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FUNCTIONAL ASSESSMENT OF INVASIVE *SALIX FRAGILIS* L. IN NORTH-WESTERN PATAGONIAN FLOOD PLAINS: A COMPARATIVE APPROACH

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Abstract

European willows (*Salicaceae*) are pioneer species in temperate zone floodplains. The species are considered invasive and introduction can lead to substantial alteration of floodplain vegetation communities and ecosystem functioning. Invasive spread of different *Salicaceae* have been attributed to differences in flood tolerance, growth and dispersal between it and co-occurring native species, suggesting a comparative approach examining key traits to be a profitable strategy in elucidating and predicting patterns of *Salicaceae* invasion. Here we study incipient *Salix fragilis* invasions in Chilean Patagonia on the western slopes of the Andes. Our approach combines vegetation transect data with dendroecological analysis to compare patterns of niche position along the hydrogeomorphic gradient, niche breadth, and growth rate among *S. fragilis* and co-occurring species. We evaluated these traits because they are thought to be key to species' capacity to colonize, survive, grow and reproduce in dynamic floodplain habitats. Transect data showed that relative to the most common native trees and shrubs, *S. fragilis* has the broadest environmental tolerance along the hydrogeomorphic gradient and has a mean niche position closest to severely disturbed and highly flooded channel margins. Moreover, growth models showed that *S. fragilis* grows faster relative to native species, especially at juvenile stages. Our data suggest that a unique set of trait values allows *S. fragilis* to occupy a previously under-occupied and abundantly distributed niche, and will continue to colonize, survive, grow and reproduce in morphodynamically disturbed river margins. This is the first report of invasive *S. fragilis* in Chile, and we comment on potential impacts to native vegetation communities, soil development and ecosystem function.

Keywords

Nothofagus antarctica, *Salix fragilis*, *Salix eucina*, Patagonian rivers; Floodplain vegetation; Vacant niche.

1 Introduction

Riparian zones are widely recognized as amongst the most vulnerable habitats to invasive plant populations (Mack et al., 2000; Tockner and Stanford, 2002). This high propensity to invasion is generally attributed to the habitat's dynamic, frequently disturbed surfaces that are continuously reworked by fluvial action and provide a large supply of bare substrate for colonizing plant propagules, as well as high hydrological connectivity that efficiently disperses them (Catford and Jansson, 2014; Pyšek and Prach, 1993; Renöfält et al., 2005). Of significant concern in riparian environments is substantial alterations to underlying fluvial processes and ecosystem functioning that invasive plant populations can cause (Chapin III et al., 1997). For example, invasive plant colonisations have been documented to alter water table depths and transform channel morphology (Caruso et al., 2013; Meier et al., 2013; Sala et al., 1996). Hydrology, geomorphology, and riparian biogeochemical cycles can all be modified as a result of plant invasion, and these modifications can trickle down to affect biological communities, often with negative consequences for native fauna and flora (Fei et al., 2014; Gerber et al., 2008; Huddle et al., 2011; Le Maitre et al., 2015; Mineau et al., 2012). *Salicaceae* build a diverse group of floodplain specialist trees and shrubs and are one of the most invasive plant genera worldwide, particularly in riparian zones of the southern hemisphere (Adair et al., 2006; Arbuckle et al., 1999; Budde et al., 2011; Caruso et al., 2013; Datri et al., 2017; Doody et al., 2014). In Patagonia, two *Salix* species are currently known to exist: native *Salix humboldtiana*, and invasive *Salix fragilis* - *Salix alba* – complex (taxonomic development to *Salix euxina* – *S. alba* – complex according to Belyaeva (2009)). Native *S. humboldtiana* reaches its southernmost extent in Chile at 38° S (Hauenstein et al., 2005), while in Argentina *S. humboldtiana* ranges further south to Santa Cruz Province. Invasive *Salix* spp. were introduced to Patagonia in the 19th century and populations currently span hundreds of kilometres in the Negro River catchment (Budde et al., 2011; Datri et al., 2017; Thomas et al., 2012, 2015; Thomas and Leyer, 2014), the Chubut River system and the Futaleufú River (Miserendino et al., 2011). In Chilean Patagonia, non-native *Salix* spp. are rarely mentioned in the peer reviewed or grey literature. As far as we can see, no vascular aquatic plants are listed as potential invaders, including *S. fragilis*.

