Crack willow changing riverine landscapes in Patagonia

L. Datri [1,2], A. Faggi [2,3] and L. Gallo [4]

[1]LIEN (Laboratorio de Investigaciones Ecológicas de la Norpatagonia) Universidad Nacional del Comahue, Neuquén, Argentina (leodatri@gmail.com)

[2]Facultad de Ingeniería, Universidad de Flores, Cipolletti, Argentina

[3] Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Consejo Nacional de Investigaciones Científicas y Tecnológicas - CONICET), Buenos Aires, Argentina

[4] INTA (Instituto Nacional de Tecnología Agropecuaria), Estación Experimental Bariloche, Argentina.

Abstract

In Patagonia (Argentina) in recent decades, the exotic species and hybrids of *Salix alba* - *Salix fragilis* complex has spread over wide areas along watercourses, taking advantage of it is sexually and vegetatively propagation. It out-competes with native vegetation, facilitated by stochastic events related to large floods of long-lasting duration higher than the average maximum of 186 m^3/sec for more than a day. We analysed the exotic willow's increase along the braiding Azul River, and the hydrological regime between 1966 and 2012. We evaluated the links between regime and tree density over time using dendrochronological data. Results showed an increase of the forest's cover from 2.1% to 70.8% over the last 46 years. The densities of exotic willows grew exponentially between 1966 and 1973, during a period which was free of higher floods. The initial native populations declined as willow's population increased. Up to 1973 there was an increase in the native populations too. Then from 1974 on, the willow showed a gradual growth coupled with a decline in the native trees. Up 1977 the willow expansion could be linked to an extreme flood that reached 392 m^3/sec (210.75%) greater than the average of the maximum flows). We concluded that plant succession in the Azul River follows a "Red Queen" effect whereby the exotic willow and native trees repeatedly reorganized the system after pulses and periods of extreme flooding events.

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Keywords

Salix alba – Salix fragilis complex, bioengineer, succession, hydrological regime

Introduction

Great progress in understanding river ecosystems has been made in the last few decades, highlighting the fact that these landscapes are very dynamic and sensitive in their structural and functional attributes (Ward *et al*., 2002; Gurnell, 2014). In recent years the links between pattern and processes across spatial and temporal scales have become evident, and also the feedbacks between physical drivers and vegetation (Holling, 1998; Bendix and Hupp, 2000; Gurnell and Petts, 2006), which are an input needed to link research with restoration management (Tockner *et al*., 2003; Gurnell *et al*., 2009). River floodplains are conditioned by energy pulses and the erosion and deposition of materials that define the structure and function of the river system. Alternating high and low flows govern its stability. The frequency, intensity and duration of both phases characterize the disturbance produced by the hydrological regime depending on the topographic position of the geomorphologic units and their vegetation cover (Corenblit *et al*., 2007). Thus every flood defines a particular form of interaction with the riverine ecosystem, producing a differential effect on the floodplain (Neiff, 1999). For this reason an altered flow regime, has direct implications on the ecological dynamics of the riparian landscape.

Alluvial floodplains are low lying surfaces composed of fluvial deposits adjacent to river channels (Balian and Naiman, 2005). They are frequently flooded and are normally covered by changing plant communities. Hydro-geomorphological factors and pioneer species are the primary drivers of early succession (Shnauder and Moggridge, 2009) which in braided rivers are characterized by high turnover rates (Tockner *et al*., 2010). Hydro-geomorphological factors include water flow, flood pulses, erosion and deposition of fine and coarse sediments. Pioneer vegetation is highly adapted to extremely variable river flow and morphology (Gray *et al*., 2006) and can trap and stabilize sediments that influence their own distribution patterns in the river channel. A closer and more complex interplay between riparian trees, woody debris jams, flood pulses, sedimentation, island and bar development results in new plants that grow by sexual and vegetative reproduction (Gurnell *et al*., 2005, Francis *et al*. 2009, Mikuś *et al*., 2013).

Usually floodplains are characterized by high or increasing levels of plant cover (Bendix and Hupp, 2000) because rivers are very efficient in transporting propagules, among which alien species may occur. Frequently exotics sprawling on the newly formed substrates outcompete native species (Caruso *et al*., 2013a, b). There is great concern when these increases occur within national parks, because the presence of those alien species threatens their conservation values.

There is evidence that shows the increase of the Eurasian *Salix alba* - *Salix fragilis* complex on flood plains along regulated and unregulated rivers in New Zealand, Australia and Argentina (Stokes & Cunningham, 2006; Caruso *et al*., 2013a, b; Thomas *et al*., 2012). *Salix* x *rubens* Schrank is the hybrid of *Salix alba* L. and *Salix fragilis* L. complex which belong to the most frequent hybridizing *Salix* species (Budde *et al*., 2011) and it is a major invasive of this complex in Patagonia (Argentina). *Salix fragilis* is a tree 15 m in height, with easily broken branches, which has been introduced in the Southern Hemisphere in colonial times (Newsholme, 2003). In recent decades, *S. fragilis* and *S.* x *rubens* it has spread over wide areas along montane watercourses and Nahuel Huapi lake (Budde *et al*., 2011), taking advantage of it is ability to propagate sexually and vegetatively (Moggridge and Gurnell, 2009, Budde *et al*., 2011, Thomas *et al*., 2012). In doing so, it could outcompete with native floodplain plants, like disperse shrubs (*Baccharis* sp., *Fabiana imbricata*, *Berberis* sp.) and with the native willow (*Salix humboldtiana*).

