Invasibility of Species-Rich Communities in Riparian Zones

ANNE-MARIE PLANTY-TABACCHI,* ERIC TABACCHI,† ROBERT J. NAIMAN,† COLLETTE DEFERRARI,† AND HENRI DÉCAMPS*

*Centre d'Ecologie des Systèmes Fluviaux du CNRS, 29, rue Jeanne Marvig, 31055 Toulouse Cédex, France, email tabacchi@cesf.cemes.fr

†Center for Streamside Studies, Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

Abstract: *Invasibility of riparian plant communities was estimated by the percentage of alien species found along the Adour River (Southwest France) and along Lookout Creek, McKenzie River, and Willamette River (Central Cascades, Oregon, U.S.A.). At the patch scale, the invasibilities of riparian plant communities were compared between one exceptionally rich site of the Adour River and patches selected in the Hoh and Dungeness watersheds (Olympic Peninsula, Washington, U.S.A.). Alien species represented 24% of 1396 species for the Adour and 30% of 851 species for the McKenzie. They represented 24% of 148 species for the Hoh drainage and 28% of 200 species for the Dungeness drainage. Similar trends were found along the Adour River and along the McKenzie River for changes in total number of species per site and in percentages of alien species per site. These trends may be related to the intermediate disturbance regimes and to the physical structure of the riparian corridors. Climatic and human factors are also involved in these longitudinal changes. Positive linear relationships were found between the total number of species and the percentage of aliens observed in each site. At the patch scale, most of the sampled communities contained alien species. Although mature vegetative patches appeared to be invasible, young communities contained more alien species than older ones. For entire corridors, a positive linear relationship was found between total species richness and percentage of alien species in each patch type for the richest site of the Adour River. This may be partially explained by landscape features considered in a successional context. We suggest the use of empirical rules, and stress the importance of riparian systems for monitoring the conservation of local and regional species pools are suggested.*

La propensión a la invasión de las comunidades de zonas ribereñas ricas en especies

Resumen: *Se estimó la propensión de las comunidades de plantas ribereñas a la invasión a partir del porcentaje de especies invasoras encontradas a lo largo del Río Adaour (Sudoeste de Francia) y a lo largo del arroyo Lookout/Río McKenzie/Río Willamette (Cascadas Centrales, Oregon, EUA). A escala de parche una la propensión de la comunidad de plantas ribereñas a las invasiones fue comparda, entre un sitio excepcionalmente rico en el Río Adour y parches seleccionados en las cuencas de Hoh y Dungeness (Península Olímpica, Washington, EUA). Las especies invasoras representaron un 24% de las 1396 especies de Adour y un 30% de las 851 especies de McKenzie. Estas también representàron un 24% de las 148 especies de la cuenca de Hoh y un 28% de las 200 especies de la cuenca de Dungeness. Tendencias similares fueron encontradas a lo largo del Río Adour y del McKenzie, para los cambios en el número total de especies y en el porcentaje de especies invasoras por sitio. Estas tendencias podrían estar relacionadas a los regímenes intermedios de perturbación y a la estructura fsica de los corredores ribereños. Los factores climáticos y humanos también se encuentran involucrados en estos cambios longitudinales. Se encontró una relación lineal positiva entre el número total de especies y el porcentaje de especies invasoras observado en cada sitio. A una escala de parche, la mayoría de las muestras de la comunidad contenían especies invasoras. Sin bien, los parches vegetativos maduros parecieron ser propensos a la invasión, las comunidades más jóvenes presentaron más especies invasoras que las comunidades más antiguas. En cuanto a los corredores en su totalidad, se encontró una relación lin-*

Paper submitted March 8, 1995; revised manuscript accepted May 19, 1995.

eal positiva entre la riqueza total de especies y el porcentaje de especies invasoras en cada tipo de parche para el sito más rico del Río Adour. Esta relación puede ser explicada parcialmente por las características del paisaje, consideradas dentro de un contexto sucesional. Se sugiere el uso de reglas empíricas y la importancia de los sistemas ribereños para el monitoreo de la conservación de grupos de especies locales y regionales.

Introduction

The invasibility of natural plant communities by alien (exotic) species continues to be a major topic in ecology. Since the early studies of de Candolle (1855), Thellung (1911–1912), and Elton (1958), researchers have attempted to relate the invasibility of a community to total species richness. The ease with which alien species can invade species-poor oceanic islands was one of the classical arguments of C. S. Elton for a causal relationship between community species richness and stability (Rejmanek 1989). Although most plant communities have been shown to be susceptible to invasions (Crawley 1987), many authors (Fox & Fox 1986; Crawley 1987; Ashton & Mitchell 1989; Sauer 1988; Malanson 1993; Planty-Tabacchi 1993) suggest that riparian zones are usually sensitive to invasion.

The position of riparian forests as edges between terrestrial and aquatic systems (Naiman & Décamps 1990; Gregory et al. 1991) tends to enhance fluxes of energy and species. But, riparian forests differ from other ecotonal systems by a high degree of hydrological disturbance from water level fluctuations. Moreover, because streams and rivers represent a connected network throughout the landscapes (Forman & Grodon 1986), they facilitate the spreading of several species at the regional scale (Tabacchi 1992; Planty-Tabacchi 1993; DeFerrari & Naiman 1994) and are well known as productive and species-rich sites (Malanson 1993; Naiman et al. 1993)

As highly variable systems, riparian zones provide pertinent information on the relationship between species richness and the presence of exotic species within a given community. We compared data sets from the Adour River (southwestern France), the McKenzie River, Willamette River, and Lookout Creek (Cascade Mountains of Oregon, U.S.A.), and the Dungeness and Hoh Rivers (Olympic Peninsula of Washington, U.S.A.) to examine relationships between species richness and the presence of exotic species and to analyze possible consequences for species conservation.