Much of the literature regarding *Salix* spp. invasion focuses primarily on mapping its geographic spread and monitoring demographic factors. For example, the *S. fragilis* populations documented are a recent geographic and bioclimatic extension of the species South American range. However, it is increasingly understood that in new regions, the wider biotic community, its functional composition and its interactions with the abiotic environment all help to determine the demographic outcomes of potentially invasive species (Catford and Daehler, 2012; Catford and Jansson, 2014; Renöfält et al., 2005). For example, regions lacking species that are functionally analogous to *Salix* spp. in riparian environments are thought to be at higher risk for invasion (Rejmánek, 2013). This suggests that a comparative approach examining the distribution of key trait values in the riparian plant community might provide novel insight into *Salix* spp. invasion and its magnitude (Arroyo et al., 2000; Pauchard et al., 2013; Rejmánek, 2013; Tickner et al., 2001).

In this paper, we take a comparative approach to better understand incipient *Salix fragilis* invasions in Chilean Patagonia on the western slopes of the Andes. Specifically, we combine quantitative vegetation transect data with dendroecological analysis to compare patterns of niche position along the hydrogeomorphic gradient, niche breadth, and growth rate among invasive *Salix fragilis* and co-occurring native species. These traits are thought to be important for colonization, growth and reproduction in floodplain habitat (Karrenberg et al., 2002; Lytle and Poff, 2004; Merritt et al., 2010), and relative differences among species may help elucidate ongoing *Salix* spp. invasion and future risk. We hypothesize that relative to co-occurring native species, invasive *Salix* spp. grow faster and occur more abundantly in more heavily disturbed riparian sites, key differences that, we argue, drive the spread of invasive populations in Patagonian riparian zones.

2 Materials and methods

2.1 Study sites

The study was conducted at three sites located in southern Chilean rivers in the administrative region “Región de Aysén del General Carlos Ibañez del Campo”, at the Paloma, Murta, and De los Ñadis rivers (**Figure 1**). The three rivers were selected considering their similar size, high ecological value and minimal hydrological or morphological alteration resulting from human management (Rivera Izam et al., 2009). All three rivers are free-flowing with braided channel patterns and flow regimes that are driven by snowmelt and rainfall, with peak discharge typically in late spring (Dussailant et al., 2012; Meier et al., 2013). Our specific sites were located on 4th or 5th order reaches with mean annual discharge ranging from 35 to 50 m³ s⁻¹, according to our on-site estimates and MOP (2016).

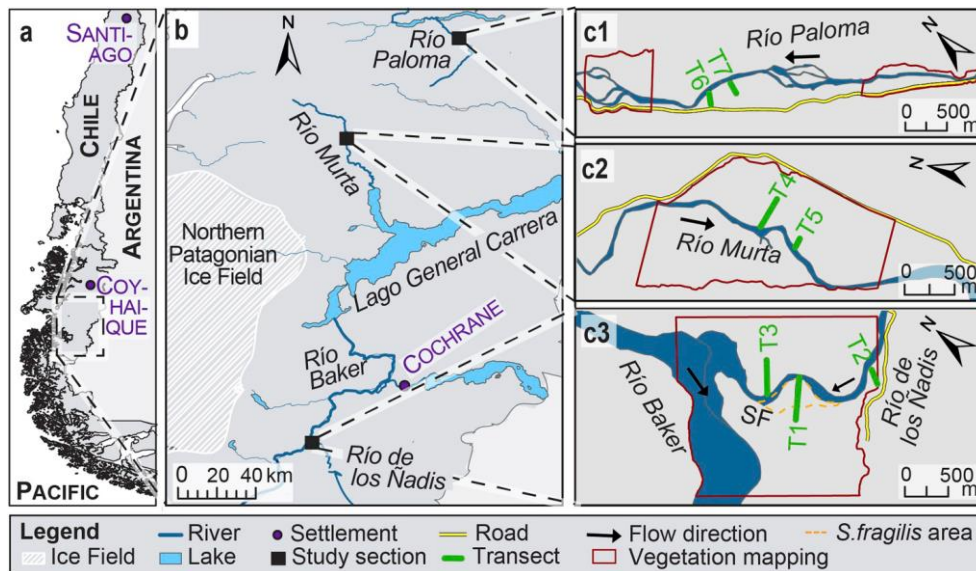


Figure 1. (a) Map of southern Chile with marking of the southern part of the Aysén region, south of its administrative capital Coyhaique; (b) Section of the administrative Aysén region showing the position of the studied river sections in the Aysén and Baker catchments; (c) Studied river reaches at Paloma River (c1), Murta River (c2) and De los Ñadis River (c3) where vegetation mapping was performed (see **Figure 2**), with the positions of the transects (T1-T7) and the area of the *Salix fragilis* inventory (SF, dashed line in c3).