The aim of this study was to contribute to a better understanding of the drivers that trigger the increase (with the probability of invasion) of the crack willow on Patagonian floodplains during recent decades. Specifically, we ask the following questions:

1- Which factors determined the expansion of the exotic willow?

2- What interactions exist with other tree species in the river floodplain?

The hypothesis that arises is that the increase of the exotic willow can be facilitated by stochastic events related to large floods of long-lasting duration. To test the hypothesis we considered the exotic willow´s increase along a braiding river, located in Southwest Argentina, firstly analysing its hydrological regime between 1966 and 2012. Secondly, we studied the spatial and compositional patterns of the floodplain vegetation over the same time

period. Finally, we evaluated the links between the hydrological regime and the changes in density of the exotic willow and native trees over time.

Methods

Study area

The study was conducted along the 10.5 km long Azul River, flowing in many anastomosing channels around alluvial bars or islands. It rises at about 200 m above sea level; it has a 9% channel slope and drains -through a delta- a basin of 1200 km^2 in the Puelo Lake National Park. The climate is temperate, characterized by cold winters with a rainy season and dry in summer. The dominant vegetation of the catchment belongs to the Andean Patagonian forest, composed predominantly by *Nothofagus* species *(N. dombeyi*, *N. pumilio*, *N. antarctica)* and *Austrocedrus chilensis.* Due to urbanization of the floodplain, forest cover was analyzed on the riverbed in the Azul Delta (Puelo Lake National Park).

A survey conducted in the National Park 20 years ago described the riparian vegetation of the Azul River as a mosaic of plant communities composed of *Salix fragilis, Baccharis* sp. and *Fabiana imbricata* on bars sand and islands and *Myrceugenia exsucca* and *Maytenus boaria* in the floodplain. In the river floodplain in recent years an increased number of patches of crack willow, exotic shrubs and herbaceous species (*Cytisus scoparius*, *Rubus ulmifolius*, *Rosa eglanteria* and *Lupinus polyphyllus*) have been reported (Faggi and Cagnoni, 1996).

Data collection and analysis

The hydrological regime was determined by using data from the lower section of the Azul River obtained from gauging stations on the river and its main tributary, the Quemquemtreu River from 1966 to 2012 (National Water Resources Subsecretary. Available in: http://bdhi.hidricosargentina.gov.ar/Filtros.aspx). Water flow and magnitude frequencies were estimated with PULSE program (Neiff and Neiff 2003), in order to obtain a measure of the regularity of flood and low-flow events. Historical maps of the riparian forest cover were obtained from two historical aerial photographs in black and white (1951 and 1995) at a scale of 1:5000, of the Azul River Delta. Both were georeferenced and processed with the Quantum 2.4.0 (Qgis) program and both were overlapped in turn on the current forest coverage obtained from a scene georeferenced (Available in: Google Earth 2013). Additionally layers of the historical evolution of the area covered by rocks, woody shrub sand the riverbed from 1951 on, were compared to estimate the development of the forest area.

Patches of woody vegetation (n: 53) were sampled on cross and alternate bars, on straight channel edges, accretion ridges, islands, plains stretches and temporary channels. We identified and characterized riparian forest patches at random, from the estimate of the cover of tree canopy, shrub and saplings, through sample plots of 10 x 10 meters. In each patch sampled, trunk diameters (DBH) were measured at breast height. In addition, in each patch the trunks of dominant and co-dominants trees were drilled at 1.30 m height to determine the age of plants (total 87 trunks) (Stoffel and Wilford, 2012). All growing plants have been recorded. Species frequency associated with each year to analyze the relationship between these over time. In forest patches this relationship was evaluated using a linear and nonlinear regression model. Weibull model was chosen for its special ability to evaluate the probability of change over time:

$$f=1-exp(-(x/lambda)^k)$$

where *x* is the frequency of *Salix fragilis*

In order to evaluate the influence of flooding regime on the detected patches a principal component analysis (PCA) relating ecological and hydrological variables, was performed. Thus the PCA allowed inferring the level of floods impact on the patches. Initially, the field variables obtained were analyzed according to a gradient established between the low water bed and floods. This information is summarized in the first two axes of a PCA. Afterward three variables (rockiness, patch age and height) were selected for consideration in a subsequent analysis of the environmental variables. The rocky coverings represent unstable areas and the oldest and highest patches, the most stable areas.

