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ORIGINAL PAPER

Half a century of changes in the riverine landscape of Limay River: the origin of a riparian neoecosystem in Patagonia (Argentina)

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Abstract Our study aims to determine the dynamic that led to the spread of exotic Salicaceae on the Limay River floodplain and its implications in shaping the current neoecosystem. We used images obtained by the HRG sensor on board the SPOT-5 satellite. We selected two images dates allowed a comparison of the floodplain under different flooding regimes programmed by the Interjuridiccional Basin Authority, at a rate of 1290 m^3/s in Spring and a flow rate of less than 400 m^3/s in Summer. To characterize the vegetation cover, the Normalized Difference Vegetation Index (NDVI) was used to compare images of September and December, also the Normalized Difference Water Index (NDWI) was applied to delineate the riverbed and floodplain in September. To evaluate the influence of flooding regime on the detected patches a Principal Component Analysis (PCA), was performed; and biotic and abiotic factors on the composition of the dominant tree species in each patch by Multiple Factor Analysis (MFA) were analized. A 58.4 % coverage of forest patches had developed on the Limay River floodplain. Patches of older trees grew on surfaces at 1.5 m above the water level. However, the surfaces not reached by floods >1.5 m have a very low rocky coverage (1 %). The analysis of the age of the trees downstream of the dam system showed that the vegetation, often exposed to high floods before the dams were built (1971), was composed of the native willow (*Salix humboldtiana*) and the exotic *Salix alba*. As the river regime was attenuated and extraordinary floods disappeared with the operation of the dam Arroyito in 1980, the first patches of *Populus nigra* spread.

Keywords Landforms · Floodplain · Salicaceae · Neoecosystem · Succession

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Introduction

The massive trees invasions of Eurasian Salicaceae species, particularly *Salix alba–Salix fragilis* complex, shaped the current structure of riparian forests in Patagonia (Budde et al. 2011; Thomas et al. 2012). Willows and poplars were introduced from Europe throughout the middle of the twentieth century, linked to fruit production and carried out in the valleys. Since then, Salicaceae species configured ecosystems with a particular structural heterogeneity and ecological complexity of which little is known so far.

The dispersion of willows and poplars on floodplains is determined by the intensity and frequency of disturbances and occurs in almost all riverine ecosystems, facilitated by their adaptive dispersion individuality (Karrenberg et al. 2002). For the Southern Hemisphere, in Southeast Australia, Stockes and Cunningham (2006) described the dispersion of exotic willows in natural and regulated river regimes. As stated by Adair et al. (2006) in Australia, *S. alba*, *S. fragilis* and *Salix rubens* are considered to be weeds of national significance due to their widespread distribution and the substantial ecological damage that they cause. Willows and poplars are early colonizers and they produce many seeds in spring and summer. Seedlings on wet surfaces can withstand floods and the effects of removal because of the favorable mechanical properties in their stems (Karrenberg et al. 2002, 2003). In particular willows have a great capacity for vegetative reproduction from living wood and exposed roots on gravel and sand (Karrenberg 2002; Moggridge and Gurnell 2009; Mikuś et al. 2013). This ability makes them very competitive and guides essential processes, such as the formation and consolidation of islands, the development of complex structures of riparian forests and plains and the stabilization of migration channels (Francis et al. 2009).

Our study aims to determine the dynamic that led to the spread of exotic Salicaceae on the Limay River floodplain and its implications in shaping the current neoecosystem. We hypothesize that the complexity of the structure and diversity of the new riparian ecosystem can be linked to macrofactors, such as the natural and artificial flow regulation of the Limay River, together with endogenous factors generated by the presence of the Salicaceae patches. To our knowledge this is the first study which analyzes the effect of dams on the development of new ecosystems in riparian vegetation in Patagonia.

Materials and methods

Study area

The study includes a stretch of 50 km of the lower reaches of the Limay River valley between the Arroyito dam and the confluence with the Neuquén River. This stretch is located in Monte (Morello1995) biogeographic region and represents the dry end of a gradient of diversity, an increase in rainfall towards the Andes. The waters of the Limay River is regulated by five hydroelectric dams: El Chocón (1971), Arroyito (1980), Alicurá (1984), Piedra del Águila (1990) and Pichi Picún Leufú (1995). The dams have added a variable control in the hydrological regime since the beginning of their activities in 1971, to the present. The Limay River originates in the Nahuel Huapi Lake, and most of its tributaries drain sixteen glacial lakes. Flood cycles of the Limay River at the confluence are characterized by two delay steps (Fig. 1).

