

# Age structure, growth performance and composition of native and invasive Salicaceae in Patagonia

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**Abstract** In northern Patagonia, riparian ecosystems are highly modified due to alien plant invasions. The establishment of non-native willows and poplars has unknown effects for *Salix humboldtiana*, the only native floodplain tree species in this region. To clarify establishment processes and to assess whether inter-specific competition among the Salicaceae taxa may occur and therefore whether the native species can coexist in the long term, we analysed age structure and growth performances of the dominant four taxa within mixed adult forest stands along the Río Negro, Argentina. Low mean ages of <15 years for all four taxa within 20 stands could be detected and suggest frequent and severe disturbances resulting in the removal of existing vegetation and subsequent creation of sites for establishment. Trees of the same stand showed the same age structure indicating joint establishment events with all taxa involved. A significant better growth performance (basal area, crown diameter) could be proved for the invasive willows. Considering the upper and middle river separately in a total of 88 studied plots, *S.*

*humboldtiana* was more frequent at the middle river stretch, while invasive willows showed an opposing pattern suggesting a downstream directed invasion process. The results showed that competition pressure in mature mixed stands could affect *S. humboldtiana*. However, these stands are usually removed by river dynamics creating new sediment bars and islands. These processes enable *S. humboldtiana* seeds to germinate frequently which may compensate for its inferior growth performance and potential impacts by the invasive willows and poplars.

**Keywords** Floodplain forest · *Salix* spp. · *Populus* spp. · Riparian landscapes · DBH · Basal area

## Introduction

Riparian ecosystems are known to be vulnerable to invasion by alien plants mainly due to the hydrological connectivity of river corridors (Ward et al. 2002) and to the frequently occurring disturbances (Renöfält et al. 2005; Richardson et al. 2007; Stohlgren et al. 1999; Tabacchi et al. 2005). It has been predicted that species invasion along rivers will continue in the future (Tockner and Stanford 2002). Invasive plant species can have severe impacts on river systems. For instance, they can change the composition and structure of vegetation, ecosystem function (Richardson et al. 2007) and ecohydrologic processes (Hultine and Bush 2011).

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**Fig. 1** Aerial view of a representative section of the upper Río Negro with vegetated islands and sand bars. The Salicaceae forests on the picture are dominated by invasive willows and poplars. In the middle of the picture, one of the studied islands is seen with adult stands where all of the four target taxa are present

Among riparian invaders, species of Salicaceae introduced for ornamental and functional landscaping play an important role. The Asian weeping willow (*Salix babylonica* L.) and the European Lombardy poplar (*Populus nigra* L. var. *italica*) are de facto the most widely planted ornamental trees worldwide (Li 1996). Eurasian willows have naturalized widely, for example in Australia (Cremer 2003), New Zealand (Glova and Sagar 1994), South Africa (Henderson 1991) and the USA (Shafroth et al. 1994). Species of Salicaceae are known to be invasive alien species around the world. In a global review of invasive trees and shrubs (Rejmánek and Richardson 2013), 14 species of *Salix* and 5 species of *Populus* are listed, including *S. alba* L., *S. babylonica* L., *S. fragilis* L., *S. × rubens* Schrank, *P. deltoides* Bartram ex Marsh, *P. nigra* L. and *P. × canadensis* Moench. In Patagonia, riparian landscapes are dominated by planted and naturalized poplar and willow trees (Naumann 1996). In the past, *Salix humboldtiana* Willd., the only native riparian tree species in the region, was very frequent forming floodplain forests at the river banks of the rivers Negro and Limay (Hauman et al. 1947). These gallery forests have vanished and have been displaced by mixed forests (Fig. 1) in which invasive Salicaceae play an important role (Correa 1984; Zalba and Villamil 2002). In the recent two decades, especially floodplain forests structured by invasive willows and poplars have occupied large areas, for example in the Río Negro region of northern Patagonia. They were introduced to Patagonia by

European settlers as windbreaks and wood source in the late nineteenth or early twentieth century (Naumann 1996; Peri and Bloomberg 2002). The increase of forests dominated by invasive Salicaceae may have altered the riparian ecosystem of the Río Negro profoundly as it could be shown in other invaded riparian landscapes (e.g. Cremer 2003; Lester et al. 1994; Holland-Clift et al. 2011). The main question in this context is whether the native *S. humboldtiana* can persist in the future despite the occupation of large areas by these introduced Salicaceae.