Results

The analysis of hydrological data showed that the Azul and Quemquemtreu River have a middle flood average of 33 m^3/sec (average of maximum floods: 186 m^3/sec and low flood: 7 m^3/sec). Both rivers are characterized by a low frequency of extreme pulses, with two annual floods peaks in winter and spring. In most of the years studied the river regime remained close to the annual average. The years 1988 and 2000 are examples of two contrasting situations with extreme and opposite pulses. In winter of 2000 was a very important flood and in 1988 a dry period throughout the year with flows below the annual average occurred (Figure 1). Between 1970 and 2012, 21 floods and 31 low floods were observed.

Forest cover over the last 46 years on the Azul floodplain showed an increase from 2.1% to 70.8% on the Azul River Delta. In 1951, the rocky riverbed did not possess patches of forest (<0.1 km^2). However by 1995 the riverbed forest had increased to 0.2 km^2 (37.5 % of the forest). At present, the forest on the riverbed is 0.4 km^2 (Figure 2). A steady density increase of the crack willow and a density decrease of native species were observed between 1969 and 1973 (Figure 3). In 1998 the willow density surpassed the density of the natives. Since 1978, the river pulse amplitude has been much smaller compared to the period between 1966 and 1977. There was some regularity in the recurrence of pulses greater than 186 m^3/sec flood. Twelve years did not exceed 186 m^3/sec at the beginning of the registration flood (1961-1973). The average recurrence was 2.4 years. Throughout this period the first individuals of *Salix fragilis* became established.

From 1977 extreme flood pulses of 14 days duration occurred, while the density of *S. fragilis* increase. Simultaneously the first species of native trees were identified, but their densities decreased as *S. fragilis* increased (Figure 3a). After this year, the amplitudes between pulses were shortened except for a period of 1000 days without extreme pulses between 1983 and 1987 (Figure 3b). At the same time the population growth of *S. fragilis* and the decline of native trees showed fluctuations because of high-intensity disturbances (Figure 3c). Increased frequency in the floods implied slower growth of *Salix fragilis* and a decrease of native trees.

The frequencies of native species and *S. fragilis* oscillated between 1970 and 1976, during a period which was free of higher floods (above a flood rate of 186 m^3/sec). The initial native populations (*Myrceugenia exsucca*, *Nothofagus dombeyi)* declined as willows increased. Up to 1973 there was an increase in the native populations, with an important increase in *Maytenus boaria*. Then from 1974 on, *Salix fragilis* populations showed a gradual increase coupled with a decline in the native trees. Up 1977 *Salix fragilis* spread could be linked to an extreme flood that reached 392 m^3/sec and lasted for four days. Similar evidence has been observed since 1987: the steady increase in the populations of *Salix fragilis* could be associated with intense disturbances and a decline in the native trees. Never the less, *Myrceugenia exsucca* increased in 1980 and 1995; *Maytenus boaria* in 1987, 1990, 1994, and 2000; *Rhaphithamnus spinosus* in 1987 and 2005 (Figure 3a, b, c).

A greater diversity of native trees could be linked to the reduction of the pulses amplitude from 1991. In the same period parity frequencies occur between native trees and willows. In 2000 an extreme 12 days flooding occurred, after which the frequency of native trees surpassed the frequency of the willows. From 2004, as the intensity of the disturbances and the days of pulse duration decreased, the ratio of native to exotic willows stabilized at frequencies near 50%. As a result of this dynamic, the nonlinear regression model confirms that there is a direct relationship between the increase of *Nothofagus dombeyi* (p-values, λ: <0.001, k: <0.0088), native trees growth (p-values, λ: <0.001, k: <0.0184) and *Salix fragilis*. While the willow is also linked to native trees like *Myrceugenia exsucca, Aristotelia chilensis* and *Luma apiculata* (p-values, λ: <0.001, k: <0.001), the best association was found to *N. dombeyi.* The richness of native trees also showed a significant association (r^2=0.7527) with increased *Salix fragilis* on the riverine landscape (Table 2).

At the end of study period the native vegetation showed an increase of richness on the floodplain. The PCA summarized the environmental information along two axes explaining 93 % of the variance. Axis 1 summarized 74.9 % of the information on a geomorphological and ecological stability gradient, showing patches of diverse forest vegetation and structural complexity. Once *Salix fragilis* invaded the riverbed free of disturbances, patches of native species *Maytenus boaria*, *Austrocedrus chilensis*, *Myrceugenia exsucca* and *Nothofagus dombeyi* advanced in the floodplain and near the same channel. Next to the willows, *Rosa* sp., *Cytisus scoparius* and *Baccharis* sp. shrubs, colonized the most unstable areas with rocky soils. Within this group, *Baccharis* sp. was the only native species. The native trees and *Fabiana imbricata*, were associated with elevated patches on the river and with older age (Figure 4).

Discussion

The process of primary succession on the floodplain near the main channel of the Azul River, activated in all historically when the amplitudes between extreme stochastic disturbances became more prolonged. This situation took place when pulses were below 186 m^3/sec (Figure 3) as native species cannot form dense stands as *S. fragilis* did above this level of flood. And probably do so hybrids *S. alba – S. fragilis* complex detected upstream near the valley of El Bolson by Budde (Budde *et al*., 2011). Since the 70s, rocky surfaces on the active riverbed began to be massively colonized by the exotic *Salix fragilis*, a species that has ecological adaptive advantages compared to native trees and other *Salix* and their hybrids.