Regional geology is dominated by the north-to-south aligned Andes, Jurassic volcanic sequences (basalts, rhyolite) and Miocene metamorphic complexes (Sernageomin, 2003). The geomorphology of the area is shaped by Pleistocene glacial dynamics, quaternary and recent fluvial dynamics, volcanic activity, tephra deposition and abundant landslides (Lara et al., 2015). More recent changes result from deglaciating Patagonian Ice Fields (Glasser et al., 2011; Iribarren Anaconda et al., 2015). Strong orographic effects and elevational change drive strong regional variation in climate, ranging from moderately seasonal hyper-humid oceanic regime to desert steppe (Luebert and Plissock, 2006). At our sites, annual precipitation for the Murta River and Paloma River catchments range from 1000 to 1600 mm year⁻¹, while the De los Ñadis River catchment is slightly drier (700–1000 mm year⁻¹), according to the WorldClim data provided by Hijmans et al. (2005). The average monthly temperature measured at Murta River ranges between 14.0 °C in the summer (January) and 3.5 °C in the winter (July) (MOP, 2016).

Among the three watersheds investigated, the extent of human land use has progressed unevenly. Along De los Ñadis River and the Paloma River, the forests were intentionally burnt in the 1940s for agricultural expansion and are currently used for subsistence farming. Livestock are also common in these two valleys, however grazing is concentrated in the upland pastures and hillslopes although cows occasionally occupy the active floodplain (Romero et al., 2014). The Murta valley, in contrast, is perhaps one of the least disturbed catchments in the Aysén Region and is the only remaining river in Chile designated as ‘*reserva de aguas*’ (water reserve) (Rivera Izam et al., 2009). It is characterized by primary forest in low elevation fluvial plains, limited human land use, and reduced wildfire. Grazing impacts are limited and comparable to the other watersheds, but presumably originate from wild animal grazers (**Figure 2 – c, Table S2** in Supplementary Material).

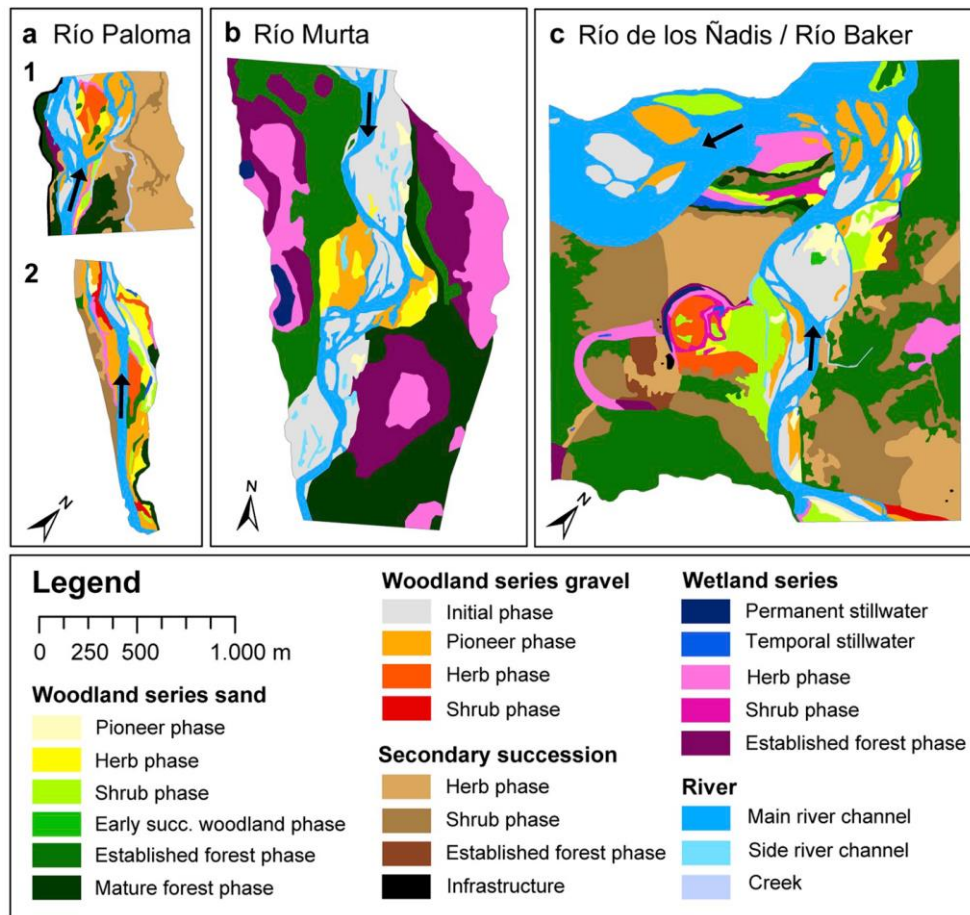


Figure 2. (a) Succession phases at study areas of Paloma River, (b) Murta River, and (c) De los Ñadis River, sorted by successional series; mapped by G. Egger in 2012, unpublished. The corresponding mapping method and succession phases are described in Egger et al. (2015). The primary successional series (woodland series sand, woodland series gravel and wetland series) are defined following the initial substrates while secondary succession is marked by agricultural land use.

