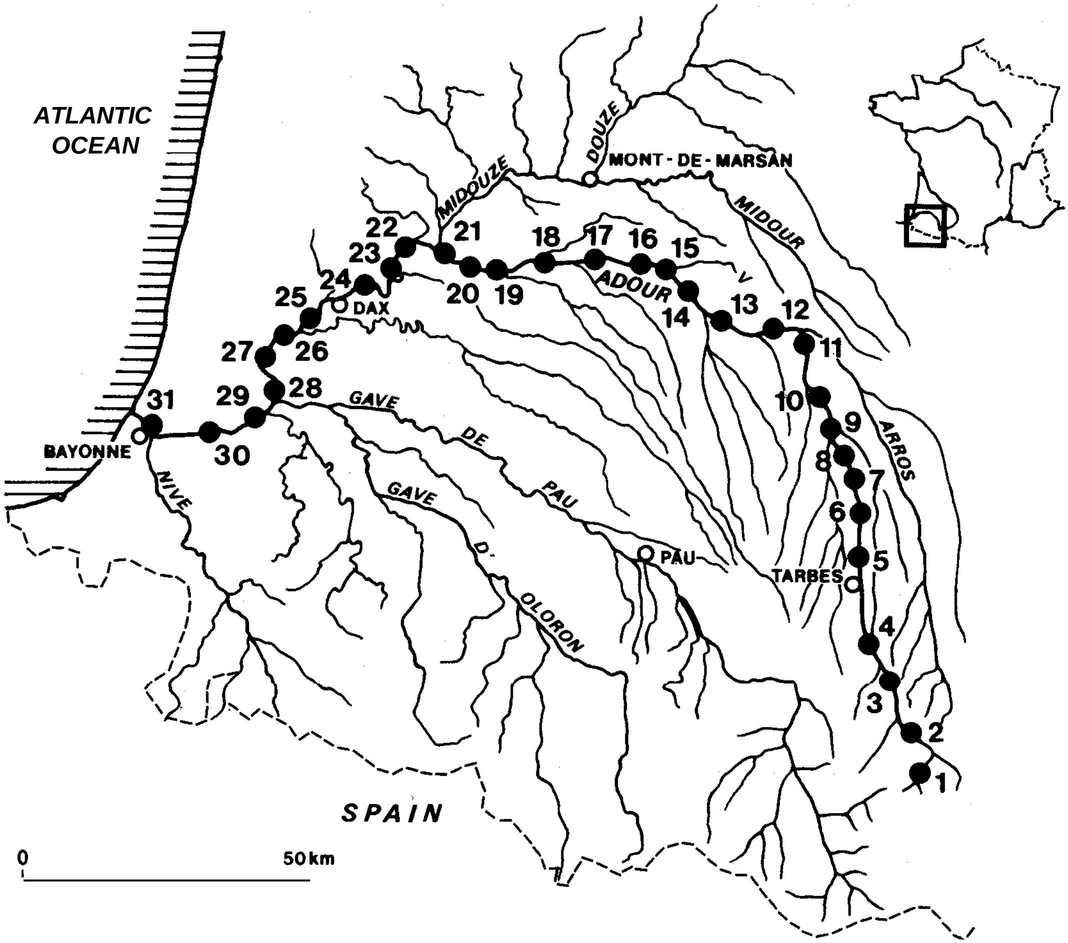

Fig. 1. Location of the 31 sampling sites along the **Adour** River, SW France.

mean water discharge, which is 350 m^3/s at the mouth.

The whole drainage basin is under an atlantic climatic influence. However, three minor climatic influences (mountain, submediterranean, subcontinental) modify the composition of the riparian vegetation along the river (Tabacchi and Planty-Tabacchi 1990). The natural corridor of the Adour River is particularly well conserved, although the lower part of the floodplain has been managed for agriculture since the XVIIth century. An important diversity of the riparian landscapes characterizes the Adour River.

Sites and methods

A total of 31 sites, each about 10 km apart, were studied along the Adour River (Fig. 1). These sites were ordinated by reciprocal averaging of 58 environmental variables (geomorphological, physico-chemical, physionomical). Ordination was made upon a complete disjunctive matrix (370 x 31). Then, the first seven component scores were used in a hierarchical cluster analysis (reciprocal neighbour clustering, ADDAD program, J. Juan, 1983). The resulting typology was compared to the zonation of the vegetation and to the species richness data.