These links between the stochasticity of the river regime and the succession process is coincidence to the dispersion of exotic willows in New Zealand (Caruso *et al*., 2013a, b).

Over 46 years the riparian ecosystem develops through different stages of succession, alternating pulses of extreme flood, and relatively long periods of stability. Then the system entered a pulse recurrence period of approximately 2.4 years. While pulses operate as a factor regulating the growth of *Salix fragilis* on the active bed, the mechanical and physiological characteristics of the exotic tree allowed their adaptation to the riverine environment and the setting of sand and rocks banks (Schnauder and Moggridge 2009, Gurnell and Petts, 2006). At the same time, and associated with this cycle in which intense floods occurred, native tree species persisted and increased the diversity of the riparian forest. With the entrance of a second period of intense pulses, the dispersion of *Salix fragilis* and native trees became stabilized. This indicates a trend across advanced succession process according to established processes in riparian landscapes led by *Salix* sp. (Gurnell and Petts, 2006).

Plants growing within river corridors both affect and respond to fluvial processes, developing bioengineering functions that modify and create niches and habitats for various species (Gurnell, 2014). Our findings confirmed the hypothesis: the stability of substrates produced over a period of very large amplitudes of disturbances between the 60s and 70s, together with the accumulation of jam wood debris of native pioneer species, such as *Fabiana imbricata*, *Myrceugenia exsucca* and *Nothofagus dombeyi*, favored the rooting of broken branches and the asexual dispersion of *S. fragilis* (Gurnell, 2014, Moggridge and Gurnell, 2009, Budde *et al*., 2011, Thomas *et al*., 2012). Then *S. fragilis* itself created the conditions for further vegetative spreading and also overcame increased frequency of flooding.

The succession process driven by *S. fragilis* now set new conditions and a system of interactions between the periods of flooding and dispersion of native trees with influence on diversity. *Nothofagus dombeyi* is a tree characteristic of humid habitats, well adapted to fire or landslides (Veblen *et al*., 2004) but not to riparian disturbances such as extreme flooding. This species grows on levees, plains or patches of substrates anchored by the exotic *Salix fragilis*. *Myrceugenia exsucca* is a riparian native tree growing along lakes shores, on floodplains (González *et al*., 2014) and in deep humid valleys, and also not well adapted to a high frequency of disturbances (Correa-Araneda *et al*., 2012). Nevertheless it has the capacity to regrow from broken trunks and produces succulent adventitious roots on submerged branches. On the Azul River *Myrceugenia exsucca* built a swamp forest, near to the delta and

the paleobed of the Golondrina stream (Figure 5). Over the floodplain we observed isolated individuals of this tree, protected by nursing effect of *Salix fragilis*, which allowed the native tree to develop on stabilized substrates.

The other two native trees are *Maytenus boaria* and *Austrocedrus chilensis*. The first one has high plasticity, grows along stream banks, and it is associated with *Nothofagus* species in the humid Patagonian region (Donoso and Wendler, 1985, Veblen *et al*., 2004), but it is also adapted to drier conditions. *Maytenus boaria* has gemmiferous roots, produces a lot of saplings and build pure stands. Our findings showed that on the Azul River, the tree cover increased notably over the last two decades forming patches with *S. fragilis* or young *A. chilensis* trees on the lower floodplains in the upper stretch of the river. Also, other native trees, like *Maytenus boaria* and *Austrocedrus chilensis*, benefited from the nursing role played by *S. fragilis* (Figure 3).

In the static regime without any disturbances introduced by the river, nothing changes. On the highly dynamic environments the landscape is always changing, and this continually generates or increases niches which can be exploited by incoming species (Corenblit *et al*., 2007). This even applied to stands of *Nothofagus* and *Austrocedrus* trees -that despite their high light requirements- could grow in between willows, which were affected by the hydrological disturbance. In the Azul floodplain the richness of native trees increase and development of each species followed an initial exponential growth and a gradual stagnation associated with the appearance of new species (Figure 6). As the willows grew on land impacted by the flood regime and the power of the waters, the native species mainly developed on more stable surfaces. In this sense, the increase in richness resulted from the complexity relations between willows with the riverine landscape and the recurrence of the disturbance, achieved by the system over time, due to endogenous factors of new abiotic/biotic relationships established among the species (Mikuś *et al*., 2013, Francis *et al*., 2009, Tockner *et al*., 2010).

The riverine landscape is not static, but it is a set of states in which each tree patch can reach a local equilibrium and continue to thrive. We can say that each different successional stage observed in the Azul River, followed the conceptual framework of the Red Queen Hypothesis (Van Valen, 1977) in the way that biotic and abiotic interactions changed the landscape. This hypothesis stated that the effective environment of each species depends on the other species in the ecosystem. Therefore, evolutionary change in one species in the ecosystem is

equivalent to a change in the effective environment of all the others. Such changes are likely to be detrimental, rather than beneficial, at the level of species adaptation to the environment. Each species must, therefore, evolve continually if it is to keep pace with changes in other species (Hoffman, 1991).