Study Sites and Methods

The Adour River in southwestern France flows 350 km from the central Pyrénées Mountains (source: 2800 m above sea level) to the Atlantic Ocean (Tabacchi et al. 1990). Its watershed (17,000 km^2) is characterized by diverse substrate, climate, and land-use. The vegetation of the riparian corridor is well developed and may be one of the richest riparian systems of western Europe (Tabacchi & Planty-Tabacchi 1990). The main riparian trees are alder (*Alnus glutinosa* Gaertn.), willow (*Salix alba* L., *Salix triandra* L.), black poplar (*Populus nigra* L.), maple (*Acer campestre* L.), ash (*Fraxinus excelsior* L., *F. angustifolia* Vahl.), elm (*Ulmus minor* L.), and oak (*Quercus robur* L.).

The McKenzie River flows 350 km from the Cascade Mountains of western Oregon (source: 1300 m above the sea level) to the Willamette River. The upper course flows within pristine riparian forests, whereas the lower course is surrounded mainly by privately owned forests and crops. The main tree species are western hemlock (*Tsuga heterophylla*, [Raf.] Sarg.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western red cedar (*Thuja plicata* Donn.), red alder (*Alnus rubra* Bong.), black cottonwood (*Populus trichocarpa* T. & G. ex. Hook.), ash (*Fraxinus latifolia* Benth.), big-leaf maple (*Acer macrophyllum* Pursh.), and Pacific willow (*Salix lasiandra* Benth.). Coniferous species largely disappear from riparian woods downstream from the McKenzie-Willamette confluence. Conversely, they dominate in mountain tributaries (Lookout Creek), where they are represented in mature stages.

The Dungeness and Hoh Rivers are located on the Olympic Peninsula of Washington state. The Dungeness River watershed is dominated mainly by western hemlock and Douglas-fir at lower elevations and by subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) at higher elevations. The Hoh River watershed is dominated by Sitka spruce (*Picea sitchensis* [Bong.] Carr.), western hemlock and western red cedar at lower elevations, and Pacific silver fir (*Abies amabilis* [Dougl.] Forbes) and western hemlock at higher elevations) (DeFerrari 1993; DeFerrari & Naiman 1994).

We estimated species richness for native and alien (exotic) species at two scales during the period of maximum development of the riparian vegetation (between May and September). At the first scale, the watershed scale, we used longitudinal studies: we examined 500-m reaches within the 10-year flood zone (Tabacchi et al. 1990). Thirty-two sites were distributed from the source to the mouth of the Adour River and 11 from the source to the mouth of the McKenzie River (Planty-Tabacchi 1993). Additional sites were studied on a shorter stream

(Lookout Creek, two sites) and on a longer stream (Willamette River, two sites) for comparison with the McKenzie River. To obtain an estimate of species richness as complete as possible we investigated each site by random walk until no new species appeared. Previous work (Tabacchi & Planty-Tabacchi 1990) showed that no area corrections were needed with this method of inventorying heterogeneous sites. Longitudinal trends were smoothed by double-weighted least squares to minimize the influence of outlier points (MacLain 1974). The longitudinal study method was not applied to the Dungeness and Hoh Rivers.

Two surveys of alien plants allowed us to consider exotic invasions at the second scale, the patch scale. For the Adour River we chose the Bernède site because it harbors an exceptional richness of species. Species were exhaustively counted for each of 30 patch types (communities) identified from both aerial infrared photographs (scale 1:4000) and species-composition analysis (Tabacchi 1992). Different patch types were analyzed by ANOVA, and *t* tests were used to detect differences in macrolocation within the landscape (zone) and for vegetation types. For the Dungeness and Hoh Rivers we measured species richness on 208, 100-m^2 (upland patches) or 50-m^2 (riparian patches) circular plots (DeFerrari & Naiman 1994). Seven patch types were selected in the Hoh watershed and six in the Dungeness watershed (alder flats were not present in this drainage). No patch-scale survey was made on the McKenzie River.

Results

Floral Richness and Alien Species

The total number of vascular plant species observed over whole river corridors was 1396 species for the Adour River and 851 species for the Lookout Creek, McKenzie, and Willamette drainage (254, 453, and 684 species, respectively; Planty-Tabacchi 1993). Alien species represented 24% (Adour) and 30% (Lookout-McKenzie-Willamette) of the total flora (Table 1). Of the 702 species identified at the Bernède site, 126 were aliens (Tabacchi 1992). This rich site on the Adour River

Table 1. Characteristics of vegetation patches identified at the Bernède site in France.