The riparian vegetation was observed from February to May 1987, within the natural corridor, as defined by Forman and Godron, 1986. The num-

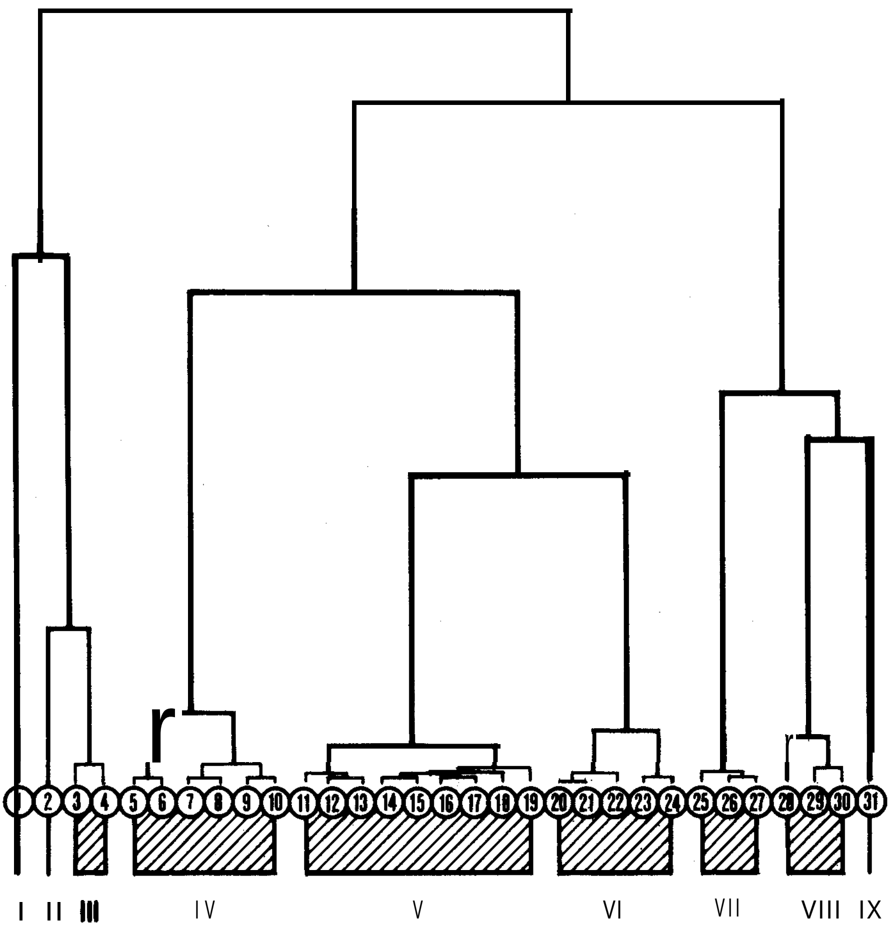

Fig. **2. Dendrogram of similarities between sampling sites according to environmental data. (Hierarchical ascendant clustering, reciprocal neighbours method). Sum of level indexes: 0.26703. Nine groups of sites (hatched zones) are created from the 31 sites studied.**

ber of vascular species (Bryophyta excluded) was considered. We showed (Tabacchi and Planty-Tabacchi, 1990) that no surface-scaling transformation (Whittaker 1975) was needed for our data.

The longitudinal changes in the composition of the riparian vegetation may be approached considering the number of common species to a given number of consecutive sites. The studied sites of the Adour River follow one another from i = 1 (spring) to i = 31 (mouth). We can define a 'window of observation' of w consecutive sites, and then move this window downstream along the series of consecutive sites, making a shift of one site. At each step, we define a group $G_{i,w}$ of w consecutive sites, the first site of which is the site i. The set of species richness corresponding to such a group is:

$$(S_i, S_{i+1}, \ldots S_{i+w-1}).$$

As an example for a window where w = 5 sites:

group	set of sites	set of species richness
$G_{1,5}$	1 2 3 4 5	S_1, S_2, S_3, S_4, S_5
$G_{2,5}$	2 3 4 5 6	S_2, S_3, S_4, S_5, S_6
$G_{3,5}$	3 4 5 6 7	S_3, S_4, S_5, S_6, S_7

We characterized each group $G_{i,w}$ by two variables:

1. $C_{i,w}$, the number of common species observed,
2. $T_{i,w}$, the expectancy of the maximum floristic affinity.

These two variables are related. Theoretically, the maximum number of common species possible within a group $G_{i,w}$ is the minimal species rich-

Table I. Characterization of the 31 sites studied from the principal trends of the mesologic analysis. (The nine groups of sites correspond to those of Fig. 2).

Sites	Order	Slope %	Altitude (m)	Hydrological influences	Climatic influences
1	2	118	1690	nival	mountain
2	3	38	700	nivo-pluvial	mountain
3–4	4	12	600-421	pluvio-nival	idem/atlantic
5 to 10	**4(5)**	3, 6	280-145	**id°** attenuated	**idem** attenuated
11 to 19	5	**1, 1**	114-20	pluvial	**submedit./atl./subcont.**
20 to 24	**5(6)**	**0,** 4	13-6	id"	**atl./Subcont.**
25 to 27	6	**0,** 4	**4–2,5**	± tidal (very low salinity)	atl.
28 to 30	**6(7)**	**o +**	2-0.5	maritime	**atl.** (Oceanic)
31	7	**0**	0	estuary	Oceanic

ness observed in this group:

$$\text{Max } C_{i\,w} = \text{Min } (S_i, \ldots S_{i+w-1}).$$

The expectancy of the maximum floristic affinity is viewed as the saturation rate of $C_{i\,w}$:

$$T_{i\,w} = C_i \text{ ,/Max } C_{i\,w}$$

Therefore, $T_{i\,w}$ varies from 0 (no common species) to 1 **(maximum** number of common species). For w = 1, it is clear that $C_{i,1}$ is the species richness, and $T_{i\,1}$ is maximum:

$$C_{i,1} = S_i \text{ and } T_{i\,1} = 1$$

Results

Site zonation

Nine groups of sites were isolated from the **dendro**gram in Fig. 2 (cut-threshold set to 90% of the maximal similarity). Main characteristics of those groups (according to the relieved trends of the **mul**tivariate analysis) are given in Table 1.