Through the Red Queen Hypothesis we could explain that many of the native species even at low densities, developed in the riverine landscape depending on how the exotic willow created changes in the disturbance regime, undisturbed areas were covered by native species and the total diversity increased. While the frequencies of native species increased, their densities remained low due to interspecific competition through the recruitment of new individuals of different species and willows, in particular. This occurred because the rates of reproduction of *S. fragilis* doubled that of all the native trees, until it stabilized in the last five years.

Conclusion

Salix fragilis was favored by stochastic pulses, during periods of decreased intensity and duration of the flood, colonizing unstable rocky substrates. At the same time it attenuated the effect of intensive flooding on the floodplain and enabled the establishment of individuals of native trees and shrubs. The accumulation of woody jams on unstable surfaces created a favorable habitat for mature forest. This set of interactions by which exotic willows and native trees repeatedly reorganized after flooding and drought pulses system, led to the current configuration of the riparian landscape, in which individuals of native trees and shrubs increase on the floodplain. A greater diversity of trees and patches of native forest in floodplain depends on the intensity and frequency of disturbances that facilitate and simultaneously regulate the colonization of exotic willows on the banks, near the river.

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Table1. Nonlinear regression models analysis (Weibull model) of native trees in relation to *S. fragilis* increase between 1966 and 2012 (46 years).

Variable	N	MSE	Sigma	Iteration	Parameters	Initial value	Estimate	SE	T	p-value	obs.
					λ	0,38	0,21	0,04	4,94	<0,0001	
Nothofagus dombeyi	46	0,07	0,27	4	*k*	-1,46	-1,76	0,64	-2,74	0,0088	
					λ	0,38	0,08	0,02	4,21	0,0001	
Myrceugenia exsucca	46	1,8e-03	0,04	2	*k*	-0,05	-1,23	0,19	-6,34	<0,0001	
					λ	0,38	1,08	0,13	8,25	<0,0001	
Austrocedrus chilensis	46	5,6e-04	0,02	6	*k*	0,23	3,37	0,53	6,30	<0,0001	
					λ	0,38	2,75	1,46	1,89	0,0653	not significant
Raphithamnus spinosus	46	1,0e-04	0,01	4	*k*	0,05	2,36	0,72	3,27	0,0021	
					λ	0,38	1,11	0,18	6,30	<0,0001	
Schinus patagonicus	46	1,7e-05	4,1E-03	7	*k*	0,03	6,18	1,35	4,59	<0,0001	
					λ	0,38	0,72	0,03	24,45	<0,0001	
Aristotelia chilensis	46	3,0e-06	1,7E-03	3	*k*	0,02	17,21	2,71	6,35	<0,0001	
					λ	0,38	0,67	0,05	14,27	<0,0001	
Luma apiculata	46	2,0e-05	4,5E-03	6	*k*	0,02	22,58	8,35	2,70	0,0097	
					λ	0,38	0,36	0,04	8,77	<0,0001	
Native plants	46	0,07	0,26	4	*k*	-1,00	-1,06	0,43	-2,45	0,0184	

Maytenus boaria not does fit the model

Table2. Linear regression analysis of tree's richness in relation to *S. fragilis* increase between 1966 and 2012 (46 years)

Multiple correlation coefficient	0,8676
Determination cofficient R^2	0,7527
R^2 ajusted	0,7471
DF	1
EE	1,0545
P-value	<0,0001
Observations	46