Patch type	*Species richness*	*Aliens (%)*	*Zone*[a]	*Vegetation*[b] *Type*	*Patches (#)*	*Area (ha)*	*Perimeter (km)*
Alder woods	125	3.2	Al	F	13	0.6	3.9
Alluvial hornbeam woods	147	3.4	Al	F	1	0.8	1.8
Alluvial oak woods	182	4.4	Al	F	134	9.9	5.5
Alluvial spiny shrublands	193	7.3	Al	SH	3	0.2	4.1
Alluvial spiny tall herbs	158	11.4	Al	PP	28	1.0	7.4
Alluvial tall herbs	260	9.2	Al	PP	49	1.7	17.1
Aquatic communities	108	10.2	Al	P	1	3.3	19.4
Artificial meadows	223	7.6	M	PP	6	0.9	33.1
Artificial poplar woods	206	9.7	Al	F	22	8.5	1.8
Artificialized patches (trails, constructions)	215	9.3	M	P	45	1.2	2.6
Ash and ash-oak woods	156	4.5	Al	F	38	1.2	1.0
Black locust woods	185	5.4	M	F	8	0.2	11.7
Crops	257	12.8	M	P	55	42.4	2.1
Douglas-fir plantations	nr[c]	nr[c]	Hl	F	6	0.6	1.4
Edgerows	207	8.2	M	SH	195	3.2	11.5
Elm-dominated woods	222	6.8	M	F	65	1.7	7.9
Embankments	479	13.6	M	P	72	1.6	10.2
Mesohygrophilous meadows	253	8.3	Al	PP	15	2.0	22.4
Mesoxerophilous meadows	221	14.0	Al	P	6	0.4	8.5
Mixed riparian woods	241	10.4	Al	F	92	5.0	7.2
Old willow–poplar woods	147	5.4	Al	F	17	1.1	1.8
Pebbles-gravel bars	445	24.3	Al	P	58	5.8	31.4
Pioneer black poplar forests	190	11.1	Al	SH	89	2.6	5.4
Pioneer white willow woods	211	9.0	Al	SH	54	1.2	21.4
Poplar-oak woods	226	9.3	Al	F	9	0.7	1.0
Silt-sand bars	276	11.6	Al	P	37	0.7	12.1
Upland clearcut regeneration	277	7.2	Hl	SH	10	1.0	0.8
Upland hornbeam-oak woods	119	2.5	Hl	F	13	4.4	9.1
Upland oak-chestnut woods	234	10.3	Hl	F	6	2.9	4.1
Upland shrubby vegetation	206	6.3	Hl	SH	5	0.2	22.6

[a] *Zones: Al = alluvial; M = mixed; Hl = hillslopes.*
[b] *Vegetation types: P = pioneer; PP = post pioneer (herbs); SH = shrubs; F = forests.*
[c] *nr: not recorded.*

also showed the most-complex landscape features because of its exceptional fluvial dynamics (Tabacchi 1992). The richest site of the McKenzie data set (Delta, site 5) showed geomorphic conditions very close to those at Bernède.

We found 52 alien species within the Dungeness and the Hoh drainages, accounting for 23% of the flora (DeFerrari 1993). This percentage is similar to that found for the Bernède site, the Adour River, and the Lookout-McKenzie-Willamette system. Using data from the total British flora, Crawley (1987) found percentages of aliens between 13 and 39% for habitats associated with running waters.

Considering the mean number of species per site, the Adour River appeared to be the richest system and to be less invaded than the Lookout-McKenzie-Willamette system (Table 1), but considerable variability was associated with these mean values. Differences also appeared when we considered woody or herbaceous species. Forty-six percent of woody species on the Adour River were aliens (only 17% for the Lookout-McKenzie-Willamette system). In contrast, the Oregon herbaceous communities were more invaded (32%) than the French ones (21%). These results were confirmed by the mean percentages of aliens per site, which were significantly higher in the Adour for woody species and significantly higher in the Lookout-McKenzie-Willamette system for herbaceous species.

For the Adour River, alien species originated mainly from North (21.5%) and South America (12.1%), Asia (22.1%), and the Mediterranean (12.3%). In North America, alien species originated from Europe and Eurasia (60.2% and 20.7%, respectively, for the three Oregon streams studied). The main alien species are given in Appendix 1 for each sampling set. For all sites the most representative families were similar. The alien flora was dominated mainly by Compositae, Poaceae, and Leguminosae. Aliens belonged to various morphological and functional groups (annuals, biennials, perennials, shrubs, trees, lianae). No alien trees were found in the Dungeness and Hoh watersheds, however, and few alien trees were identified along the Oregon rivers. Woody alien species were far fewer at the American sites than at French ones.

Longitudinal Trends

On the Adour and McKenzie Rivers, species richness exhibited longitudinal trends, increasing from the source to the piedmont (transitional zone between mountain and lowland domains) as the riparian corridor widened (Figs. 1a and 2a). The slope of this portion of the curve was lower for the McKenzie because of the more physically constrained corridor. Higher species richness was found within the middle course, where intermediate disturbance levels induced considerable spatial heterogeneity. For the Adour River, the Bernède site (site 13) showed high values (near 700 species per 500 m) because of geomorphic instability. Similar observations were noted for the Delta site (site 5) of the McKenzie River. The lower course of both rivers showed low levels of species richness because of more specialization with respect to disturbance regime (longer but less frequent floods). But species richness increased again downstream with the onset of temperate environmental conditions (Atlantic coast for the Adour, Willamette valley for the McKenzie). As for total species richness, longitudinal trends of the percentage of alien species were similar for both the Adour and the McKenzie Rivers (Figs. 1b and 2b). Maximum values were observed in the lower course, reaching 40% for the Adour and 60% for the McKenzie.