Despite uneven human development among watersheds, the studied floodplains permit a rare opportunity to examine vegetation structure along an intact and complete hydrogeomorphic gradient. The headwater regions feeding all three rivers remain forested with no evidence of fire, and minimal animal grazing (Astorga et al., 2018). As natural, seasonal flood pulses are still intact, the active floodplains where our study takes place are routinely scoured by natural floods and their beds and plains reshaped by natural fluvial processes, which remain the predominant forces structuring the local vegetation community.

2.2 Vegetation transects

In January 2016 we sampled tree and shrub vegetation in floodplains using 10×20 m plots. Plots were oriented with their long axis perpendicular to the river channel and following the main hydrogeomorphic gradient (Corenblit et al., 2015). Consecutive plots were placed end-to-end, forming variable length transects traversing the entire floodplain gradient. In total, we sampled vegetation in 106 plots distributed among seven transects and three riparian sites, comprising a total area of 21,200 m². In total, 54 plots at the De los Ñadis River, 16 at the Paloma River and 21 plots at Murta River were sampled. Cover was visually estimated for each tree and shrub species by visually projecting the crown canopy cover on the ground. The estimation was done within three classes: adults, juveniles, and recruits. For tree species, we defined adults as individuals > 3 m in height and juveniles between 0.5 m and 3 m. Recruits were defined as individuals with heights up to 0.5 m, which captured seedlings, saplings and suckers. For shrubs, these thresholds were modified to account for their smaller stature. Shrub individuals up to 0.1 m were considered as recruits, between 0.1 m and 0.5 m as juveniles, and taller individuals as adults. Cover for each class of every species was visually estimated in 5% intervals, except for the range 0–5%, where a 1% interval

was used. We identified all stems to species level with the help of experts (Alicia Marticorena, Herbario de Concepción, UDEC) and reference literature (Lautenschlager-Fleury and Lautenschlager, 2014; Riedemann and Aldunate, 2014). In each plot we also recorded environmental data regarding soil texture, consisting of the percent ground cover of four substrate types: cobble (> 63 mm), gravel (63 mm - 2 mm), sand (2 mm - 0.063 mm) and silt (< 0.063 mm) (Wentworth, 1922). We additionally estimated the ground cover for water, open ground, driftwood, herbs and moss. Percentages of each environmental variable were estimated visually using the same intervals as the vegetation survey.

2.3 Stem growth

Growth data for the most important floodplain species was estimated by analysing tree rings. To sample tree rings, we sawed off disks for small individuals and for larger ones took increment cores using a Pressler drill. All tree ring samples were prepared using standard technique and the number of tree rings counted with the help of an optical microscope (Fritts, 2001). Total plant height, basal diameter and the plant height at the cutting point were also recorded. For multi-stemmed species, the length of the longest stem was measured. On one single gravel bar at De los Ñadis River (marked as 'SF' with a dashed line in **Figure 1 - c3**) all heights and breadth of *S. fragilis* stems were measured and their position was marked on an aerial photo (Google Earth Image © 2016 DigitalGlobe). We examined tree ring samples from all size categories for each species, in order to feed species-specific growth models.

2.4 Data analysis

Growth models for both, vertical height and basal diameter increment, were constructed for each species. Both linear and logarithmic functions were explored and those with higher R-squared retained. Because rapid seedling-juvenile growth is important in avoiding total submergence of leaf organs during floods, additional growth models were constructed for a recruitment phase subset for each species (Parolin, 2002). Growth models for recruitment subsets were based on ages from 1 to 6, varying slightly among species due to differences in availability of field samples.

We examined community composition pattern and its relationship to environmental variables using Non-Metric Multidimensional Scaling (NMDS). Distance matrices were constructed using Bray-Curtis dissimilarity metric after a Wisconsin double standardization of the species-plot matrix. Plots without vegetation were omitted. Subsequently, we mapped fitted vectors of environmental variables onto the ordination, selecting only significant relationships (p -value < 0.05). All analyses were performed in R software (R Core Team, 2016) using *vegan* package (Oksanen et al., 2016) and the function *metaMDS*.