This clustering reflects the topological order of the sites. According to the 58 environmental variables used, the general ldngitudinal zonation appears clearly.

The mountain zone (sites 1 to 4) is clearly separated from the other groups (Fig. **2),** while in the mid course, the upper alluvial plain (sites 5 to 10) is separated from the lower sites. The confluences mark clearly discontinuity zones: this is the case of the Midouze River, the Gaves River and the Arros River (Fig. 1). The limit between the upper alluvial plain (sites 5 to 10) and the upper mid-course (sites 11 to 19) results from the combined effects of climatic and hydrologic influences of the Arros River valley. The Gaves valley influences in the same way the limit between sites 27 and 28.

Species richness of the riparain vegetation

A total of 900 **taxa** were identified along the **Adour** corridor, of which 101 were woody species (33 trees, 63 shrubs and 9 lianas); 342 species of the species found were **ruderal,** and 120 species alien (introduced) species. We referred to the whole species of vascular plants (Bryophyta excluded) in this analysis of the species richness.

Table 2 indicates the frequency distribution of the species. About one third of the species (298) were found in only one site. The presence of these exclusive species depends on local particular conditions. Altogether, about 50% of the observed species were represented in 3-4 sites or less. This reflects the large heterogeneity in the physionomy of the corridor **along** the **Adour** River. Finally, only nine species **(1%)** were present in more than 27 sites (90%): ***Alnus*** *glutinosa* Gaertn., ***Dactylis glomerata*** L., *Poa trivialis* L., ***Rubus fruticosus*** L. ***aggr.sp.***, ***Urtica*** *dioica* **L.,** *Ranunculus* ***repens*** L., *Galium aparine* L., *Mentha* ***aquatica*** L. *Phalaris* ***arundinacea*** L.. No species were found in the whole 31 sites sampled.

The mean value of the species richness (Table 3,

Table 2. Number of species (N) found in one site (n = 1), in two sites (n = 2), . . . in 31 sites (n = 31).

n (number of sites)	n (number of species)
	298
2	106
3	83
4	65
5	48
6	34
	33
8	24
9	18
10	21
11	19
12	15
13	14
14	12
15	12
16	13
17	14
18	9
19	10
20	6
21	8
22	9
23	4
24	4
25	6
26	2
27	3
28	2
29	3
30	4
31	0
Total	900

column w = 1) was 167.3 ± 16.9 (.05 confidence limit). If we distinguish an epilittoral zone (1) (flooded more than two times a year), and a littoral zone (2) (flooded not less than one time a year) (Nilsson, 1981), mean richness values are respectively: 47.8 ± 7.0 and 119.5 ± 16.5. The lower value results from stressful1 conditions. However, the midcourse with an important geomorphological activity (sites 10 to 15) shows values significantly above average for the epilittoral zone, in agreement with an 'optimal degree of disturbance', as stated by the intermediate disturbance hypothesis (Connel 1978, Houston 1979).

Longitudinal change of the species richness

The species richness changes longitudinally from the source to the mouth. An analysis of this change may utilize three characteristics of each site (Fig. 3): (i) the number of species exclusive to the site (amounting 298 species, as shown in Table 2), (ii) the number of species that are not observed upstream the site (new species or specific gain), (iii) the number of species that are not observed downstream the site (disappearing species or specific loss).

The sum of gains or losses are both equal to 900.

The curve of cumulative exclusive species (c) appears with a nearly constant slope (constant rate of local specialization). The two major discontinuities correspond to the site 17 (high and steep banks, favourable to subxerophilous vegetation) and to the site 31 (estuarine conditions, halophilous vegetation). The tidal influence (including oceanic influence) is indicated by an increasing degree of specialization of the riparian flora from site 27 (stronger slope).

The curve of cumulative gains (a) shows schematically three subsegments, with different slopes: (i) the mountain zone (sites 1 to 5), where the commonest species of the corridor appear rapidly; (ii) the medium zone (5 to 13) which is highly dynamic and characterized by a strong climatic gradient; (iii) the lower course, with a relatively low rate of new species, except in the estuarine zone (site 31).

Symmetrical remarks can be made for the cumulative losses (b). The mountain zone shows a progressive loss of mountain elements (few of them persist until the mid course). The apparition of thermophilous elements near the Adour/Arros confluence leads a slight increase of slope (sites 9 to 14). Downstream from the site 15, the rate of loss increases, with the change of flood regime (Table 1).