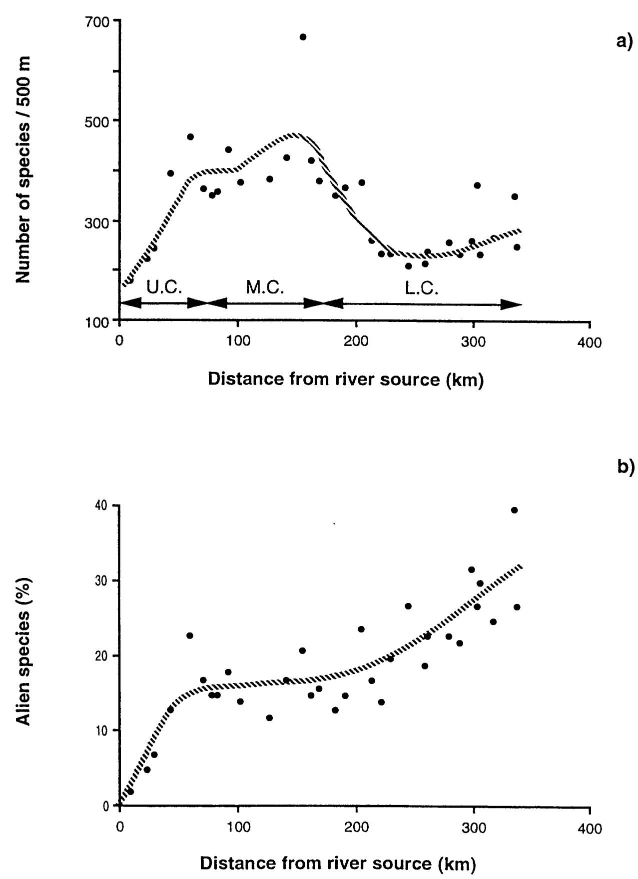

Figure 1. Longitudinal trends observed for the Adour River (32 sites), France: number of species observed in each 500-m long stretch versus the distance from the source of the river (U.C. = upper reach, M.C. = middle reach, L.C. = lower reach [the piedmont is located between the upper and the middle reaches]) (a) and the percentage of alien (exotic) species observed in each 500-m long stretch versus the distance from the source of the river (b).

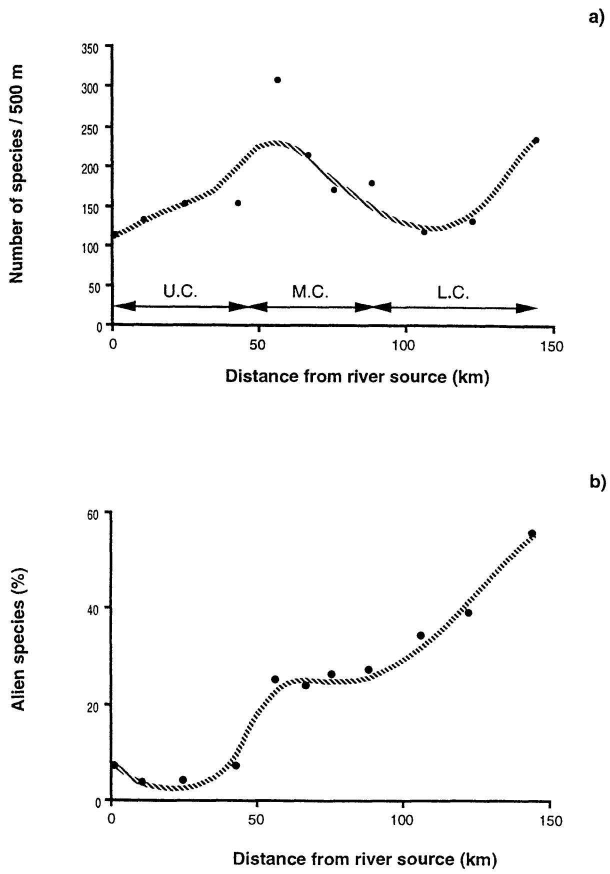

Figure 2. Longitudinal trends observed for the McKenzie River, Oregon: number of species observed in each 500-m long stretch versus the distance from the source of the river (U.C. = upper reach, M.C. = middle reach, L.C. = lower reach [the piedmont is located between the upper and the middle reaches]) (a) and percentage of alien (exotic) species observed in each 500-m long stretch versus the distance from the source of the river (b).

The percentage of alien species also increased from the source to the piedmont. Because the boundary between confined and unconfined stretches of river was sharper for the McKenzie valley than for the Adour valley, the first sharp increase in exotic species corresponding to the piedmont occurred farther downstream for the Ardour than for the McKenzie. The percentage of exotic species remained constant (below 20% for the Adour and above 20% for the McKenzie) from the piedmont downstream. Finally, the percentage of alien species increased rapidly for both river systems in the lower courses. There was a significant linear relationship (least-squares regression) between the total number of species (*Nt*, $Nt > 0$) and the number of alien species (*Na*, $Na > 0$) for the two systems: Adour River: $Na = 0.18\ (Nt) - 0.9$, $r = 0.64$, and $p = 0.0001$; McKenzie River: $Na = 0.60\ (Nt) - 62.0$, $r = 0.87$, and $p < 0.0001$.

Species Richness of Landscape Patches

At the Bernède site of the Adour River, 1154 patches were identified from aerial photographs on 107 ha of riparian, upland (hillslopes) and mixed landscape. They corresponded to 30 patch types (Table 1), of which one (Douglas-fir plantation) was not sampled.

The total number of species and the percentage of aliens in each patch type were not correlated with total patch area (Table 2). The richest patch types were alluvial gravel bars and embankments associated with cultivated areas. The least-rich patches were relatively stable upland and alluvial forests (oak, hornbeam, and alder).