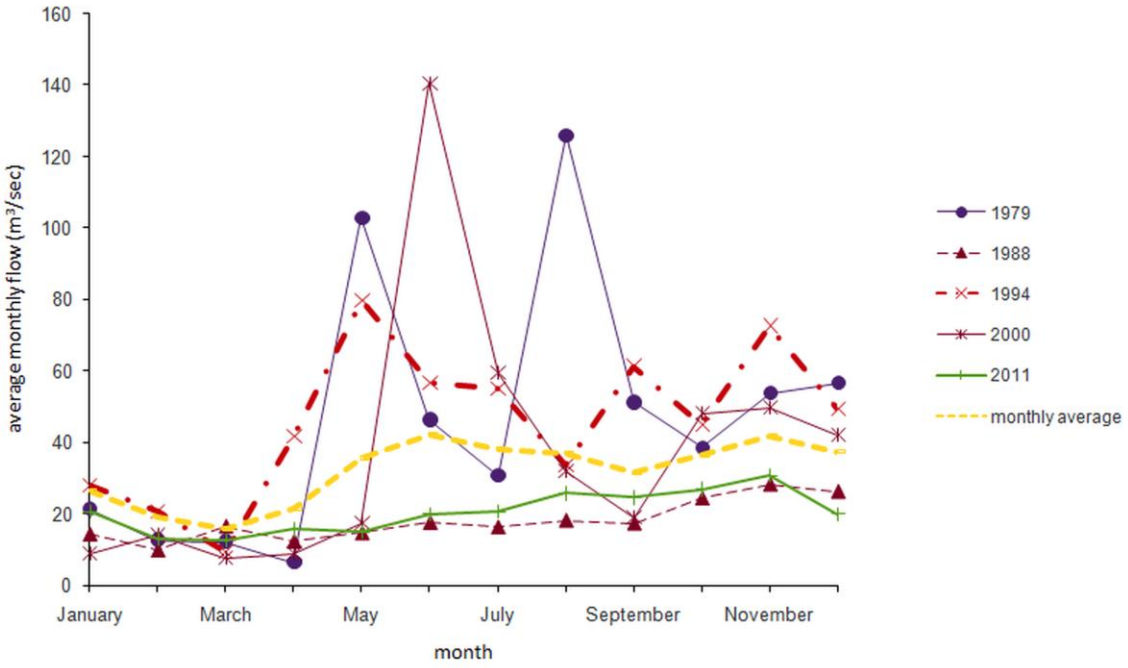

Fig. 1. Significant flood years of hydric interannual regime in the Azul River between 1970 – 2012.

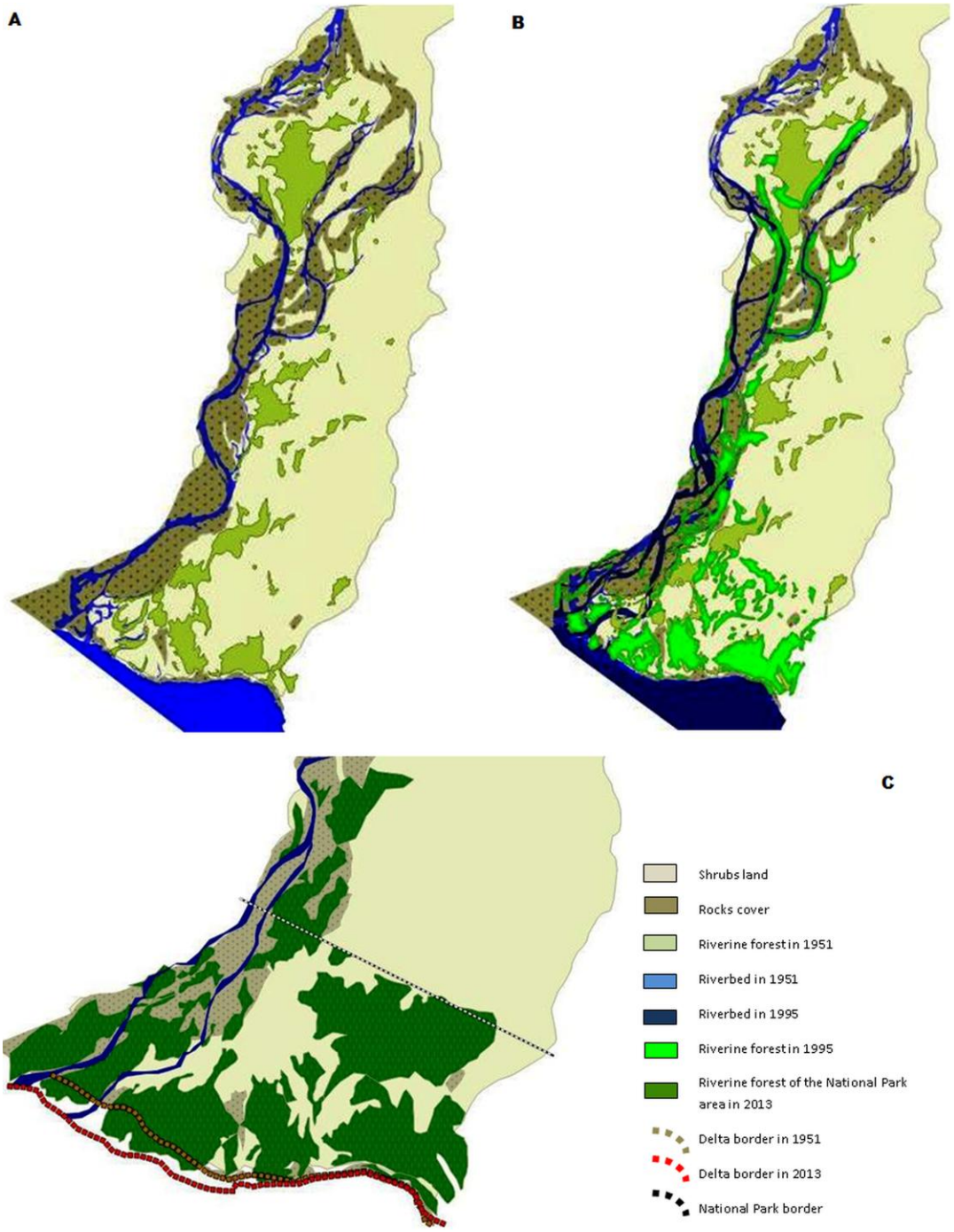

Fig. 2. Advance of vegetation cover on the Azul River floodplain. A) Forest, shrubs and rocks cover on the floodplain in 1951. B) Forest, shrubs and rocks cover on the floodplain in 1951 and 1995. C) Forest cover on the floodplain and riverbed at the delta of the Azul River in 2013. Own elaboration with aerial photographs provided by the Lago Puelo National Park, the Provincial Forest Management of Chubut and Google Earth (Software Qgis 2.4).