For a given site, the balance between the species newly observed (gains) and the species which disappear downstream (losses) can be expressed by the difference between gains and losses or a-b (Fig. 4). This difference illustrates the longitudinal change

Table 3. **Values** of $C_{i,w}$ (number of common species), according to the first site (i = 1 to 31) of a given section, and to the number of consecutive sites (w = 1 to 10) constituting this section. For the column w = 1, $C_{i,w}$ corresponds to the species richness observed in site i. Mean value and standard deviation are indicated for each series (w = 1 to 10) constituting this section. For the column w = 1, $C_{i,w}$ corresponds to the species richness observed in site i. Mean value and standard deviation are indicated for each series (w = 1 to **10),** and significative difference (= 5%) by ' + ' (above average) or by ' – ' (below average).

i	W									
	1	2	3	4	5	6	7	8	9	10
1	131-	46-	23-	22-	9 -	6 -	5–	4 -	4 -	3 -
2	151-	81	73+	39	33	28	26+	23+	23+	14
3	121–	93+	63+	37	32	25	22	20+	17+	13
4	247 +	158+	81+	55+	45+	45+	33+	29+	24+	23+
5	232+	105+	63+	46+	45+	41+	32+	23+	21+	20+
6	152	85	59+	58+	43+	33+	28+	22+	20+	17+
7	141	77+	68+	46+	37-k	31+	23	18	18+	16+
8	188+	148 +	94+	61+	51+	44+	33+	28+	24+	18+
9	284 +	137 +	86+	69+	55+	46+	37-k	30+	22+	20+
10	187 +	loo+	74+	64+	50+	43+	33+	20+	19+	17+
11	204+	119+	79+	63+	54	44	31+	26+	17+	13
12	188+	134+	80+	63+	50	30+	26+	21+	16	13
13	279 +	120+	82+	55+	35	33 +	28+	18	15	14
14	197+	109+	59+	36	33	26	21	17	14-	14
15	179	84	45–	39	28	20-	16-	15–	13-	10–
16	152	59-	44-~	28-	20-	18-	14-	13-	11–	19–
17	147	71-	41-	27-	19-	17-	13-	12-	12-	13
18	201+	87	46-	29-	22-	16-	15-	13-	13-	11–
19	169-	68-	35–	27-	20-	18-	16-	16-	14-	12-
20	141–	50–	34-	21-	19–	16-	15-	15-	14-	9 -
21	129-	57-	30-	25-	19–	18-	16-	15-	10–	7–
22	110-	40-	31-	23-	22-	21-	17-	12-	8 -	4–
23	118-	50-	35–	27-	26-	23-	20-	14-	8 -	
24	120-	56–	42-	32-	26-	16-	12-	8 -		
25	131-	63-	47-	33-	19-	17–	15–			
26	132-	84-	47-	23-	20-	11–				
27	150-	65-	31-	25-	14-					
28	145–	46-	33-	17-						
29	119–	51-	32-							
30	144-	51-								
31	196+									
Mean	167.3	83.3	53.7	38.9	31.3	26.4	21.9	18.0	15.5	13.2

of the composition of the riparian vegetation. It approaches zero when no sensible change (excepting the exclusive component) is observed. This is the case of the section between sites 12 and 24, corresponding to the mid course, as defined earlier (Fig. 2). Therefore, this section appears as an equilibrium zone for the floristic balance. It differs from the upstream section or mountain zone where a-b > 0 and from the downstream section or lowland zone where a-b < 0.

Longitudinal co-occurrence and scale effect

The above analysis of gains and losses gives a first idea of the longitudinal change of the species richness. It is necessary to go further in the analysis, and to consider the relationships between sites at finer scales.

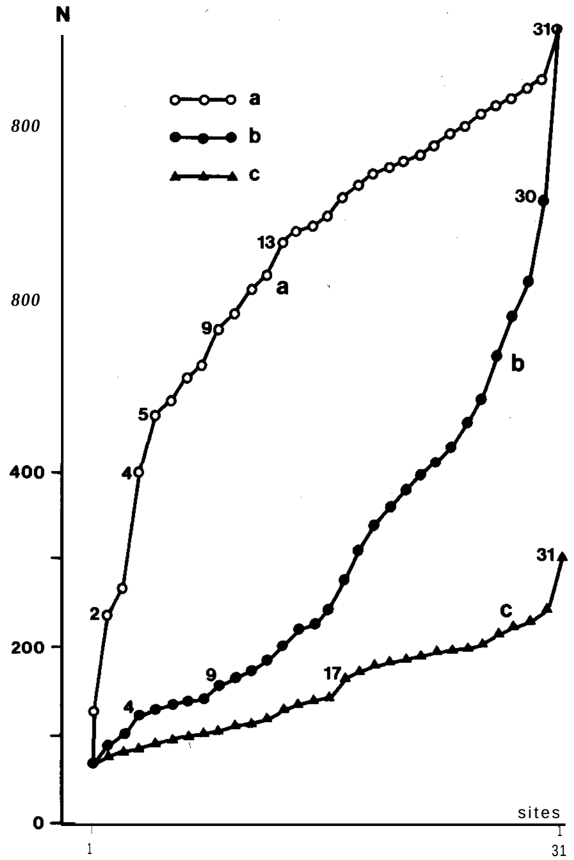

Fig. 3. Spatial evolution along the **Adour** River of: a: cumulative number of species not observed upstream from the given site (sum of gains a = 900). b: cumulative number of species disappearing downstream from the given site (sum of losses b = 900). c: cumulative number of exclusive species to the given site (sum of exclusives c = 298). The position of some of the 31 sites is recalled on the curves.