Depending on patch type, the percentage of alien species varied from 2.5 to 24.3%. One-third of the patch types showed percentages of alien species above 10%, mainly within the riparian zone. Disturbed and young communities (< 15 years of age) were generally more invaded than stable and mature communities. The proportion of aliens was correlated with the edge length of each patch type when considering either untransformed data ($r = 0.37$, $p = 0.005$) or values corrected by the log of the area ($r = 0.38$, $p = 0.04$). No significant differences were demonstrated for total species richness by patch type, but the percentage of alien species was different among the various vegetational types ($F = 8.61$, $p < 0.0001$). T tests revealed differences only between young and mature vegetative types for total species richness ($p = 0.02$) and for the percentage of alien species ($p = 0.001$). Significant differences were also found between pioneer herbaceous stages and pioneer forests for

Table 2. Total and mean values observed for species richness and percentage of aliens for the longitudinal studies (mean ± 95% C.I.) of the Adour River, France, and the three rivers in Oregon, U.S.A.

	Adour River (32 sites)			*Lookout-McKenzie-Willamette system (15 sites)*		
	Total	*Woody*	*Herbaceous*	*Total*	*Woody*	*Herbaceous*
Total number of species	1396	174	1222	851	118	733
Aliens in the flora (%)	24	46	21	30	17	32
Species richness per site	314.2 ± 36.7	37.2 ± 4.0	276.9 ± 33.4	199.0 ± 41.6	34.9 ± 3.2	164.0 ± 41.0
Aliens per site (%)	17.90 ± 2.9	27.0 ± 4.3	16.6 ± 2.8	26.4 ± 9.3	12.0 ± 7.1	29.6 ± 9.6

the percentage of aliens ($p = 0.03$). For the Adour River, there was a significant linear relationship between *Nt* (total number of species) and *Na* (number of alien species) for each patch type: Na = 0.16 (*Nt*) − 11.8, $r = 0.82$, and $p < 0.0001$.

Similar results were found for the number of alien species in all patch types from the Dungeness and Hoh Rivers (Table 3). Young and disturbed communities showed the highest number of aliens, and within the forested patches riparian communities contained more alien species than uplands. When all patch types were considered, significant differences in the number of alien species were revealed by ANOVA ($p < 0.001$). The number of aliens and percent cover were negatively correlated with patch age for both riparian zones (Dungeness: $r = -0.87, p < 0.001$; Hoh: $r = -0.73, p < 0.001$) and upland zones (Dungeness: $r = -0.79$, $p < 0.001$; Hoh: $r = -0.71$, $p < 0.001$). Despite their age (11-39 years), however, the alder flats from the Hoh River were highly invaded because of the favorable winter light regime after leaf fall.

Discussion

The species richness of plants have been shown to vary considerably along riparian corridors (Nilsson et al. 1989). Despite a strong influence of the fine structure of the riparian corridor on variations in species richness at local scales, some additional factors have been proposed to explain the principal longitudinal trends (Décamps & Tabacchi 1994). Patterns found for total number of plant species along the Adour and McKenzie Rivers suggest a maximum diversity at an intermediate level of disturbance (here, in the middle course). These results agree with those of Nilsson et al. (1989), who found trends in modal values in the middle course of Swedish rivers. Other factors are related mainly to the hydrological disturbance regime and to the physical structure of the riparian woods. Moreover, human activities within and around the riparian corridor result in the introductions of many aliens, as well as of native ruderals (Nilsson et al. 1989; Tabacchi et al. 1990; Tabacchi 1992; Planty-Tabacchi 1993). These plants are favored by both natural and anthropogenic disturbance.

Table 3. Number of alien species encountered within different patch types of the Dungeness and Hoh watersheds in Washington, U.S.A.

	Number of alien species		*Number of plots*	
Patch type	*Dungeness*	*Hoh*	*Dungeness*	*Hoh*
Cobble bar	32	24	10	10
Riparian shrub	24	19	10	10
Riparian forest	14	4	8	4
Alder flat	—	12	0	10
Upland clearcuts	25	18	35	29
Upland young forests	3	4	5	8
Upland mature forest	1	0	1	2

Total Species Richness and Number of Alien Species

Invasibility has been related to species-poor communities (Elton 1958), poorly adapted native species (Sculthorpe 1967), disturbance (Mitchell 1974; Sousa 1984), and the presence of empty niches (Elton 1958; Harper 1977; Johnstone 1986). Ashton and Mitchell (1989) proposed three main mechanisms to explain the susceptibility of environments to invasions: disturbance or alteration of habitat, absence of predators, and absence of effective competing species. Many authors (Fox & Fox 1986; Macdonald et al. 1986, 1989; Crawley 1987, 1989; Malanson 1993) indicate a maximum number of alien plants in mesic or riverine environments. The dynamic aspects of the riparian zone, as an ecotone between aquatic and terrestrial landscapes (Naiman et al. 1988; Naiman & Décamps 1990; Gregory et al. 1991), and the particular spatial structure of the riparian landscapes (shifting mosaic within a corridor) are known to contribute strongly to species richness (Forman & Godron 1986; Kalliola & Puhakka 1988; Solbrig 1991).

The proportions of alien species in the American sites seems to be slightly higher than those in the French sites. It is surprising that French sites are not more invaded than the American ones, given the longer time they have been exposed to anthropogenic introductions. These observations agree with hypotheses based on the potential exchanges between floras from different continents (Di Castri 1989), and in this context the response of riparian zones does not seem to differ from that of other systems. Although these percentages varied widely in our samples, mean values in riparian zones were around 20–30%.

Samples from sites along rivers (McKenzie and Adour) or from patches at one site (Bernède) indicated that the richest communities are also the more invasible. Similar relationships between the number of native species (or all species) and the number of alien species were found by MacDonald et al. (1986, 1989), Kruger and Taylor (1979), and Kruger et al. (1989) for natural reserves of the Cape (South Africa) and of the Mediterranean-type climate regions of California. Macdonald et al. (1986) suggested that such a pattern could result from an increase in habitat diversity rather than from the differences in the area of the reserves compared. Contrasting results by Fox and Fox (1986) should be considered carefully, however, because the authors deduced a trivial negative relation between the percentage of alien species and the total richness of the sampled regions (Rejmanek 1989).