In order to answer this question, a promising approach is to clarify establishment processes by analysing the age structure of the native and invasive Salicaceae involved in the frequently occurring mixed forests: Is *S. humboldtiana* capable of establishing when invasive forests are already developed or was the native species already present when the invasive ones spread out? Or are the stands even the result of joint establishment events?

Moreover, it is not clear whether invasive Salicaceae have the potential to affect *S. humboldtiana*, for example through heavy shading and other competition processes. A first investigation revealed a better vegetative reproduction capacity of invasive willow hybrids in comparison with *S. humboldtiana* (Thomas et al. 2012). Measurements of growth performance in relation to the age of the trees in mixed forest stands help to assess whether interspecific competition may occur in older life stages in Salicaceae forests and therefore whether the native species can coexist in the long term.

Therefore, the following questions were addressed in this study:

- (1) What is the age structure of adult mixed Salicaceae forests in the active zone of the Río Negro?
- (2) Do native and invasive taxa possess different growth performances indicating potential disadvantages for *S. humboldtiana* in the adult life stage?

The Negro River in Patagonia with its dense forests consisting of native and invasive Salicaceae is well suited as a model area for analysing such questions. Moreover, the land-use intensity and invasion history is rather heterogeneous along the course of the river. This aspect is associated with the following question:

- (3) Do tree composition and performances of native and invasive Salicaceae change in the course of the river?

## Methods

### Study area

The research was conducted at the Río Negro in northern Patagonia, Argentina (Fig. 2). The Río Negro drains a catchment area of 65,000 km<sup>2</sup> (Cushing et al. 2006), and the valley is surrounded by the dry shrubby Patagonian steppe. The mean annual precipitation is less than 250 mm, and the mean annual temperature is 14–20 °C (Gut 2008). The two tributaries, the Río Limay and the Río Neuquén, which rise in the Andean Mountains, join at 225 m a.s.l. to form the Río Negro near the city of Neuquén. From there, it flows approximately 630 km to the Atlantic Ocean crossing the Patagonian high plateau (Cushing et al. 2006). The river has a mean annual discharge of 900 m<sup>3</sup> s<sup>-1</sup> with pronounced water level fluctuations (DPA, Departamento Provincial de Aguas Río Negro). The natural flow regime is governed by snowmelt in the Mountains, but since the onset of dams at the Rivers Limay and Neuquén during the 70 s of the last century, flood disturbances are irregular and depend on energy requirements. The Negro River itself is not regulated by dams, but water is withdrawn for intensive agriculture. Human impact along the river is characterized by land use, especially fruticulture and grazing. The river still shows natural dynamics and flows in its natural shape slightly meandering and forming exposed vegetated islands (Fig. 1). The Río Negro is subdivided in the upper (Alto Valle), middle (Valle Medio) and lower stretch (Valle Inferior). The upper river valley is the principle region of Argentina for apple and pear production. Hence, the valley is characterized by large fruit plantations, mostly at the northern side of the river, which stretch to the river shores. Plantations are usually enclosed by planted alien poplar and willow rows. Downstream in the middle river valley, large plantations are fewer with farming and cattle breeding being more important. The original vegetation along the river is composed of *S. humboldtiana* as the only native tree species and the natural shrubby steppe vegetation (e.g. *Larrea spp.*, *Prosopis spp.*, *Baccharis spp.*) (Gut 2008).