For this, we used the two variables: (1) $C_{i,w}$, the number of common species, and (2) $T_{i,w}$, the expectancy of a maximum floristic affinity (see methods). Values are given in Tables 3 and 4, and general trends are presented in Fig. 5. The number of sites w gives a measure of the spatial scale of study from 10 km (**w** = 1) to 100 km (**w** = 10).

Two patterns were defined, drawn up by both variables.

1. the variation of $C_{i,w}$ or $T_{i,w}$ accordingly to the variation of i (from 1 to 31) **gives** the longitudinal change of $C_{i,w}$ or $T_{i,w}$.

2. the variation of $C_{i,w}$ or $T_{i,w}$ accordingly to the variation of w (from 1 to 10) gives the resolution change of $C_{i,w}$ or $T_{i,w}$. We call this latter relation a 'scalar gradient' because (1) the increase of w (number of sites in a group) corresponds to a change of scale (each site is representative of a 10 km long stretch), and (2) values are monotonously decreasing when w is increasing.

For each variable $C_{i,w}$ and $T_{i,w}$ a gradient can be read in two different ways from a site i_o:

- an ascending scalar gradient, integrating progressively upstream sites. For example (Table **3)**, from site i_o = 3 1, the successive values of $C_{i,w}$ are: 196, 51, 32, 17 . . .
- a descending scalar gradient, integrating progressively downstream sites. For example (Table **3)**, from site i_o = 4, the successive values of $C_{i,w}$ are: 247, 158, 81, 55 . . .

These two examples are illustrated in Fig. 5 (dotted line).

General trends are the same for $C_{i,w}$ and $T_{i,w}$. Figure 5 shows that longitudinal trends (i.e., $C_{i,w}$ versus i) are roughly conserved when increasing the length of stretches (w). The higher values of species richness were found from site 4 to site 15. This is a well conserved zone, with floods of high frequency but of low duration. Riparian woods are generally natural, and each site shows a high physionomical diversity (wide ecological spectrum of the riparian flora). The zone located downstream to sites **16**– 17 gets more stable conditions, with floods of low frequency, but of long duration. In this zone, the Midouze River, seriously affected by pollution (paper manufacturing), causes the disappearance of hydrophytes within the main channel of the stream for 50 km. The lower values of species richness of the lowland results from an old management tradition since the **XVIIth** century: the floodplain is covered by man-controlled marshy grasslands and riparian woods (oak groves and alder groves). The maritime zone (downstream from site 28) shows a high degree of human influence (species richness of the estuary is only restored by **haline** specialization and a large amount of alien species).

The expectancy of the maximum floristic affinity within a given section ($T_{i,w}$) is shown in Table 4. For each value of w, above average values are found in the upper course, and below average values in the lower course. More precisely, **con-**