Statistical evidence for a relationship between invasibility and total species richness seems clear for mesic or riverine environments. What is not clear, however, is why the richest communities or sites are also the most invasible. Our results suggest that the linear relationship between total species richness and alien species richness is significant for different scales (patches versus watersheds), across different regions, and for different sites along the same river. We discuss this relationship along two gradients (upstream-downstream gradient and successional gradient) in an attempt to identify factors inducing invasibility in riparian zones.

Invasibility Along Rivers

We suggest that the invasibility of riparian communities is proportional to species richness, independent of location. For the number of species, similar trends were found for changes in the percentage of alien species along the Adour and McKenzie Rivers. The trends allow us to delineate three main regions along the rivers. Although a sharp increase in the percentage of aliens may be related to the riparian corridor widening at the piedmont, a plateau in the number of species appeared in the middle reaches. Then, in the lower reaches of the rivers, the percentage of aliens increased again. Examination of total species richness of each site shows that the richest zone, the middle reach, is not the most invaded. Data from the middle reach suggest that, despite a high level of species richness, (1) riparian communities may resist invasions or (2) landscapes features of the riparian corridor may reduce the establishment of invaders. The maximum diversity of habitats in the middle reach should be favorable for the establishment of alien species. As shown for naturally disturbed zones along the Adour at Bernède (Tabacchi 1992), alien populations did not differ significantly in their colonization strategies from native pioneer populations. Thus, it is difficult to explain this relatively low percentage of aliens only by competitive effects. One explanation would be a low level of physical fragmentation at the external edge of the riparian corridor, which may limit introductions from the surrounding environment. But hydrological disturbances should be favorable to alien species when new gravel bars are established within the corridor itself.

The higher invasibility of lower stream reaches may be explained by three factors. First, the human impact on the riparian corridor is greater. The corridor becomes more fragmented, and cultivation adjacent to the floodplain increases. Second, changes in the hydrological regime may induce increased specialization for native riparian plants. Along the Adour River, for example, the helophytes become more numerous as the species richness of the riparian communities decreases (Tabacchi & Planty-Tabacchi 1990). As species become more specialized, the community may be more susceptible to invasion by specialized alien species. Third, lessons from colonization dynamics in Bernède lead us to believe that a warming of the climate at lower elevations would be more favorable to exotic species than to the native community (Tabacchi 1992).

The downstream increase of alien species along the McKenzie and Adour Rivers are similar to trends described by Nilsson et al. (1989) for ruderal species. But a fundamental question is whether or not native ruderals behave as alien species along the rivers in terms of life history and competitive and spatial strategies?

Invasibility Among Patch Types

Analysis of the relationship between the species richness of a community and the percentage of aliens at the patch scale lead us to suggest that invasibility is greater for young communities, disturbed communities, and patches exhibiting higher edge-to-area ratios.

Pioneer communities are more invaded because of a greater level of ruderality (Grime 1979) of numerous alien species (Baker 1965; Heywood 1989). But this is not the case for many alien species in older patches along riparian systems (Planty-Tabacchi 1993), and we found no clear differences when considering the colonization of littoral patches in Bernède by alien and native pioneer communities (Tabacchi 1992). Moreover, only mature communities in the French watershed showed significant alien components. Results from older patches of primary succession and patches of secondary succession in Bernède, and within the riparian patches of the Hoh and Dungeness Rivers, suggest that the trapping of propagules following floods may also play an important role in invasions. The results of the study of the Atchafalaya Delta (Louisiana, U.S.A.) agree with this hypothesis (Rejmanek et al. 1987). It appears that the invasion process may also be widely influenced by the permeability of the landscape at the patch scale (Forman & Godron 1986). This permeability may be considered through static boundaries (edge effect) or from a dynamic, seasonal point of view. The significant relationship between the percentage of alien species and the total patch perimeter suggests that edge effects are highly involved in the sensitivity of the communities. Hence, it is not surprising to see that embankments around agricultural and littoral communities are the most invaded in Bernède. Moreover, the fact that, for the Hoh River, the alder flats were widely invaded may be related to their seasonally opened canopy, which contrasts to the closed canopy of the coniferous forests.

Conclusions

The invasion of riparian zones by alien species appears to be strongly influenced by disturbance regimes and local landscape structure. Despite longitudinal continuity, riparian corridors are differently affected by invasions according to the various hydrological and geomorphological zones along the river. The similarity of results obtained for the McKenzie and Adour Rivers leads us to suggest that invasions may be predictable along the rivers from the point of view of species richness.

The exceptional species richness found in riparian systems lies, in a large part, in the development of patches and interfaces, along the edge of the corridor itself and the edge of patches inside the corridor. At the patch scale the comparison of the results obtained from the Bernède study site and from the Hoh and Dungeness Rivers indicates that important differences in invasibility may be observed along successional gradients, with riparian zones probably being more sensitive to invasion than upland zones. The landscape structure participates actively in this process at the patch scale. The spatial configuration of the shifting mosaic, as well as the permeability of patch edges and the canopy, are also important.