To compare species' niche positions and breadth along the main hydrogeomorphic gradient we first reduced the soil texture variables (cobble, gravel, sand and silt) to the primary axes of a principal component analysis (PCA) on the correlation matrix. Variation among substrate particle size classes is expected to change as a function of water energy, thus we used the primary axis as an indicator of the principal hydrogeomorphic gradient. Niche positions and breadth along this axis were estimated for each species using abundance weighted means (Laliberté and Legendre, 2010) and Rao's Quadratic entropy (Botta-Dukát, 2005), respectively. Abundance weighted mean thus expresses the average position of species' cover along the main hydrogeomorphic gradient, while Rao's Q expresses the average variability in environmental conditions. Both statistics are weighted by cover, with larger individuals carrying more influence.

3 Results

The vegetation sampling along the transects revealed three tree and four shrub species (**Table 1**). Most species were sampled in at least two sites, except *Nothofagus pumilio* and *Discaria chacaye*. *Salix fragilis* was not present within our plots at Murta River, but these transects nevertheless provided valuable comparative data for growth and

environmental analyses. Except for *S. fragilis*, all woody species are native to Patagonia. Native tree species are exclusively from the family *Nothofagaceae*, while for shrubs' taxonomic membership was more varied.

Table 1. Woody species sampled in north-western Patagonian floodplains. The species habit, scientific name, plant family and their occurrence in the three studied rivers are indicated. All species are native except *Salix fragilis*, which is considered as invasive.

Habit	Species	Family	Murta River	Paloma River	De los Ñadis
Tree	<i>Nothofagus antarctica</i> (FORST.) OERST.	<i>Nothofagaceae</i>	X	X	X
	<i>Nothofagus dombeyi</i> (MIRB.) OERST.	<i>Nothofagaceae</i>	X	–	X
	<i>Nothofagus pumilio</i> (POEPP. & ENDL.) KRASSER	<i>Nothofagaceae</i>	–	X	–
	<i>Salix fragilis</i> L. ^a	<i>Salicaceae</i>	–	X	X
Shrub	<i>Discaria chacaye</i> (G.Don) Tortosa	<i>Rhamnaceae</i>	–	–	X
	<i>Baccharis obovata</i> Hook. & Arn.	<i>Asteraceae</i>	X	X	X
	<i>Escallonia virgata</i> (RUIZ & PAV.) PERS.	<i>Escalloniaceae</i>	X	–	X
	<i>Berberis empetrifolia</i> LAM. EX POIR.	<i>Berberidaceae</i>	X	X	X ^b

^a We determine the *Salix* species according to its morphological characteristics as *Salix fragilis*. New changes in taxonomy revealed a new name for *S. fragilis* L.: *S. eucxina* (Belyaeva, 2009). To determine the species unequivocally further genetic analysis would be necessary.

^b *B. empetrifolia* was present at the De los Ñadis River but not mapped due to its very low occurrence.

3.1 Community structure and environment

The primary axis of the PCA explained 58.5% of measured environmental variation, and described the hydrogeomorphic gradient we observed in the field (**Figure S1** and **Figure S2** of Supplementary Material). Low scores corresponded to open sites near the river channel with coarse substrates of cobble and gravel, while high scores indicated more distal sites with finer substrate (**Table 2**).

Table 2. Eigenvalues for each substrate parameter along the first principal component axis.

Environmental variable	PC1
Silt	0.59
Sand	0.24
Gravel	-0.50
Cobble	-0.58

Along this gradient, plant cover increased from bare cover to over 70% cover in the least disturbed sites (**Figure 3**). Plant cover estimates greater than 50% occurred in only a handful of sites (4%), and the majority of sites (70%) had cover estimates lower than 10%. *S. fragilis* had a mean cover of 8% where it was present and a maximum cover of 50%, representing 22 and 55% greater average cover in comparison to the mean and maximum cover estimates of the most frequent and abundant native tree, *N. antarctica*. Relative to native species, invasive *S. fragilis* demonstrated amongst the largest Rao's Q and the smallest community weighted mean along the primary environmental axis (**Table 3**).