### Survey method

For all analyses, the most dominant and forest-building taxa were chosen: (a) *S. humboldtiana*, (b) willows of

the *S. alba*–*S. fragilis* complex including the hybrid *S. × rubens* (hence called *S. × rubens*), (c) a hybrid of this complex and *S. babylonica* (hence called *S. babylonica* hybrid), as well as d) *Populus* spp. (*P. nigra*, *P. deltoides* and their hybrid *P. × canadensis*).

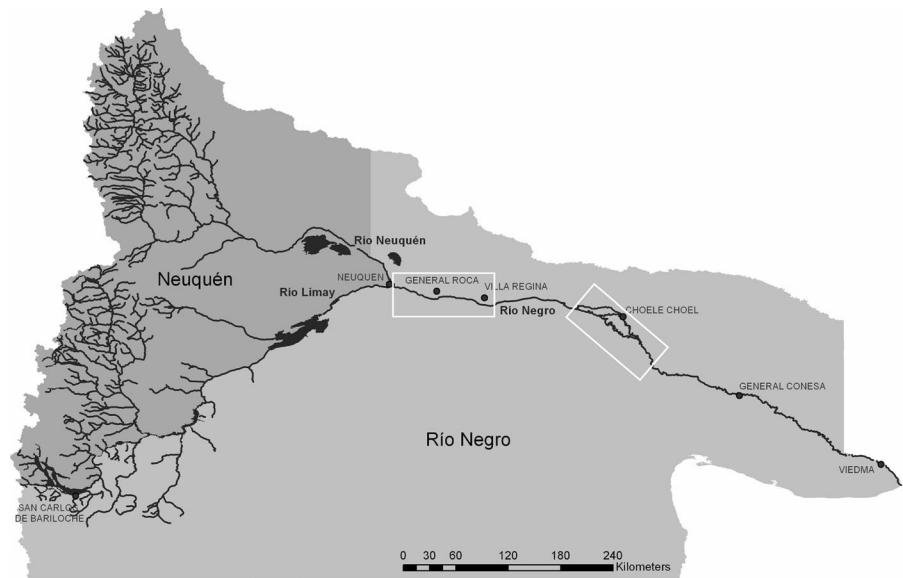
### Age structure and age–DBH relationship

Wood core samples of trees were taken on a total of 20 islands within the active zone of the Río Negro, northern Patagonia (Fig. 2). Thereof, 10 islands were located at the upper and 10 at the middle river stretch. Islands were selected since they are the sites with the least human influence across the whole floodplain. All the islands studied were characterized by the occurrence of mixed adult forest stands where all of the four target taxa were present (Fig. 1). In each stand, samples from three individuals per taxon were taken to determine the age of the stands summarizing a total of 60 randomly chosen trees per taxon. Wood cores were taken at breast height (1.3 m) with an increment borer for growth analysis (Suunto, 300 mm). For the exact age determination, a microscope was used for counting the annual rings. Relations between diameter at breast height (DBH) and age from analysed core samples were explored for each taxon by regression analysis with linear and asymptotic models. These models were compared and tested for their suitability using ANOVA. For this purpose, even from the multi-stemmed *S. × rubens* only one trunk was measured per individual. Differences in age among the taxa were analysed using one-factorial ANOVA followed by Tukey's method of honestly significant differences. Additionally, age was related to taxon and river stretch using two-factorial ANOVA followed by Tukey's method of honestly significant differences.

### Growth performance

Measurements of growth performance were taken in each of fifteen individuals per taxon in five adult mixed forest stands on five islands along the river. Age was determined using wood cores as described above. Tree height, DBH (of all trunks when several existed of one individual), mean crown diameter (average north–south and east–west expansion) and crown base height (the height where the crown of a tree begins) were measured in the field. Basal area of each individual was determined using the DBH and

**Fig. 2** The Río Negro in northern Patagonia, Argentina. All samples were taken in the marked sections in the upper and the middle river stretch



including multiple trunks when present. Differences among the taxa were analysed using ANOVAs followed by Tukey's method of honestly significant differences. Additionally, basal area was related to age and taxon using ANCOVA.