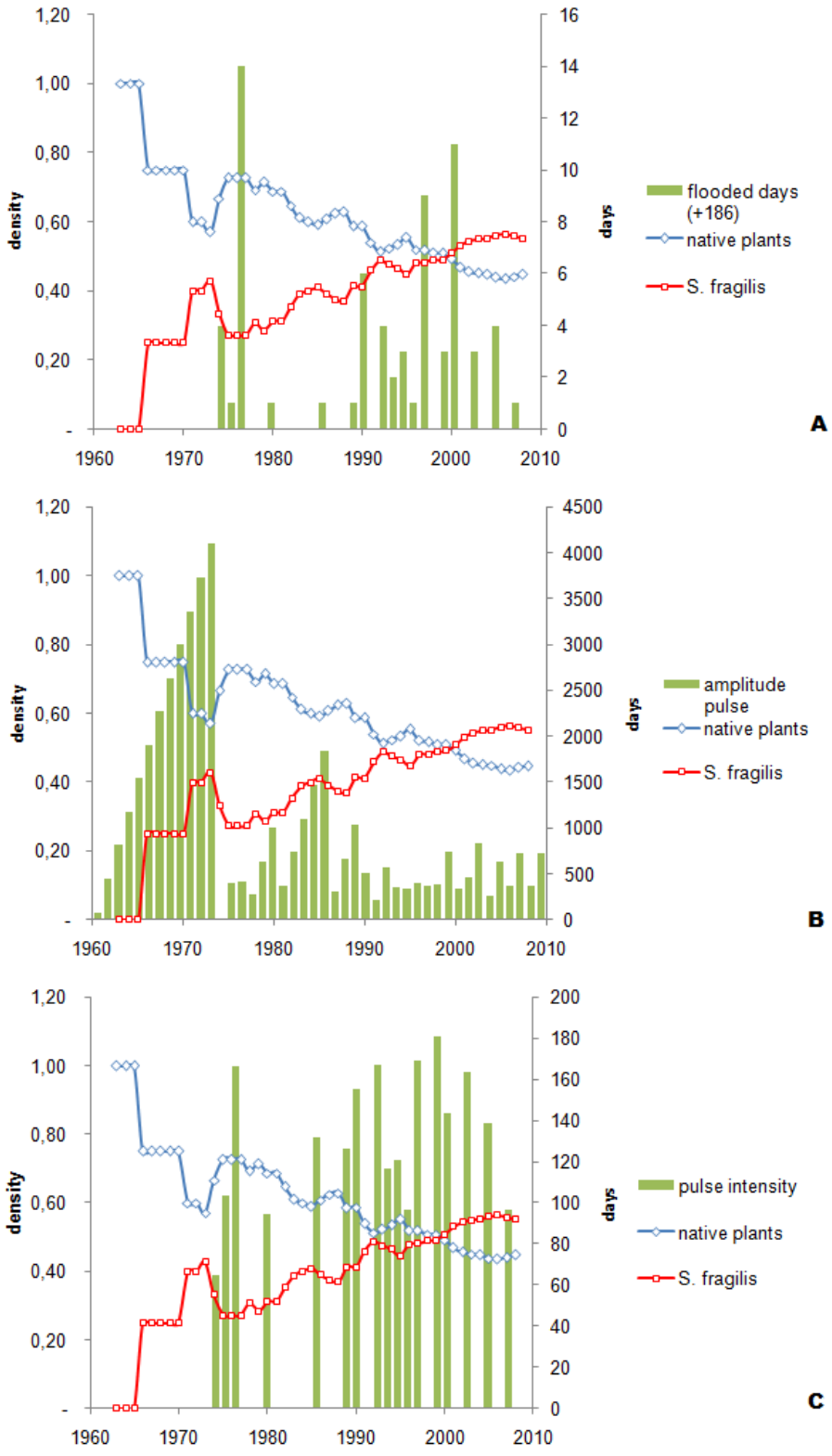

Fig. 3. Pulse regime of the Azul River between 1970 – 2012. Growth of native and exotic willows related to A) annual flood duration of more 186 m3/sec. flows. B) pulse intensity. C) pulse amplitude.