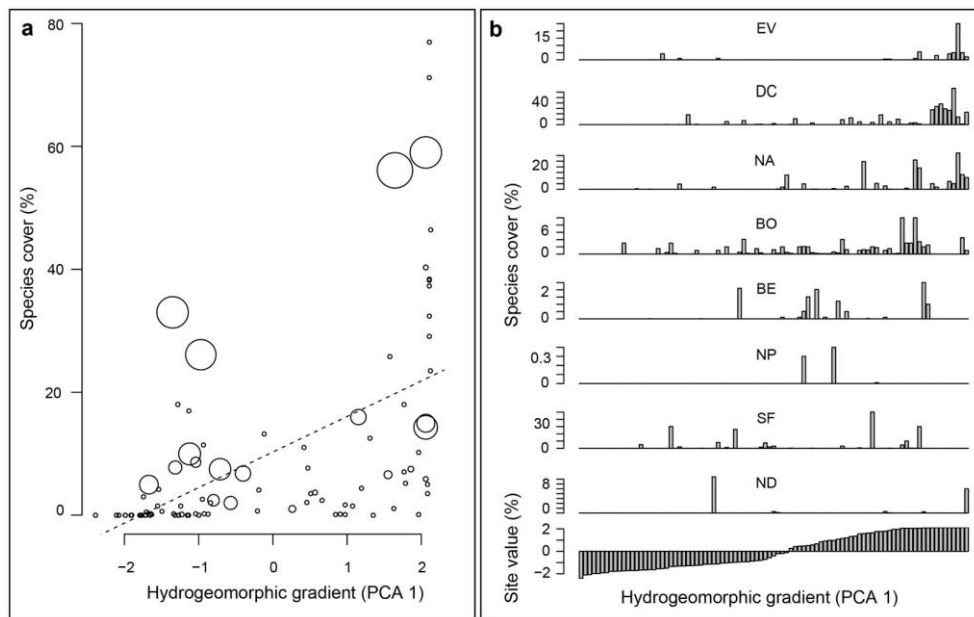


Figure 3. Plant cover along the main environmental axis of hydrogeomorphic variation. (a) Total plant cover of the entire community increases with decreasing flood disturbance (PC1). Values range from -2 (most disturbed) to 2 (least disturbed) as inferred from sediment grain size. Bubble size is proportional to *Salix fragilis* cover, demonstrating potentially high cover of this species even at relatively disturbed sites. The dotted line shows a linear regression. (b) Sites are sorted by their position along the hydrogeomorphic gradient (PC1), the value of which is indicated by the bottom barplot. Upper barplots indicate cover for each species at each site. Species are sorted from bottom to top in order of increasing abundance-weighted-mean of along the hydrogeomorphic gradient. Two-letter codes for each species are as follows: *Salix fragilis* (SF), *Nothofagus antarctica* (NA), *Nothofagus dombeyi* (ND), *Nothofagus pumilio* (NP), *Escallonia virgata* (EV), *Discaria chacaye* (DC), *Baccharis obovata* (BO) and *Berberis empetrifolia* (BE).

Table 3. Weighted mean and Rao's Q indicate measures of each species relative to niche position and breadth along the main axis of environmental variation (see methods for details) are listed.

Species	Weighted mean	Rao's Q
<i>Nothofagus antarctica</i>	1.63	0.36
<i>Nothofagus dombeyi</i>	0.24	1.17
<i>Nothofagus pumilio</i>	0.77	0.03
<i>Salix fragilis</i>	0.45	1.03
<i>Discaria chacaye</i>	1.67	0.43
<i>Baccharis obovata</i>	0.99	0.84
<i>Escallonia virgata</i>	1.71	0.57
<i>Berberis empetrifolia</i>	0.84	0.51

The NMDS analysis (dissimilarity index Bray Curtis = 0.140; Nonmetric fit: $R^2 = 0.982$; Linear fit: $R^2 = 0.87$) revealed complementary patterns of community structure. The first axis highlighted compositional differences among the three rivers, driven mainly by the absence of *S. fragilis*, and *D. chacaye* in Murta River and De los Nadis River, respectively (**Figure 4**). This primary axis, however, was associated with little measured environmental variation, excepting a minor increase of drift wood at Murta River. Most measured environmental variables correlated with the secondary axis and described the main hydrogeomorphic gradient, from flood-disturbed cobble substrates to low-disturbed sandy plains. Species ordination scores along the secondary axis reflected shifts in life form along the floodplain gradient, with sandier and less disturbed sites dominated by tree species (*N. antarctica*, *N. pumilio*, and *N. dombeyi*) and highly flooded, disturbed sites dominated by shrubs (*Escallonia virgata*, *D. chacaye*,

Baccharis obovata, *Berberis empetrifolia*). A secondary pattern was also apparent, where seedlings and juveniles demonstrated higher association to more disturbed and coarse substrates than adults of the same species. The relatively low species scores along the secondary axis for *S. fragilis* relative to co-occurring species were congruent with estimates of its niche position in more disturbed sites with higher proportions of gravel and cobble.