#### *Composition, age and performance along the river*

Additionally, 88 randomly distributed plots (10 m<sup>2</sup>) were established on 12 islands along the river. To get an idea of the natural age structure, Salicaceae taxa composition and frequency along the river, these plots were not only located in mature mixed forest stands, but reflected a wide range of habitats where minimum one stem >5 cm DBH occurs. The plots represent different vegetation structures, ranging from almost vegetation-free to dense forests. Fifty-four plots were located at the upper river stretch and 34 plots at the middle stretch (Fig. 2). Within these plots, all stems with DBH > 5 cm were measured. In total, 442 trees of *S. humboldtiana*, 430 *Populus* spp., 284 *S. babylonica* hybrids and 177 *S. × rubens* were identified. Age was derived from DBH using the linear model of the regression analyses described above. For all four target taxa, the basal area, that is the area covered by stems, within each plot was determined. Furthermore, the following variables were determined for all taxa: mean and maximum age of trees over all individuals,

mean number of individuals per plot (only plots counted where the respective taxon was present) and frequency of occurrence in the plots. Age, DBH, basal area and number of individuals were related to taxon and river stretch as explanatory variables using two-factorial ANOVAs followed by Tukey's method of honestly significant differences. All analyses were made with the software package R (version 2.12.2, R Development Core Team 2011). Constancy of variance and normality of errors were checked using diagnostic plots (Crawley 2007).

## Results

### Age structure and age–DBH relationship

Age–DBH relationship is best explained by linear models. Regression analyses revealed significant linear relationships of age and DBH for each taxon (Table 1). Two-factorial ANOVA results with taxon and river stretch as explanatory variables and age as response variable only revealed significant differences between the taxa, but not between the upper and middle river stretch. Furthermore, no interactions between the explanatory variables could be detected. Thus, only the results of the one-factorial ANOVA with age and taxon as variables were considered ( $F_{3,235} = 5.304$ ,  $p = 0.0014$ ). For all four taxa, the

**Table 1** Regression analysis of DBH and age for each taxon ( $n = 60$  individuals per taxon)

species	Parameter		df	F-statistic	p value
	a	b			
<i>Salix humboldtiana</i>	0.692	1.121	1,58	89.9	2.148e–13***
<i>Populus</i> spp.	–0.002	1.72	1,58	26.84	3.121e–06***
<i>Salix babylonica</i> hybrid	–6.934	2.698	1,58	72.12	9.205e–12***
<i>Salix</i> × <i>rubens</i>	–5.711	1.679	1,58	43.98	1.135e–08***

Levels of significance ( $p$ ) are denoted with \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$

studied individuals on the 20 densely forested islands exhibited a mean age of <15 years. *S. humboldtiana* ( $12.8 \pm 3.5$  years, mean  $\pm$  SE), *Populus* spp. ( $13.1 \pm 2.4$  years) and *S. × rubens* ( $13.7 \pm 3$  years) did not differ significantly in age. The *S. babylonica* hybrid showed a slightly higher mean age ( $14.8 \pm 2.9$  years), significantly different from *S. humboldtiana* and *Populus* spp. The oldest *S. humboldtiana* was 29 years old, *Populus* spp. 19 years old, while the oldest *S. babylonica* hybrid and *S. × rubens* were 23 years old.