Riparian systems play host to many specialized or endangered species (Naiman et al. 1993). But conservation techniques applied to riparian systems should directly preserve landscape configuration (habitat diversity and complexity, including connectivity) and also the general structural integrity of a community, species diversity, and the proportion of functional groups. In the case of systems inhabited by rare species, these techniques often focus on the autoecology of species and often do not consider the biotic and abiotic context of the surrounding habitat. In addition, riparian zones may be temporary regional reservoirs of species during drastic environmental changes. Our results show that, despite the high number of plant species found along rivers, riparian zones are very sensitive to invasions (Crawley 1987). Unfortunately, little is known about the consequences of these invasions on regional and local pools of native species. For this reason riparian systems should be carefully considered in species conservation programs.

Finally, how can riparian plant communities tolerate moderate invasions without a strong level of species exclusion? Fortunately, in most cases, natural disturbance creates considerable spatial and temporal heterogeneity. Such a patchy environment appears to allow the coexistence of aliens and natives at the local scale. This may explain why so few aliens in riparian corridors appear to exclude native riparian species completely (Planty-Tabacchi 1993; De Waal et al. 1994). But the balance between native and alien species may be endangered in two ways. A drastic change in the disturbance regime may favor alien species. Also, local environmental change independent of the natural patch dynamics may promote the invasion of some "latent" species. Perhaps the best way to limit invasions is to maintain the original disturbance regime, which may favor native over alien species.

The hypothesis that rich communities are the most invaded is confirmed by our data. Fortunately, simple regression models may offer an efficient tool for predicting species richness in river conservation programs. Further studies will be needed to assess the accuracy of this relationship for other riparian-riverine systems; in the meantime, we suggest that conservation measures focus on physical and functional linkages between riparian and terrestrial communities. For conservation to be successful, it will be necessary to take into account local landscape features (location, age, nature of patches), regional landscape features (geomorphological zone, connectivity), and characteristics of the biotic communities (composition, richness, successional stage).

Acknowledgments

Research on the Washington Olympic Peninsula was supported by grants from the U.S. Man and the Biosphere Program and the University of Washington, the Center for Streamside Studies, and the Olympic Natural Resources Center. Research on the Lookout-McKenzie-Willamette system was supported by Oregon State University and by the Centre National de la Recherche Scientifique (France). We thank A. McKee, F. Swanson, and J. Sedell, (U.S. Forest Service, Forestry Science Laboratory, Corvallis, Oregon) and R. Frenkel (Department of Geography, Oregon State University) for their assistance with fieldwork. The study of Bernède site was partially supported by a grant from the Man and the Biosphere Programme of France.

Literature Cited

Ashton, P. J., and S. M. Mitchell. 1989. Aquatic plants: patterns and modes of invasion, attributes of invading species and assessment of control programmes. Pages 111–154 in J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley and Sons, Oxford, United Kingdom.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147–172 in H. G. Baker, and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–451 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonisation, succession, and stability. Blackwell Scientific Publications, Oxford, United Kingdom.

Crawley, M. J. 1989. Chance and timing in biological invasions. Pages 407–424 in J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley and Sons, Oxford, United Kingdom.

de Candolle, A. 1855. Geographie botanique raisonnée. Librairie de Victor Masson, Paris.

Décamps, H., and E. Tabacchi. 1994. Species richness along river margins. Pages 1–20 in A. G. Hildrew, P. S. Giller, and D. Raffaelli, editors. Aquatic ecology: scale, pattern and process. Blackwell Scientific Publications, Oxford, United Kingdom.

DeFerrari, C. M. 1993. Exotic plant invasions across landscape patch types on the Olympic Peninsula. M.S. thesis. University of Washington, Seattle.

DeFerrari, C. M., and R. J. Naiman. 1994. A multi-scale assessment of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247–258.

De Waal, L. C., L. E. Child, P. M. Wade, and J. H. Brook, editors. 1994. Ecology and management of invasive riverside plants. John Wiley and Sons, Chichester, United Kingdom.

Di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. Pages 1-29 in J. A. Drake et al. editors. Biological invasions: a global perspective. John Wiley and Sons, Chichester, United Kingdom.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen & Company, London.

Forman, R. T. T., and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York.

Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57-60 in R. H. Groves, and J. J. Burdon, editors. Ecology of biological invasions. Cambridge University Press, Cambridge, United Kingdom.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540–551.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, United Kingdom.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31-60 in J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley and Sons, Chichester, United Kingdom.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Review **61**:369–394.

Kalliola, R., and M. Puhakka. 1988. River dynamics and vegetation mosaicism: a case study of the river Kamajohka, northernmost Finland. Journal of Biogeography **15**:877-901.

Kruger, F. J., and H. Taylor. 1979. Plant species diversity in cape fynboss: gamma and delta diversity. Vegetation **41**:25–93.

Kruger, F. J., G.J. Breitenbach, I. A. W. Macdonald, and D. M. Richardson. 1989. The characteristics of invaded Mediterranean-climate regions. Pages 181–213 in J. A. Drake et al. editors. Biological invasions: a global perspective. John Wiley and Sons, Chichester, United Kingdom.

Macdonald, I. A. W., F. J. Powrie, and W. R. Siegfried. 1986. The differential invasion of southern Africa's biomes and ecosystems by alien plants and animals. Pages 205–225 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Oxford, United Kingdom.

Macdonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hammann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215–256 in J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley and Sons, Oxford, United Kingdom.

Malanson, G. P. 1993. Riparian landscapes. Cambridge University Press, Cambridge, United Kingdom.

MacLain, D. H. 1974. Drawing contours from arbitrary data points. The Computer Journal **17**:318–324.