Analysis of spectral data

Use of satellite image In this study, we used images obtained by the HRG (High Resolution Geometric) sensor on board the SPOT-5 satellite. The HRG sensor has three bands (Green = 545 nm, Red = 645 nm, Near-IR = 835 nm) at a 10 m spatial resolution, SWIR (1665 nm) at a 20 m resolution, and a panchromatic band at 5 or 2.5 m spatial resolution. Two SPOT-5 images (K/J 681/428) were acquired on 21 September 2013 and 2 December 2013 of CONAE (National Commission on Space Activities of Argentina).

The two selected images dates allowed a comparison of the floodplain under different flooding regimes programmed by the Interjurisdiccional Basin Authority, at a rate of 1290 m^3/s in Spring (September) and a flow rate of less than 400 m^3/s in Summer (December). The images were atmospherically corrected by means of the Dark Object Subtraction technique (DOS) with the software ENVI 4.7 (Schroeder et al. 2006).

Development of the digital mask The study area was delimited by a digital mask, considering the geomorphological boundaries of the Limay River floodplain between Arroyito and its confluence with the Neuquén River. The same mask was used to remove the urban

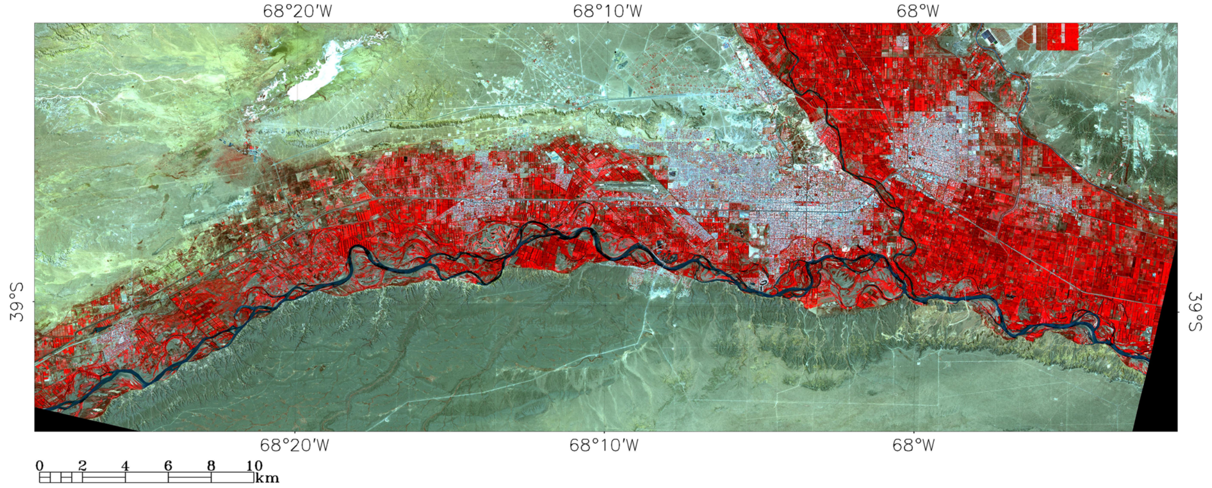

Fig. 1 Location of the Limay River valley in relation to its confluence with the Neuquén and Negro Rivers

and rural areas in order to obtain information from the riparian forests with a minimum of human intervention.

Choice of environmental indexes To characterize the vegetation cover, the Normalized Difference Vegetation Index (NDVI) was used to compare images of September and December. In addition, the Normalized Difference Water Index (NDWI) was applied to delineate the riverbed and floodplain in September (Davranche et al. 2010).

Hydrological information This was extracted from the database of the National Secretariat for Water Resources and corresponds to the gauging station at Balsa Las Perlas. PULSE software was used to study the recurrence of floods according to a sinusoidal function over time.