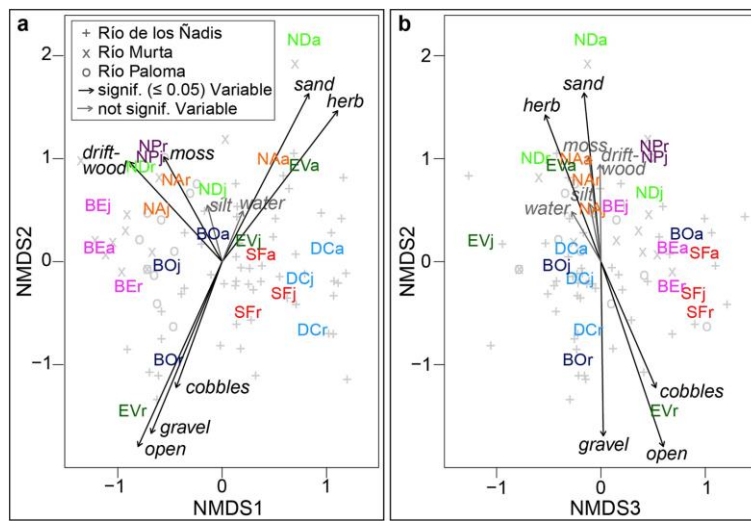


Figure 4. (a) NMDS for the vegetation cover data for axis 1 vs. 2 and (b) axis 2 vs. 3 for seven transects pooled across Murta River, Paloma River and De los Nádís River (n = 78 plots). The studied species, classified into three life stages of recruitment (r), juvenile (j) and adult (a), were *Salix fragilis* (SF), *Nothofagus antarctica* (NA), *Nothofagus dombeyi* (ND), *Nothofagus pumilio* (NP), *Escallonia virgata* (EV), *Discaria chacaye* (DC), *Baccharis obovata* (BO) and *Berberis empetrifolia* (BE). Plots without vegetation were omitted.

3.2 Dendroecology and growth

Trees demonstrated linear growth for height and basal diameter, at least within the age spans sampled by us (**Figure 5**, and **Table S1** of Supplementary Material). For the recruitment subset, model fits tended to have lower R-squared values, reflecting both larger variability in growth during this life stage and fewer data points to model it. Estimated coefficients for average growth rate indicated that *S. fragilis* grows vertically at 34.7 cm year⁻¹, the fastest growth rate among all species sampled. Recruitment stage models of vertical growth subsets showed that differences between *S. fragilis* and native trees are even more pronounced. This is a consequence of a 23% faster vertical growth rate of juvenile *S. fragilis* relative to growth rates averaged over its entire life span. In contrast, vertical growth rates for native trees were similar or even slower during recruitment phases. For example, *N. antarctica* grew faster, at 27 cm year⁻¹ on average during its whole life span than during recruitment, when it grew 20.4 cm year⁻¹, on average, a 24.5% decrease in vertical growth rate.