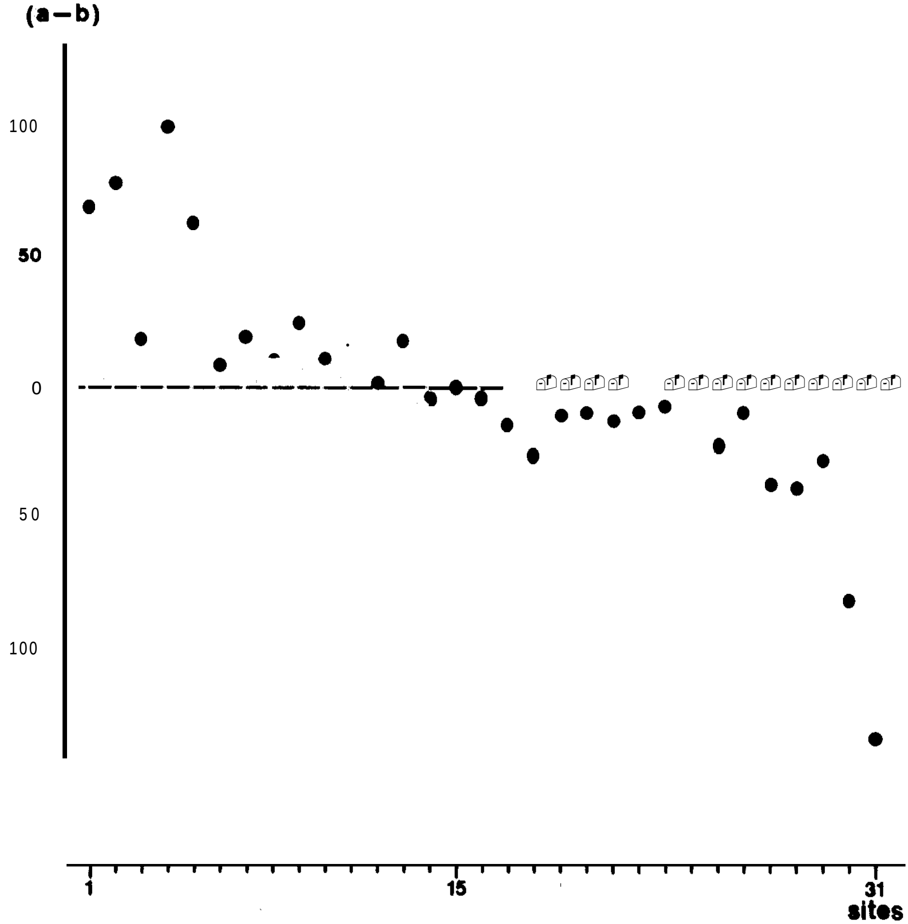

Fig. 4. Longitudinal floristic balance, given for each site by the difference between:
- the number of species observed in the site, but not observed upstream (see 'gains' of Fig. 3).
- the number of species observed in the site, but not observed downstream (see 'losses' of Fig. 3.). Values (a-b) expressed in number of species.

sidering the column w = 2 in Table 4, minimum and maximum values of $T_{i,2}$ may be analyzed as follows. Minimum values were found for the following couples of sites : 1 and 2 (35.1 %), 20 and 21 (35.5%), 30 and 31 (35.4%). These values indicate rapid changes respectively due to: transition from higher to lower altitudinal sites, Midouze tributary influence, and estuarine influence. Maximum values were found for sites 3 and 4 (76.9%), 8 and 9 (78.9%). These sites are located in transitional zones. Therefore, zones of discontinuity and of continuity show respectively low and high values of $C_{i\ w}$ and $T_{i,\ w}$.

Discussion

The scalar gradients, as defined above, are significantly described as a hyperbolic function relating $C_{i,\ w}$ (or $T_{i,\ w}$) and w (Fig. 6). This relation allows one to compare the gradients for an analysis of floristic connectance in an upstream or in a downstream direction from a given site. For example, we may consider the successive values (in %) of $T_{i,\ w}$: the ratio between the observed number of common species and the maximum number of common species (Table 4). The descending gradient from i_0 = 1 to i = 10 integrates progressively downstream

Table 4. **Values of** $T_{i,w}$ **= ratio between the observed number of common species and the maximum number of common species (or expectancy of the maximum floristic affinity within the given section). Values are expressed in percent.**

i	w 1	2	3	4	5	6	7	8	9	10
1	100	35.1–	19.0-	18.2-	7.4-	5.0-	4.1-	3.3-	3.3-	2.5-
2	100	66.9-k	60.3 +	32.2+	27.3+	23.1 +	21.5+	19.0 +	19.0 +	11.6+
3	100	76.9+	52.1+	30.6 +	26.4+	20.7 +	18.2+	16.5 +	14.0+	10.7
4	100	68.1+	55.3 +	39.0+	31.9+	31.9+	23.4 +	20.6 +	17.0+	16.3 +
5	100	69.1+	44.7 +	32.6-k	31.9-t	29.1+	22.7 +	16.3+	14.9+	14.2+
6	100	60.3 +	41.8+	41.1+	30.5+	23.4+	19.9+	15.6+	14.2+	12.1+
7	100	54.6	48.2+	32.6 +	26.2+	22.0 +	16.3	12.8–	12.8	11.3+
8	100	78.7+	50.3 +	32.6+	27.3-c	23.5 +	17.6+	15.6+	15.8+	12.2+
9	100	73.3 +	46.0+	36.9 +	29.4+	24.6+	20.7+	19.7 +	15.0+	13.6+
10	100	53.5	39.6+	34.2 +	26.7+	*24.0* +	21.7+	13.6	12.9 +	11.6+
11	100	63.3 +	42.0+	33.5 +	30.2+	28.9+	21.1+	17.7 +	11.6	9.2-
12	loo	71.3+	42.6+	33.5+	32.9 +	20.4+	17.7 +	14.3	11.3–	10.1
13	100	60.9+	45.8+	36.2 +	23.8 +	22.4 +	19.0+	12.8 –	11.6	12.7 +
14	100	60.9+	38.8	24.5 +	22.4	17.7–	14.9-	13.2	12.7	12.7 +
15	100	55.3	30.6 –	26.5	19.0-	14.2-	12.4-	13.6	11.8	9.1-
16	100	40.1-	29.9-	19.0-	14.2-	14.0-	12.7-	11.8-	10.0–	8.2-
17	100	48.3 –	27.9-	19.1-	14.7 –	15.5–	11.8-	10.9-	10.9 –	11.8+
18	100	51.5–	32.6-	22.5 –	20.0-	14.5 –	13.6-	11.8-	11.8	10.0
19	100	48.2-	27.1 –	24.5 –	18.2-	16.4–	14.5 –	14.5	12.7	10.9
20	100	35.5 –	30.9 –	19.1-	17.3-	14.5 –	13.6-	13.6	12.7	8.2-
21	100	51.8-	27.3-	22.7 –	17.3-	16.4–	14.5 –	13.6	9.1-	6.4-
22	100	36.4-	28.2-	20.9 –	20.0-	19.1	15.5	10.9 –	7.3-	3.6–
23	100	42.4 –	29.7 –	22.9 –	22.0	19.5	16.9	11.9–	6.8-	
24	loo	46.7 –	35.0-	26.7	21.7	13.4-	10.1–	6.7 –		
25	100	48.1–	35.9	25.2-	15.1–	14.3 –	12.6-			
26	100	63.6+	35.6	19.3 –	16.8 –	9.2–				
27	100	44.8 –	26.1–	21.0-	11.8–					
28	100	38.7 –	27.7-	14.3 –						
29	100	47.9-	26.9-							
30	loo	35.4-								
31	loo									
Mean	**100**	54.2	37.2	27.2	22.3	19.1	16.3	13.8	12.1	10.4