Land covers classification Several classifications were performed in order to obtain different land covers:

The Spring NDWI was estimated and a filter edge was applied. An unsupervised algorithm K-means classification with a threshold of 5 % and 9 iterations was performed. The iterations are related to the threshold and the classification algorithm defines when changing classes of pixels do not change above 5 %. Then the number of iterations is defined as no more change and the number of classifications in accordance with the process of validation with field data (Richards 2013). Finally, the class belonging to the river was removed by adjustment intervals and a vectorized flooded area. A summer unsupervised classification based on NDVI, with the use of the K-means algorithm, with a threshold of 5 % and 9 iterations was performed.

Field assessment Stratified sampling of the vegetation and field recognition of the fluvial geomorphology were carried out on 60 plots of 10 × 10 m. Woody species composition (*S. alba*, *S. rubens*, *Populus nigra*, *Salix humboldtiana*) were analyzed. Each patch was characterized, according to the fluvial landforms of Ward et al. (2002). The following variables were estimated:

(A) Percentage of soil and rock cover, (B) Height of the vegetation patches in diverse fluvial landforms was measured in relation to the water level during drought periods, (C) The vegetation patch age was estimated by counting tree growth rings of the larger trees which were characterized by their DBH (diameter at breast height: 1.30 m), (D). Species frequencies were determined considering adult trees and their saplings. (E) Total plant diversity was calculated applying the Shannon–Wiener index (Table 1).

Validity of coverages obtained Georeferenced points of sampled areas were loaded to estimate the validity of the coverage of willow and poplar plots obtained. The areas enclosed by vectorized 1290 m^3/s riparian lines, were superimposed on the vegetation cover to assess the impact of floods on the Salicaceae patches. The digital image processing and presentation of maps was performed with SOPI developed by the National Commission on Space Activities of Argentina (CONAE) and QGis 2.4.

Table 1 Indicators used for environmental characterization in the floodplain ecosystem

State indicator	Function indicator
Coverage of willows and poplars	Role in the succession process
Patch age	Age of colonization
Height	Flood pulse influence
Diversity	State of plant succession
Rocks	Degree of soil stability
Bare soil	Hydro-xeromorphic gradient
Hydrological pulses	Influence of stochastic pulses and flow regulation

Statistical analysis of hydrological, geomorphological and ecological variables

The integration of the raster format for a flow of 400 m^3/s with the vector layer built on the classification of the flood of 1290 m^3/s, resulted in a map showing the fluctuation of the flooded riparian forest interface (Fig. 2). Secondly, the integration of the Spring NDWI unsupervised classification image, led to a map of the bed and flooded plain with an estimated flow of 1290 m^3/s (Fig. 3). On this map the 60 georeferenced surveyed plots were located. In this way the plots were seen to fall into three categories: (1) Bed with a flow of 400 m^3/s (estimated level = 0.55 m); (2). Floodplain with a flow of 1290 m^3/s (estimated level = 2.5 m); (3) Floodplain with free flow to 1290 m^3/s (estimated level = >2.5 m). The data validation matrix showed a 92 % of landforms identified in the field which were adjusted to the characteristics of the surface detected on the satellite image.

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 impact of the floods on the patches. Initially, the field variables obtained were analyzed according to a gradient established between the low water bed (400 m^3/s) and the free flow plain below 1290 m^3/s floods. Four variables were then selected: geomorphology units recognized in the field, tree cover, diversity and areas free of vegetation. This information is summarized in the first two axes of a PCA. Afterwards three variables (rockiness, patch age and height) were selected for consideration in a subsequent analysis of the environmental variables.

To evaluate the influence of multiple biotic and abiotic factors on the composition of the dominant tree species in each patch by multiple factor analysis (MFA) was performed. This analysis allowed the connection of a larger number of predictor variables (height, patch age and rockiness), correlated with each other with a relatively low number of cases of dominant species. All analyzes were performed with R-version 3.1.2.

Results

Flooding occurred when the Limay River flow reaches 1290 m^3/s, which happened with a recurrence of 2.16 years. The recurrence of the maximum flood at 1290 m^3/s after the start of operations of the first dam on the Limay River (El Chocón, 1971) increased from 1.37 years to almost double (2.66 years).