#### Growth performance

Regarding the individuals used for growth performance measurements, the age did not differ significantly between taxa ( $F_{3,56} = 0.600$ ,  $p = 0.6185$ ) with means of 14.4–15.9 years. However, great differences could be observed concerning basal area ( $F_{3,56} = 4.461$ ,  $p = 3.979e-05$ ) and crown diameter ( $F_{3,56} = 22.055$ ,  $p = 1.478e-09$ ) (Fig. 3a, b). The *S. babylonica* hybrid achieved the highest means concerning basal area and crown diameter followed by *S. × rubens*, which could reach high basal areas due to multiple stems. Their performances differed significantly from *Populus* spp. and *S. humboldtiana*. Likewise, for tree height ( $F_{3,56} = 5.937$ ,  $p = 0.00137$ ) and crown base height ( $F_{3,56} = 3.289$ ,  $p = 0.02714$ ), significant differences could be observed (Fig. 3c, d). *S. humboldtiana* reached a significantly lower tree height than *Populus* spp. and the *S. babylonica* hybrid, which was not different from *S. × rubens*. However, *S. × rubens* had a significantly lower crown base height than *S. humboldtiana*. ANCOVA results of basal area in relation to taxon and age revealed significant differences between both explanatory factors and significant interactions between them (Table 2). Considering the increase of basal area along the age gradient, *S. humboldtiana* and *Populus*

spp. performed significantly worse in comparison with the two invasive willow hybrids (Fig. 4).

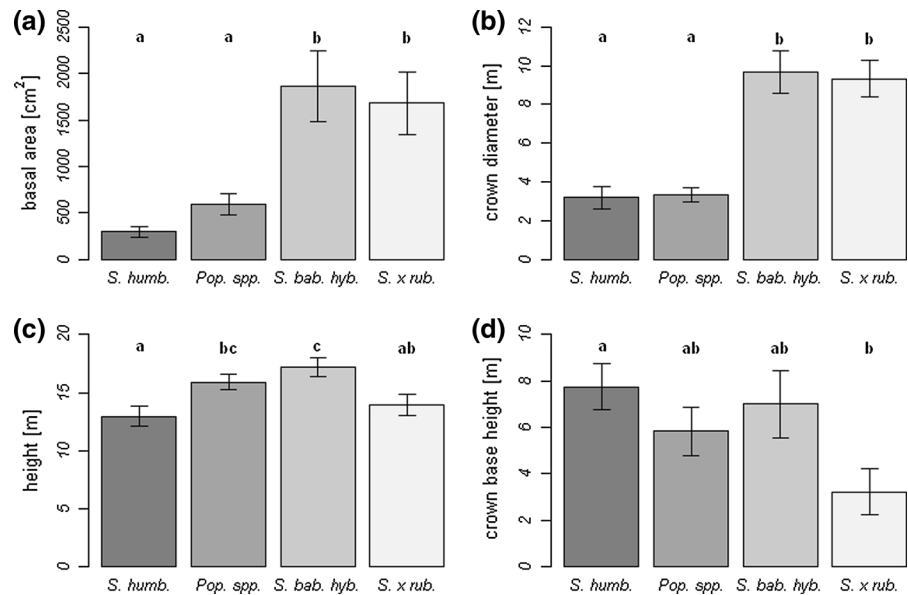
#### Composition, age and performance along the river

ANOVA results revealed significant differences for the response variables age, DBH and basal area among taxa in the randomly distributed plots along the river (Tables 3, 4).

Low mean ages could be observed on the 88 plots for all taxa (Table 4). The river stretch influences the age of the taxa significantly (Table 3). For all taxa, the mean age was higher in the middle river stretch with significant results for *S. humboldtiana* and *Populus* spp. (after post hoc comparisons using the Tukey HSD test). Concerning the DBH of all individuals, significant differences between the taxa and river stretch could be proved (Table 3). *S. humboldtiana* and *S. × rubens* reached significantly lower diameters than the *S. babylonica* hybrid and *Populus* spp. The mean DBH of the *S. babylonica* hybrid and *Populus* spp. was significantly higher at the middle river stretch.