sites, with successive values (in %) of $T_{i,w}$: 100, 35.1, **19.0, 18.2, . . . , 2.5.** In the first case (descending gradient), the differences between successive values indicate a discontinuity for values of w between 4 and 5. In the second case (ascending gradient) a discontinuity between sites 8 and 7 is indicated by the successive values (in %) $T_{8,3}$ = **50.3%,** $T_{,,4}$ = **32.6%,** the following values being closer to 32.6%: 30.5, 29.1, 23.5.

Therefore, generalizing to other gradients, a new zonation may be based on an analysis of Tables 3 and 4.

Site 1 is clearly separated from the other mountain sites (2, 3, 4). Another discontinuity appears also between sites 4 and 5 when considering the descending gradient of Table 4 but not when considering the ascending gradient ($T_{,,4}$ = 29.1%). The zone corresponding to sites 4 and 5 is rather a zone where mountains and lowland floras coexist.

The previous results are in accordance with those obtained from a cluster analysis based of environmental data (Fig. 2). This is not always the case. For example, groups IV and V are separated by the Arros River confluence in Fig. 2 (limit between sites 10

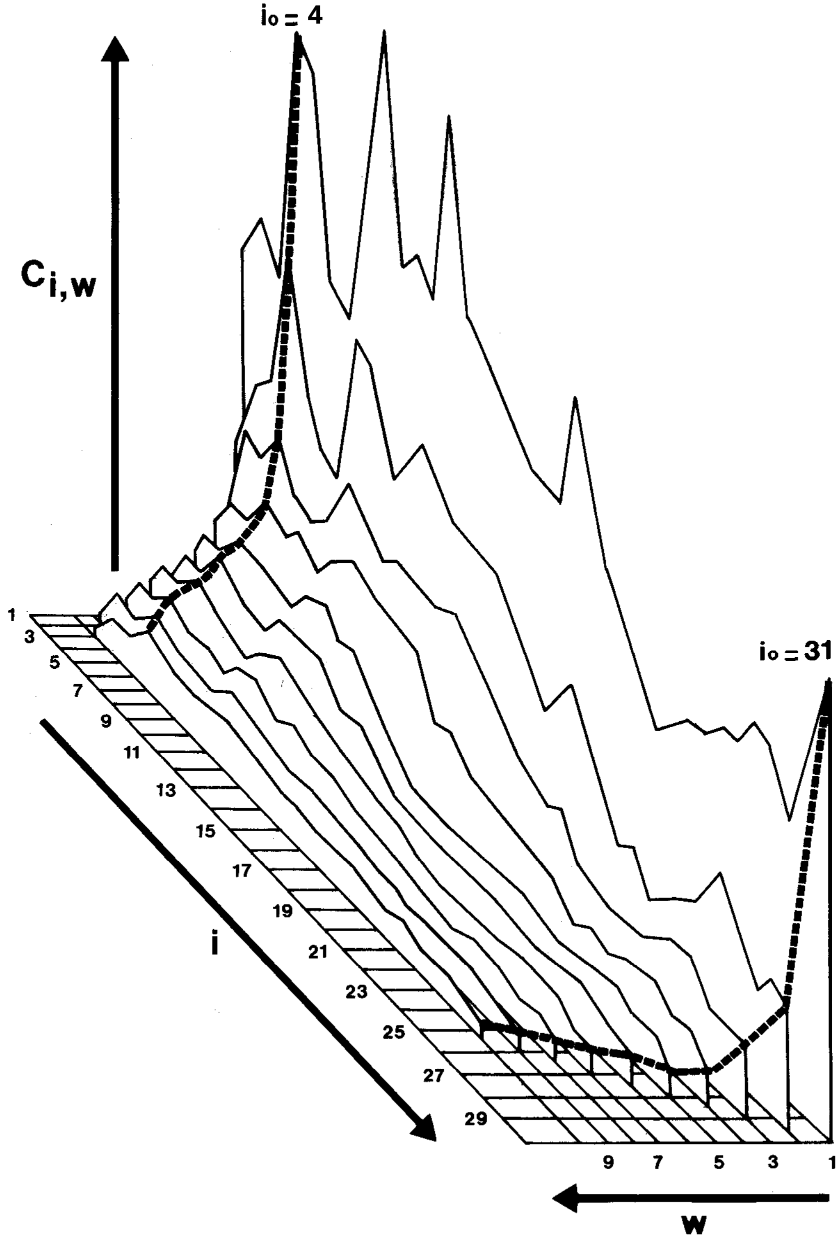

Fig. 5. Trends of the variable $C_{i,w}$ (number of common species), from site i = 1 to site i = 31, for various observation windows (w = 1 to 10). Values are conventionally reported to the median site of each observed section. Dotted lines illustrate two examples of scalar gradients: descending from i_o = 4 and ascending from i_o = 31 (see text for further explanations).

and 11). However, this influence of the Arros River extends largely upstream and downstream when analyzing the observed number of common species in Table 3: columns 1 to 3 show that the upstream limit is between sites 7 and 8 whereas the downstream limit is between sites 14 and 15.