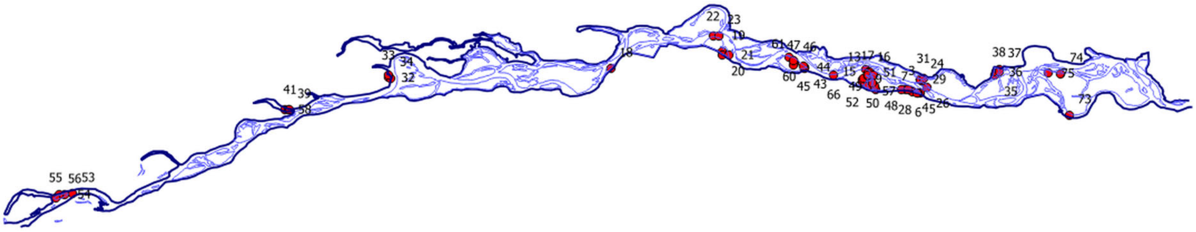

Fig. 2 Limay riverbed with a flow of 400 m^3/s at the shore line and a flow of 1290 m^3/s. The *red points* represent the location of the sample plots

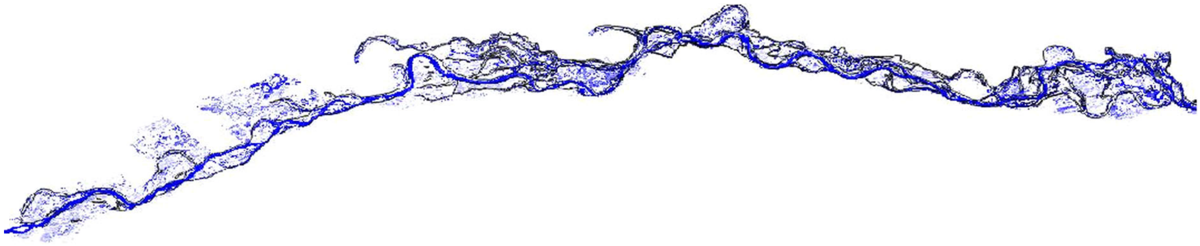

Fig. 3 Limay floodplain with a 1290 m^3/s flow

The cover of the riparian forest was estimated by an NDVI unsupervised classification of a summer image to detect. We recognized forest patches of *Salix* sp., *P. nigra* and of mixed Salicaceae forest. The base image corresponded to the dry season, giving at the same time information about the forest productivity and maximum seasonal water limitation. It also allowed for a better definition of the main course of the river and its active secondary channels (Fig. 4).

A 58.4 % coverage of forest patches had developed on the Limay River floodplain. Patches of older trees grew on surfaces at 1.5 m above the water level. The most unstable areas, estimated by the degree of rockiness, were related to the bed and floodplain surfaces. However, the surfaces not reached by floods >1.5 m had a very low rocky coverage (1 %).

The PCA summarized the environmental information along two axes explaining 90.4 % of the variance. Tree cover, vegetation and diversity were the main predictors. Axis 1 summarized 69.8 % of the information on a geomorphological and ecological stability gradient, showing patches of diverse riparian vegetation and structural complexity (Table 2).

Diversity varied along a geomorphological gradient ranging from levees to swamps. Tree cover increased in wet and stable gradient zones, such as wetlands and levees, and decreased in the most unstable landforms (bars). Areas without vegetation were associated with the riverbed and the arid steppe. On the contrary, stable and humid geomorphological units had higher vegetation cover (Fig. 5).

Salix alba and *Populus nigra* were the dominant species in the riparian forest patches. Patches with less cover were composed of *S. humboldtiana*, *S. rubens*, *Populus deltoides* and the hybrids *S. alba* × *S. matsudana* and *S. alba* × *S. humboldtiana* (Table 3). Around 40 % of the sampled area had no forest cover. A massive coverage of *Fraxinus* sp. and *Acer negundo* saplings, associated with shrubs (*Rosa canina, Crataegus* sp., *Discaria trinervis, Eleagnus angustifolia* and *Prosopidastrum globosum*) was recorded.