Regarding mean basal area per plot, where the respective taxon was present, only *Populus* spp. and *S. × rubens* showed significant differences, with *Populus* reaching higher mean values. Although all taxa reached higher mean basal areas in the middle than in the upper valley, the results were not significant. The mean number per plot did not differ significantly between the taxa and between in the upper and middle river stretch. In contrast, differences could be observed in terms of frequency. *S. humboldtiana* was much more frequent in the middle than in the upper stretch. Also *Populus* spp. was slightly more frequent at the middle valley, while the *S. babylonica* hybrid and *S. × rubens* showed converse results (Table 4).

**Fig. 3 a–d** Growth performance of different taxa in mixed forest stands (mean  $\pm$  SE). Different letters indicate significant differences ( $p < 0.05$ ) among taxa according to Tukey's method of honestly significant differences



**Table 2** ANCOVA results of basal area in relation to taxon and age

	<i>df</i>	<i>SS</i> <sup>a</sup>	<i>MS</i> <sup>b</sup>	<i>F</i> -statistic	<i>p</i> value
Taxon	3	27,287,202	9,095,734	12.1555	3.842e−06***
Age	1	7,548,012	7,548,012	10.0871	0.002511**
Taxon: age	3	7,739,224	2,579,741	3.4476	0.023103*
Residuals	52	38,910,653	748,282		

Levels of significance (*p*) are denoted with \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$

<sup>a</sup> *SS* sum of squares

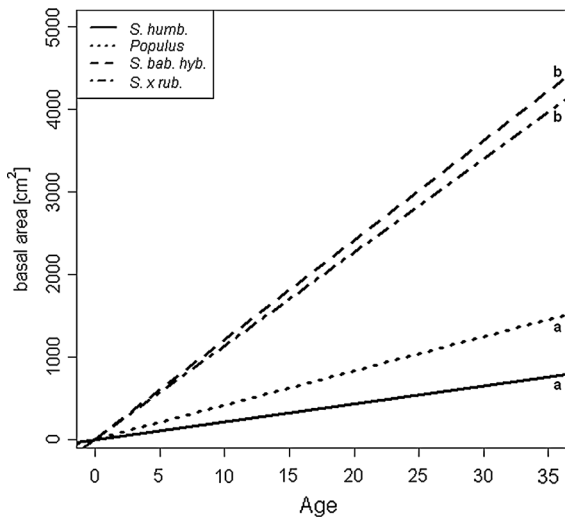
<sup>b</sup> *MS* mean sum of squares

## Discussion

Trees of the same stand showed the same age structure indicating one single or very few establishment events with native and invasive Salicaceae involved. Small variations in age could be explained by different reproduction strategies with the invasive willows depending more on vegetative propagation (Budde et al. 2011; Thomas et al. 2012) which occurs throughout the year. In contrast, sexual reproduction is restricted due to a short period of seed release and seed viability. The detected low age of adult mixed stands suggests frequent and severe disturbances within the active zone of the Río Negro. Major floods may allow for the establishment of stands by removing existing vegetation or by creating new islands when sediments are deposited (Bendix and Hupp 2000). Indeed, all states of island development could easily

be detected in current aerial views of the Río Negro with small shallow islands with no or almost no vegetation establishment to large islands of higher elevations covered by dense Salicaceae forests (Fig. 1). Also land loss by erosion leading to the disappearance of adult forests can be observed on islands. The low mean age of the floodplain forest stands coincides with the results of, for example Karrenberg et al. (2003) who found a mean age of <10 years of willow stands within the active zone of the near-natural Tagliamento in Italy.