Considering Table 4, the value of T,,, $_2$ = 40.1 indicates a subdivision not suggested in Fig. 2. Indeed, floristic data of Table 4 makes clear a discontinuity between sites 16 and 17. This discontinuity is also indicated by a change of sign (from + to –) when looking at column 2 in Table 4. It is also apparent in Fig. 4. Therefore, the major change in the floristic composition between sites 16 and 17, as

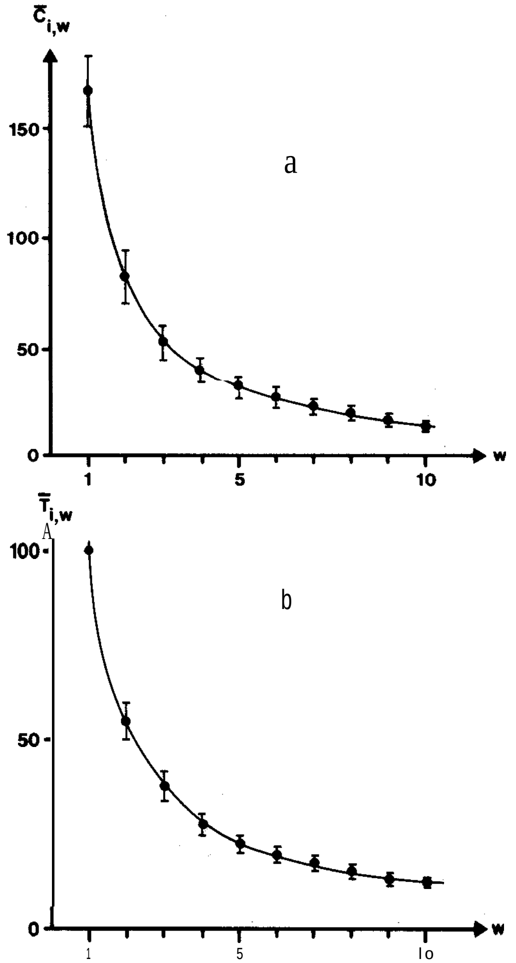

Fig. 6. Mean values of $C_{i,w}$ (a) and $T_{i,w}$ (b) as a hyperbolic function of w ('mean scalar gradients'). Respectively: R^2 = .9892 and R^2 = .9950. Other scalar gradients show similar patterns.

revealed by an analysis of the riparian vegetation along the river (Table 4), is not indicated in a zonation utilizing mesologic data (Fig. 2).

On the contrary, the limits of group V (Fig. 2) appear in Table 4, with $T_{10,2}$ = 53.5% (Arros confluence) and $T_{,,2}$ = 35.5% (Midouze confluence).

In the downstream part of the river, group VII of the Fig. 2 is floristically well characterized but should include site 28. Otherwise, group VIII (sites 29 and 30) is clearly separated from the estuary (site 31).

Finally, zones of discontinuity (low values of $C_{i,w}$ and of $T_{i,w}$) and zones of continuity (high values of $C_{i,w}$ and of $T_{i,w}$) appear as downstream orientated (high scalar gradients) from site 1 to site 24, and as upstream orientated (low scalar gradients) from site 25 to site 30. The oceanic influence (tide and climate) may explain the major part of this difference.

Conclusion

The floristic connectivity, of the Adour River corridor, as defined by Merriam (1984), was measured by an analysis of the two variables $C_{i,w}$ and $T_{i,w}$, that express both longitudinal and scalar structures.

The values of $C_{i,w}$ and $T_{i,w}$ are highest in the 4th to 6th order parts'of the river, where the riparian landscape shows a maximum environmental heterogeneity. This result is in agreement with the intermediate disturbance hypothesis (Connel 1978; Huston 1979; Ward and Stanford 1983b).

More precisely, the Adour River corridor cannot be assumed to be floristically continuous. Rather, it falls between a pristine, theoretically continuous (Vannote *et al.* 1980), and a regulated, serially discontinuous stream (Ward and Stanford 1983a). Most of these discontinuities are easily recognizable environmental factors, such as confluences of tributaries or climatic boundaries, which control the longitudinal zonation of the riparian vegetation. However, in many examples, zonations based on riparian vegetation and on environmental data do not exactly coincide. In fact, environmental discontinuities may correspond to two types of change in the riparian vegetation: these are zones of slow change (high level of floristic connectance) or zones of sharp change (low level of floristic connectance).

Finally, this analysis of the connectance of the riparian vegetation shows that the floristic relationship along various stretches of the Adour River is not orientated in a single direction. Upstream orientated relationships may interfere with downstream ones, in accordance with upstream or downstream migrations of the species.

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