Figures 6 and 7 show the distribution of trees and saplings of 4 dominant species (*P. nigra*, *S. alba*, *S. humboldtiana* and *S. rubens*) which were associated with patches of different ages. The MFA analysis explained 71.26 % of the variation. The first latent variable (patch rockiness and age) explained 40.42 % of the variation. The second axis was linked to patch height and explained 30.84 % of the variation. *S. alba* and *S. humboldtiana* were the oldest plants, preferably growing in levees. *P. nigra* depends more height, colonizing plains and channel networks. The rest of the geomorphological units showed a variable gradient of rockiness. Saplings of *P. nigra* were associated

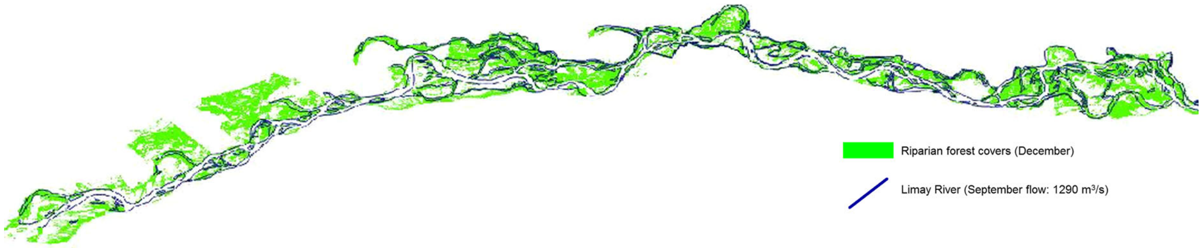

Fig. 4 Coverage of riparian forest in summer obtained by unsupervised classification with NDVI analysis on SPOT 5 image

Table 2 Riparian vegetation and structural complexity obtained with PCA compared to fields campaigns

Geomorphological unit detected in the field	Geomorphological and ecological unit to PCA
Crossbar and islands	Open forest on islands
Alternating bars and accretion	Bars
Plains	Open forest plains
Channel network	Channel network
Levees	Forests on levees
Secondary channels	Swamps

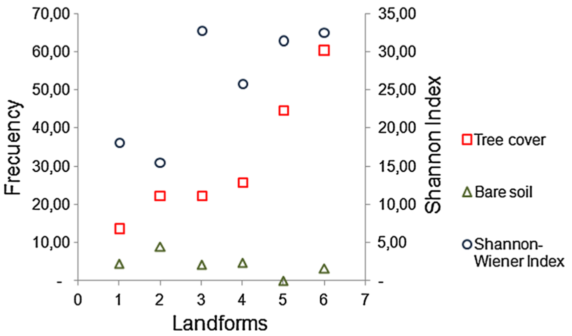

Fig. 5 Diversity, tree cover and bare soil in each geomorphological study unit (*1*: open forest plains; *2*: channel networks; *3*: bars; *4*: open forest on island; *5*: swamps; *6*: forest on levees)

with greater rockiness, next to *S. rubens* and *S. humboldtiana*. *S. alba* saplings were associated with swamps, on low lands.

As the analysis of the age of the trees downstream of the dam system showed that the vegetation, often exposed to high floods before the dams were built (El Chocón Dam 1971), was composed of the native willow (*S. humboldtiana*) and the exotic *S. alba*. As the river regime was attenuated and extraordinary floods disappeared with the operation of the dam Arroyito in 1980, the first patches of *P. nigra* spread. These patches increased from 1991, almost exponentially, after the start of operations of the other dams, such as Alicurá (1984), Piedra del Aguila (1991) and Pichi Picún Leufú (1995) (Fig. 8).

Discussion

Dispersion of willows and poplars in relation to hydrological dynamics

Plant diversity finded, showed that anthropogenic river regulation, altering macro environmental factors, changed the direction of the natural succession characterized by native shrubs and trees and favored the expansion of exotic Salicaceae. In the Limay floodplain, the natural and anthropogenic river regulation first caused stochastic events, and then more regular ones after 1980, with the main effects being on the successional process on the floodplain. Natural regulation occurred due to 16 glacial lakes and five reservoirs that absorbed the intensity of frequent floods. Later, dam operations imposed artificial regulation. Successful colonization of alien trees was also influenced by new ecological relationships in stable locations within the hydromorphic gradient, such as swamps and levees. In agreement with Tabacchi et al. (1996), who analyzed 14 rivers in arid and semiarid

Table 3 Characterization of the dominant woody species

Dominant species	Patches	Frequency (%)	Presence in patches
Salix alba	14	23.33	31
Populus nigra	12	20.00	42
Salix humboldtiana	4	6.67	16
Salix rubens	2	3.33	13
Populus deltoides	2	3.33	6
Salix alba x humboldtiana	One	1.67	2
Salix alba x matsudana	One	1.67	7
Without any trees	24	40.00	