*S. humboldtiana* is known to be the first colonizing pioneer tree of newly formed sediment banks along river margins. In the Paraná delta, Argentina, for example, *S. humboldtiana* forests generally represent the first successional stage and are replaced by *Tessaria integrifolia* (South American alder) stands after less than 20 years (Caso et al. 2010). Likewise,



**Fig. 4** Basal area related to age of different taxa in mixed forest stands explained by linear function. Different letters indicate significant differences ( $p < 0.05$ ) among taxa according to Tukey’s method of honestly significant differences

*S. humboldtiana* forms monospecific stands in the Amazonian floodplain followed by *Cecropia latiloba* after 10–20 years (Parolin et al. 2002). In Patagonia, in contrast, there is no successive tree species that displaces *S. humboldtiana* while invasive Salicaceae co-occur as first colonizers. Despite the absence of successional followers, it seems that this particular Salicaceae composition is not forming older stands due to strong natural disturbance events. Beyond the active floodplain zone, in the absence of disturbances by floods, solitary trees of all the four studied taxa that grow on pastures can reach higher ages (>40 years according to ring core analyses, data not shown).

Changes in light quality due to heavy shading by invasive species turned out to be an important factor in the suppression of native vegetation (Reinhart et al. 2006). In the study, both the introduced willow hybrids form crowns about three times larger than *S. humboldtiana*. Additionally, the native willow has

**Table 3** ANOVA results of age, DBH, basal area and number of individuals in relation to taxon and river stretch along the Río Negro

	<i>df</i>	<i>SS</i> <sup>a</sup>	<i>MS</i> <sup>b</sup>	<i>F</i> -statistic	<i>p</i> value
<b>Age</b>					
Taxon	3	147.4	49.12	3.0388	0.028135*
River stretch	1	1,286.8	1,286.75	79.5985	<2.2e–16***
Taxon: river stretch	3	220.8	73.61	4.5535	0.003511**
Residuals	1,325	21,419.4	16.17		
<b>DBH</b>					
Taxon	3	7,497	2,498.9	49.8854	<2.2e–16***
River stretch	1	3,500	3,500.5	69.8806	<2.2e–16***
Taxon: river stretch	3	991	330.4	6.5965	0.0002005***
Residuals	1,325	66,373	50.1		
<b>Basal area</b>					
Taxon	3	32,610,169	10,870,056	3.2064	0.02479*
River stretch	1	8,913,779	8,913,779	2.6293	0.10690
Taxon: river stretch	3	1,658,992	552,997	0.1631	0.92105
Residuals	158	535,639,020	3,390,120		
<b>Number</b>					
Taxon	3	550.8	183.599	2.5706	0.05621
River stretch	1	16.1	16.052	0.2247	0.63611
Taxon: river stretch	3	299.9	99.966	1.3996	0.24499
Residuals	158	11,284.9	71.423		

Age and DBH refer to all measured individuals, basal area and number are means measured per plots

Levels of significance (*p*) are denoted with \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$

<sup>a</sup> *SS* sum of squares

<sup>b</sup> *MS* mean sum of squares

**Table 4** Age, DBH, basal area, number and frequency of the four target taxa on 88 plots along the Río Negro (54 plots in the upper valley, 34 in the middle valley)

Taxon	Mean age $\pm$ SE of individuals	Max age of individuals	Mean DBH (cm) $\pm$ SE of individual	Mean basal area (cm <sup>2</sup> ) per plot	Mean number of individuals per plot	Frequency in plots (%)
Upper valley						
<i>Salix humboldtiana</i>	7.4 $\pm$ 2.7	18.6	8.97 $\pm$ 3.00	639.03	9.11	35
<i>Populus</i> spp.	7.3 $\pm$ 4.5	34.4	12.55 $\pm$ 7.76	1,553.99	9.09	60
<i>Salix babylonica</i> hybrid	8.0 $\pm$ 3.2	17.5	14.56 $\pm$ 8.68	1,552.59	6.89	67
<i>Salix</i> $\times$ <i>rubens</i>	9.0 $\pm$ 2.1	16.2	9.56 $\pm$ 3.53	558.55	6.85	37
Middle valley						
<i>Salix humboldtiana</i>	8.9 $\pm$ 4.3	39.5	10.68 $\pm$ 4.85	1,383.62	12.95	65
<i>Populus</i> spp.	10.7 $\pm$ 6.1	50.2	18.45 $\pm$ 7.96	2,134.22	6.00	65
<i>Salix babylonica</i> hybrid	9.8 $\pm$ 4.2	20.2	19.48 $\pm$ 11.39	1,787.42	4.63	24
<i>Salix</i> $\times$ <i>rubens</i>	10.3 $\pm$ 3.1	16.5	11.74 $\pm$ 5.33	742.96	5.71	21