Mitchell, D. S., editor. 1974. Aquatic vegetation and its use and control. United Nations Educational, Scientific, and Cultural Organization (UNESCO), Paris.

Naiman, R. J., and H. Décamps, editors. 1990. The ecology and management of aquatic-terrestrial ecotones. Man and the biosphere series, vol. 4. Parthenon Press, Carnford, United Kingdom.

Naiman, R. J., H. Décamps, J. Pastor, and C. A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. Journal of the North American Benthological Society **7**:289–306.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications **3**:209–212.

Nilsson, C., G. Grelsson, M. Johanson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. Ecology **70**:77–84.

Planty-Tabacchi, A. M. 1993. Invasions des corridors riverains fluviaux par des espèces végétales d'origine étrangère. Thesis. Toulouse University, Toulouse, France.

Rejmanek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley and Sons, Chichester, United Kingdom.

Rejmanek, M., C. E. Sasser and J. G. Gosselink. 1987. Modelling of vegetation dynamics in the Mississippi River deltaic plain. Vegetatio **69**:133–140.

Sauer, J. D. 1988. Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Berkeley and Los Angeles, California.

Sculthorpe, C. D. 1967. The biology of aquatic and vascular plants. Edward Arnold, Ltd., London.

Solbrig, O. T., editor. 1991. From genes to ecosystems: a research agenda for biodiversity. The International Union of Biological Sciences, Paris.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353–391.

Tabacchi, E., A. M. Planty-Tabacchi, and O. Décamps. 1990. Continuity and discontinuity of the riparian vegetation along a fluvial corridor. Landscape Ecology **5**: 9–20.

Tabacchi, E., and A. M. Planty-Tabacchi. 1990. Evolution longitudinale de la végétation du corridor de l'Adour. Botanica pirenaico-cantabrica **5**:455–468.

Tabacchi, E. 1992. Variabilité des peuplements riverains de l'Adour. Influence de la dynamique fluviale à différentes échelles d'espace et de temps. Thesis. Toulouse University, Toulouse, France.

Thellung, A. 1911-1912. La flore adventice de Montpellier. Bulletin de la Société des Sciences naturelles de Cherbourg **38**:57–572.

Appendix 1.

Main alien species found within the Adour River, Oregon Rivers, Bernède site, and the Dungeness and Hoh watersheds.

Species	*Adour River*	*Oregon rivers*	*Bernède*	*Dungeness-Hoh*
Woody Species				
Acer negundo (Aceraceae)	x		x	
Buddleja davidii (Buddlejaceae)	x			x
Castanea sativa (Fagaceae)*	x		x	
Cytisus monspessulanus (Fabaceae)		x		
Cytisus scoparius (Fabaceae)		x		x
Juglans regia (Juglandaceae)	x		x	
Parthenocissus inserta (Vitaceae)	x			
Robinia pseudacacia (Fabaceae)	x			
Rubus discolor (Rosaceae)		x		x
Rubus laciniatus (Rosaceae)		x		x
Vitis vinifera (Vitaceae)	x		x	
Herbaceous Species				
Agrostis tenuis (Poaceae)				x
Amaranthus albus (Amaranthaceae)	x		x	
Amaranthus retroflexus (Amaranthaceae)	x		x	
Bidens frondosa (Asteraceae)	x		x	
Cirsium arvense (Asteraceae)		x		x
Cirsium vulgare (Asteraceae)		x		
Conyza bonariensis (Asteraceae)	x			
Conyza canadensis (Asteraceae)	x		x	
Crepis setosa (Asteraceae)		x		
Cyperus eragrostis (Cyperaceae)	x		x	
Dactylis glomerata (Poaceae)		x		x
Datura stramonium (Solanaceae)	x		x	
Daucus carota (Apiaceae)		x		
Digitalis purpurea (Scrophulariaceae)		x		x
Elodea canadensis (Hydrocharitaceae)	x		x	
Erigeron annuus (Asteraceae)	x		x	
Galium aparine (Rubiaceae)		x		
Helianthus annuus (Asteraceae)	x		x	
Holcus lanatus (Poaceae)				x
Hypericum perforatum Hypericaceae)		x		
Hypochaeris radicata (Asteraceae)		x		x
Impatiens glandulifera (Balsaminaceae)	x			
Lactuca muralis (Asteraceae)				x
Lapsana communis (Asteraceae)				x
Leucanthemum vulgare (Asteraceae)				x
Lolium multiflorum (Poaceae)	x		x	
Lotus corniculatus (Fabaceae)		x		x
Lycopersicon esculentum (Solanaceae)	x		x	
Melilotus alba (Fabaceae)		x		
Myosotis scorpioides (Boraginaceae)		x		
Oenothera biennis (Oenotheraceae)	x		x	
Oenothera parviflora (Oenotheraceae)	x		x	
Panicum capillare (Poaceae)	x		x	
Paspalum paspalodes (Poaceae)	x		x	
Phalaris arundinacea (Poaceae)		x		
Plantago lanceolata (Plantaginaceae)				x
Poa trivialis (Poaceae)		x		x
Ranunculus repens (Ranunculaceae)				x
Reynoutria japonica (Polygonaceae)	x			
Rumex acetosella (Polygonaceae)				x
Rumex obtusifolius (Polygonaceaea)		x		
Senecio sylvaticus (Asteraceae)				x
Sporobolus indicus (Poaceae)	x		x	
Taraxacum officinale (Asteraceae)				x
Trifolium repens (Fabaceae)		x		x
Veronica persica (Boraginaceae)	x		x	
Xanthium macrocarpum (Asteraceae)	x		x	

**Rare within the riparian zone.*