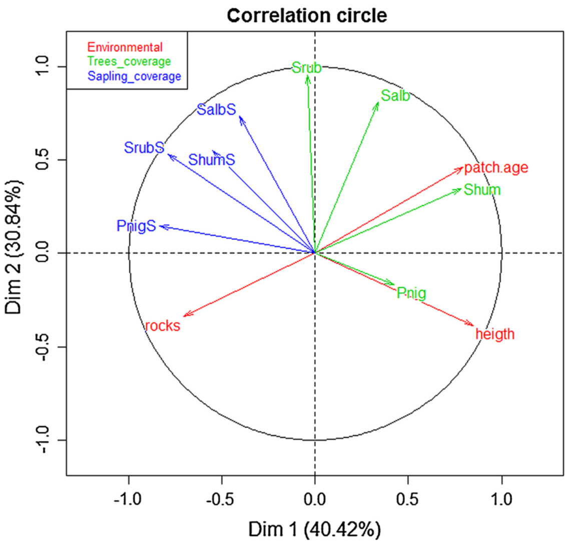

Fig. 6 Relations between dominant tree and sapling coverage and environmental predictors

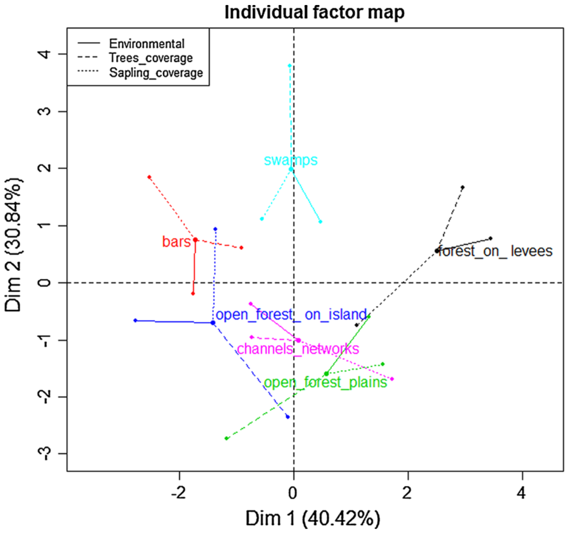

Fig. 7 Representation of an individual (landform) in a configuration with respect to the average behavior of that individual

regions of USA, France and Spain, in the Limay River, micro factors caused by tree growth, established new ecological relationships in the riparian forest, influencing the diversity and the structure of the riverine neoecosystem.

In our study, the floodplain diversity was also conditioned by the invasions of species from the Limay valley which had previously been introduced due to the diversification in rural activities in Patagonia. This situation explained the spread of exotic species like *S. rubens*, *S. alba* × *S. matsudana* and *P. nigra*. While the poplar invasion along the floodplain was synchronized with the flow regulation between the 1960 and 1980s, fruit production favored the introduction of diverse cultivars of exotic species of Salicaceae which were introduced as wind shelter belts. Irrigation channels, drainage and active river channels acted as biological corridors and favored spontaneous tree dispersal. By the early 1990s the right conditions existed for sexual and asexual dispersal of willows and poplars. As stated by many authors (Gurnell 2014; Hupp and Rinaldi 2007; Francis et al. 2009; Tockner et al. 2003) in unregulated European rivers natural stochastic changes and fluvial geomorphology create normal conditions for succession which was directed by different Salicaceae species. Mechanical adaptations allowed Salicaceae species to colonize relatively stable substrates quickly and to become established on alluvial bars along the riparian corridors (Gurnell 2014; Karrenberg et al. 2002, 2003). In the Limay River, as the regulation of hydrological regime did not cause any changes in the seasonal flood cycle, a similar willow and poplar succession process took place, as reported for unregulated European rivers, in contrast to the situation described by Greet et al. (2013) in the Murray River in Australia where regulation altered the hydrological cycle.

The low genetic variability and clonal capacity of the native *S. humboldtiana*, compared with Eurasian willows and poplars, made the species vulnerable to competitive exclusion (Thomas et al. 2012; Budde et al. 2010). In Hauman et al. (1947), reported the low presence of the native tree along the Patagonian riverbanks. The synchronized colonization of *P. nigra* and *S. rubens* after floods higher than 1290 m^3/s installed a new emerging interspecific competition with the native willow in the channels, strips and island plains. This unprecedented event affected the native *S. humboldtiana* populations in the last stages of the succession more than at the beginning, due to the massive invasion of *P. nigra* and hybrid willows, such as *S. rubens* (*S. alba* × *S. fragilis*) and *S. alba* × *S. humboldtiana* (Figs. 6, 7).