Mean age, maximum age and DBH refer to all measured individuals, basal area and number of individuals are means measured per plot

sparser crowns due to the slim, gracile leaves in contrast to the invasive hybrids and their broader leaves. This may have a severe effect not only on *S. humboldtiana*, which is highly intolerant to shade (Parolin et al. 2002), but also on native shrubs and herbaceous vegetation. It is known that the biomass productivity can increase in ecosystems due to the invasion by highly productive species (Vilà et al. 2011). Although no data for biomass production are available, it is obvious that the superior performance of the invasive willow trees and the increase of Salicaceae forests, dominated by invasive taxa, result in higher biomass production. For example, the *S. babylonica* hybrid achieved a basal area that was six times higher than that of *S. humboldtiana*.

Thicker and older trees could be observed for all taxa in the plots at the middle river stretch. This fact may be explained by lower and less frequent disturbances by flood events due to increased meandering and branching of the river. *S. humboldtiana* exhibited a higher abundance and frequency in the middle valley, whereas it was vice versa in the case of the invasive willow hybrids. This could reflect invasion history suggesting an early invasion in the upper river stretch since agriculture, that is fruit plantations, is more intensive in the upper valley with, consequently, more Salicaceae planted next to the river shores. A later downstream colonization due to the spread of downstream floating twigs can be assumed.

High floods that remove vegetation create new space for establishment of alien species (Richardson et al. 2007), but in our case also for indigenous *S. humboldtiana* seedlings. *S. humboldtiana* as well as the *Populus* taxa which produce a large amount of viable seeds rely more on sexual reproduction than the invasive willows. The latter generate no or only few seeds in capsules and only few male individuals of the *S. alba-fragilis* complex and *S. babylonica* hybrids could be observed along the Río Negro (personal observation). The spread of vegetative dispersal units is supposed to play a key role in the rapid distribution of invasive willows (Budde et al. 2011, Shafroth et al. 1994, Thomas et al. 2012). While sexual reproduction requires bare-ground sites and sufficient humidity without intensive inundations for establishment, vegetative recruits are less dependent on environmental conditions and have higher survival rates (Moggridge and Gurnell 2009).

However, strong disturbances with the creation of new sediment bars and islands enable *S. humboldtiana* seeds to germinate frequently. Stands of older life stages, where competition due to the great growth performance of the invasive willow hybrids would probably affect *S. humboldtiana*, are removed by river dynamics. These considerations let us assume that, despite its inferior growth performance and potential impacts by the invasive Salicaceae, *S. humboldtiana* will not become an endangered species at the Río Negro



in the nearby future if water levels and flow conditions allow for natural disturbance processes and therefore seedling establishment. However, these natural and necessary processes are susceptible to river regulations preventing the creation of bare-ground habitats and the removal of mature vegetation (Catford et al. 2011).

For a long-term prediction of coexistence, other properties have to be taken into account such as the question as to what extent *S. humboldtiana* is threatened via hybridization processes with invasive willows. Willows are known to frequently hybridize (e.g. Adair et al. 2006, Argus 1974, Thiebault 1998). The flowering periods of the different willow taxa along the Río Negro overlap (in September and October, pers. observation). Hybridizations between *S. humboldtiana* and *S. babylonica* as well as willows of the *S. alba-fragilis* complex are possible (Borodowski and Suárez 2004; Hunziker 1992). Thus, natural hybridizations could be possible in the study area with the consequence that the willow hybrids could expand their range by introgression. Moreover, new species such as *S. matsudana* could be observed at the margins of the River Negro and could affect the floodplain system in the future.

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