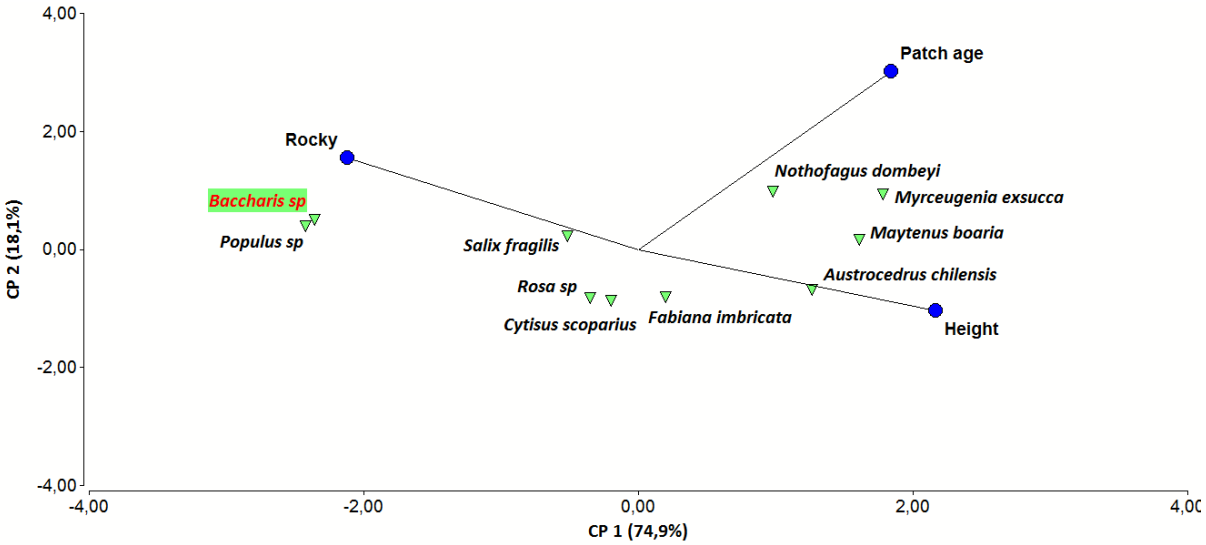

Fig. 4. The PCA shows the distribution of patches of woody vegetation in relation to age, height and rockiness. Axis 1 shows the influence of the disturbances gradient. Baccharis sp. (marked in red) is the only native species in areas reached by frequent disturbance.

Fig. 5. Azul River floodplain. A) Myrceugenia exsucca swamp forest, in the Golondrina stream in Puelo Lake National Park. B) Native shrubs and S. fragilis saplings, on the Azul riverbed next to the mouth at Puelo lake C) Willows on transverse bars and wood debris jams. These structures favor the willow's dispersion and landforms` stability. D) Willow and Nothofagus riparian forest on the floodplain. E) Austrocedrus chilensis and willows on bars in the floodplain. F) A pure stand of Maytenus boaria surrounded by willows in the Azul Delta.

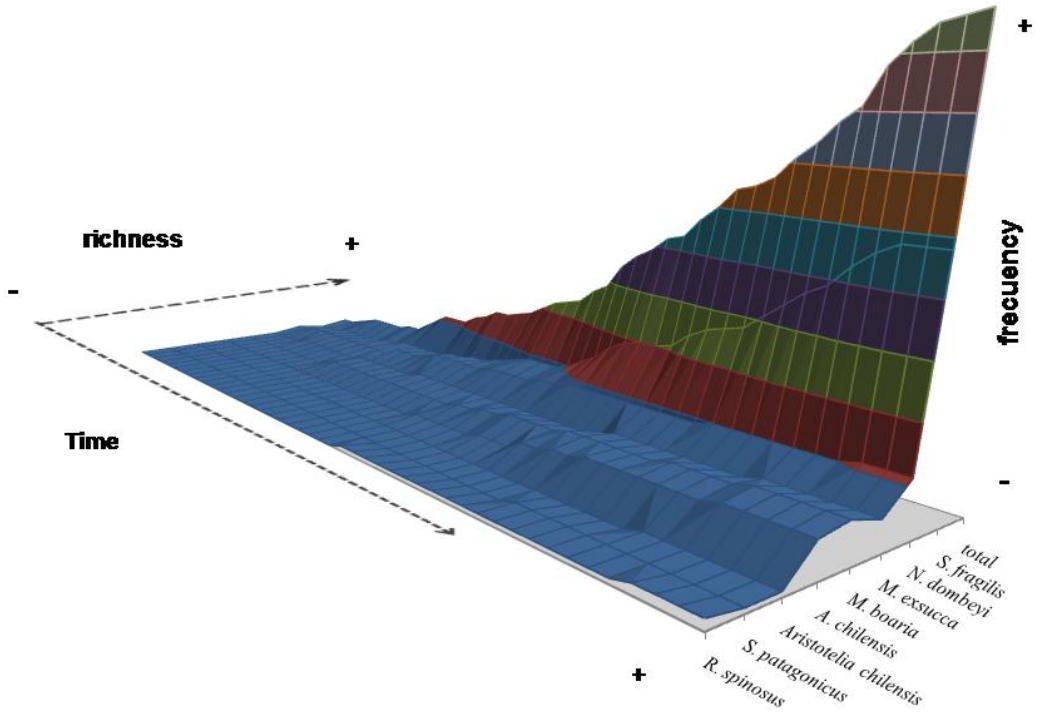

Fig. 6. Conceptual model. Representation of common use in the adaptive landscape and its implications for the evaluation of the dispersion of the species and the changes in the landscape. The increased frequency of willows is accompanied by the increase in trees richness over time.