In Patagonia, plant succession was similar to that of Italian rivers (Hupp and Rinaldi 2007), but we found that *P. nigra* settled on more unstable fluvial landforms in the Limay River. While poplars have flexible stems during their early ontogeny years, the stems grow stiff

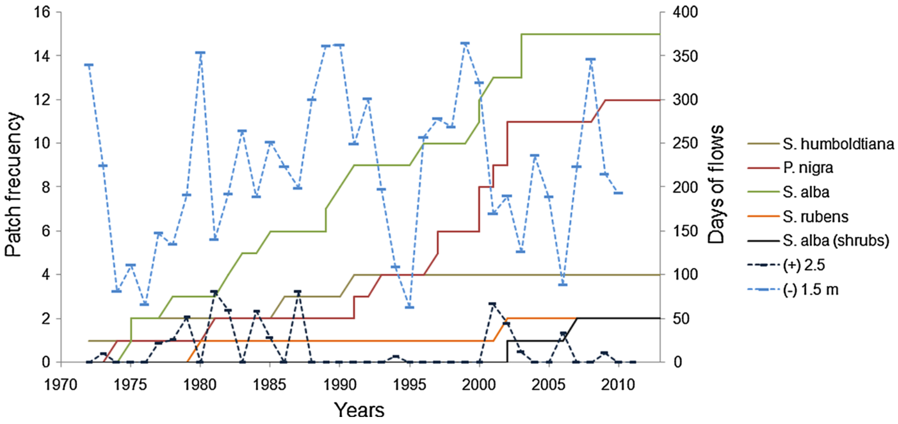

Fig. 8 Evolution of the patches dominated by different species of Salicaceae between 1972 and 2012 in relation to hydrological flood pulses

and erect in the mature phase. This latter condition makes poplar patches vulnerable to removal and falling over. In this case, asexual dispersion takes place and new areas are created in previously vegetation free areas. Moggridge and Gurnell (2009) stated that *P. nigra* in the Tagliamento River had less successful asexual reproduction than *Salix*. According to the same authors, asexual reproduction of willows facilitates sexual reproduction of other species and protects the establishment of new patches because willows performed very well as bioengineers in the geomorphological stabilization. Similarly, *Salix* sp. in regulated rivers in Southeastern Australia (Stockes and Cunningham 2006) showed alternation of sexual reproduction on stability zones and asexual dispersion in areas of disturbance. Willows, favored by these conditions, showed an initial colonization of *S. alba* in the 1970s, followed by *P. nigra* in the 1990s, as seen in the dendrochronological records of the Limay River (Fig. 5).

Hupp and Rinaldi (2007) described *P. nigra* as a pioneer species on terraces, bars and river banks in Italy. However in the Limay River in Argentina, *P. nigra* colonized the more unstable sites, such as the riverbed itself and active bars, in coincidence with Bendix and Hupp (2000). These areas were usually covered by herbs (*Rumex crispus, Polygonum* sp., *Xanthium* sp.) and some low bushes, as occurs in rivers of Northern Virginia, USA.

In the Limay river the construction of embankments and jetties produced more stable substrates suitable for colonization. As proposed by Tockner et al. (2000), Francis et al. (2009) and Little et al. (2013), hydrological cycle disturbances favor greater temporal and spatial heterogeneity and the establishment of an environmental gradient which allows connectivity between the components of the new system. Flood pulses exceeding 2.5 m in height affected most of the riparian vegetation of the Limay River. *Populus nigra* patches increased during a flood period of less than 1.5 m for more than 200 days free of floods exceeding 2.5 m between 1987–2000, which explains part of the change in the exotic forest (Fig. 5). At the same time a delayed development of new patches of *P. nigra* from 2002 and *S. alba* from 2004 was related to the colonization of other exotic species, such as *Fraxinus pennsylvanica* and *Acer negundo*. These species were associated with stable sites dominated by older patches of willows and poplars.

Endogenous processes in the neo riparian ecosystem

In theoretical terms, the succession processes that occurred in the Limay floodplain fit the island biogeography model of MacArthur and Wilson (1967). This predictive model basically states that the number of species on an island is a balance between immigrants and a natural rate of extinction. In our case islands are the vegetation patches. Increase the rate of immigrants, favored by asexual and sexual dispersion of Salicaceae and the number of species/abundance rises. Increase the rate of extinction, by stochastic events triggered by flood pulses and the number falls. As the results showed, the native willow *S. humboldtiana* was more vulnerable to extinction as it does not have so many adaptive advantages as the exotic willows and poplars. Two factors that affected the vegetation cover were: (1) the distance from other sources, like irrigation channels that promoted

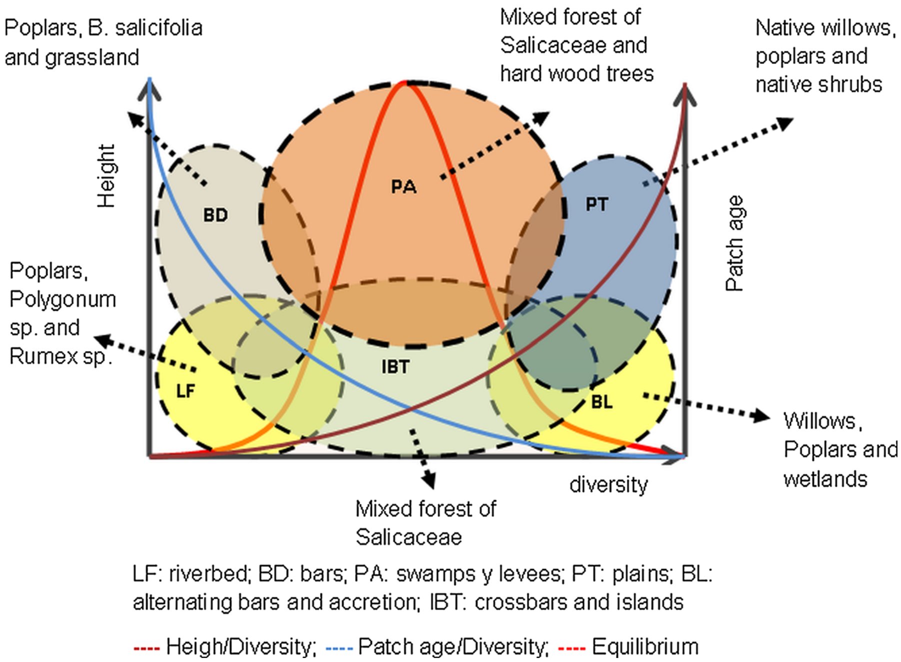

Fig. 9 Model of representation of variables that explain the distribution and species diversity in the riparian ecosystem

invaders (2) patch size and height: extinction rates were larger on small islands or at sites near to water and susceptible to erosion.

Patch height, age and diversity explained the changes that occurred in the system and the model summarizes how the system organizes itself (Fig. 9). The height at which the patches were located in relation to the most frequent water level, expressed the influence of the disturbance introduced by the hydrological regime and water availability conditions of plants. In this arid Patagonian environment the invasion of Eurasian willows and poplars was limited to the riverbed and areas below the 1.5 m flood level. Above these, a greater diversity of exotic and native species occurred. Beyond the flooding area there was a natural limit to the invasion of riparian species and an overall reduction of diversity. In terms of conservation, the invaded areas posed a threat for the conservation of *S. humboldtiana*, but offered an opportunity to study the species dynamics on areas under productive use.

Conclusions

The massive invasions of willows and poplars were triggered by the artificial regulation of the Limay River due to the construction of hydroelectric dams. *S. alba* initially colonized the more stable surfaces, such as levees, temporary channels and abandoned channels, primarily by asexual reproduction. This facilitated the subsequent installation of *P. nigra* in small mixed patches of willows and poplars. Finally, *P. nigra* advanced on relatively stable surfaces and emerging bars during periods of floods of low frequency and magnitude. The plant communities in the post-step regulation stage, far from representing a climax stage, are temporal intermediate succession stages growing on more stable substrates, as a result of the attenuation of the hydrological regime and the construction of infrastructure for the protection of the riverbanks and urban settlements.

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