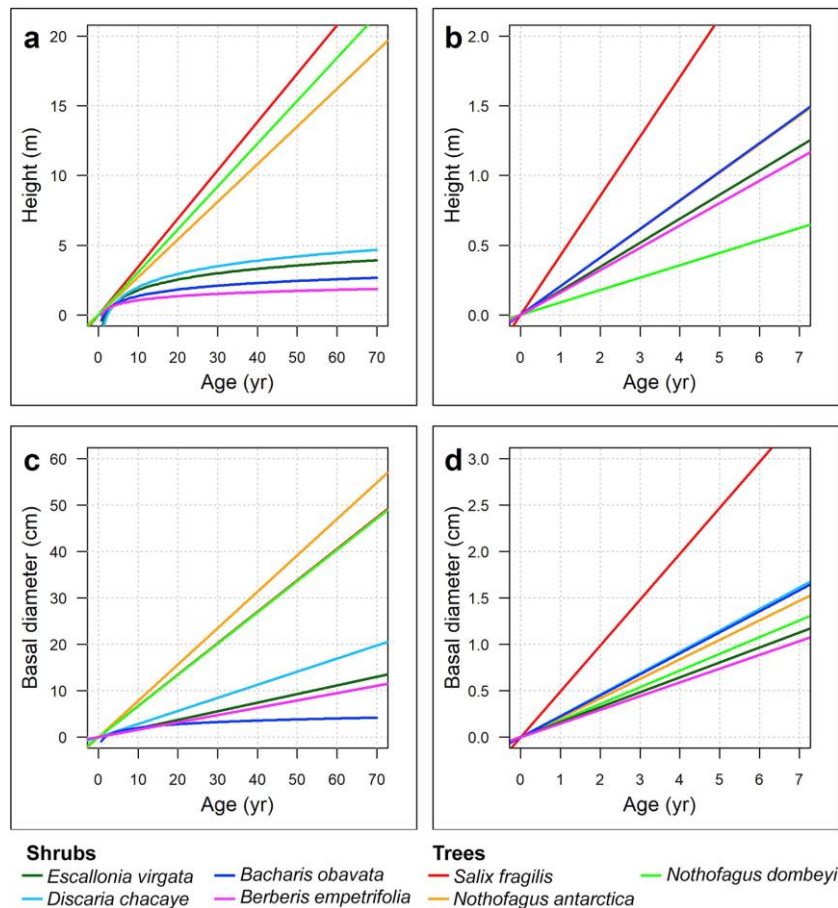


Figure 5. Species growth models representing (a and b) vertical height-age relationships and (c and d) basal diameter-age relationships for entire life span sampled and for juvenile subsets, respectively. The function, R-squared, goodness-of-fit and sampling size of each regression model appear indicated in **Table S1** of Supplementary Material.

Similar to vertical growth, models of basal increment indicated higher growth rates for *S. fragilis* than native species during recruitment phases. Over the entire time span considered, however, basal growth rates for *N. antarctica* were slightly higher than *S. fragilis*. Within species, average basal growth tended to be lower during recruitment than over the entire life span, although this pattern was especially pronounced among the native tree species.

In contrast to trees, shrubs demonstrated a logarithmic vertical growth over sampled life spans, reaching maximum heights between 1.24 m (*B. empetrifolia*) and 5.03 m (*D. chacaye*). Shrubs *D. chacaye* and *E. virgata* are long-lived species (individuals > 40 years-old observed), while a maximum age of 16 years was observed for *B. empetrifolia* and 6 years for *B. obovata*. This latter species resprouts from the base and individuals may actually be much older.

3.3 Historical reconstruction of *Salix fragilis* colonization

We sampled all *S. fragilis* stems at a single gravel bar at De los Ñadis River (**Figure 1 - c3**) and used growth models (**Figure 5**) to reconstruct the colonization history of a 16.5 ha patch over the past two decades. The great majority (88%) of the 249 stems sampled were less than 7 years old at the time of sampling in January of 2016. Population reconstructions indicated that in 1995 the gravel bar population consisted of only 16 individuals, or 1 ind ha⁻¹. By 2009, 14 new trees recruited into the bar, increasing average density to 2 ind ha⁻¹. A dramatic increase in the local population occurred during the 2009–2016 time period, with 219 recruiting individuals increasing average density to 15 ind ha⁻¹ (**Figure 6**). During field work, we found sprouting driftwood of *S. fragilis* at the water's edge and observed that young recruits on the gravel bar were relatively more abundant close to water in highly flood-disturbed and non-vegetated areas. No germination of *S. fragilis* was observed and all flowering individuals were female, so new recruits are presumed to originate asexually, although we cannot discount seed dispersal from other regions.

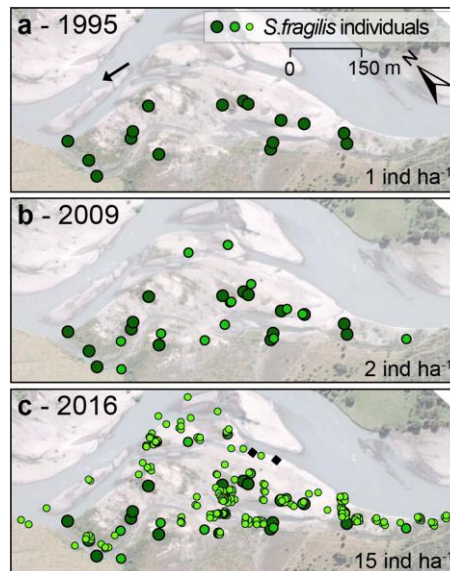


Figure 6. Position of the *Salix fragilis* L. individuals mapped within the active gravel bar zone of De los Ñadis River, illustrated in three different moments: (a) 1995, (b) 2009 and (c) 2016, using as a reference the age of the plants sampled in 2016 (Google Earth Image © 2016 DigitalGlobe). Note that some points are overlapped due to the scale of the figure.

4 Discussion

Our approach revealed core differences in growth and ecology between *Salix fragilis* and the native woody species in Patagonian floodplains. Environmental data indicated that the mean niche position of *S. fragilis* is located mainly within the active river tract, in highly disturbed sites where vegetation cover of native species is low and largely consists of young seedlings and juveniles. At the same time, its broad niche breadth along the hydrogeomorphic gradient indicates that it also grows and persists in more vegetated, multi-species communities that experience less flood disturbance. Moreover, dendroecological analyses showed that *S. fragilis* has higher growth rates relative to native species, especially during juvenile stages.

The exceptional niche position, breadth, and growth of *S. fragilis* in Patagonian floodplains are likely all associated to the species' vigorous capacity for vegetative regeneration. The epithet, “fragilis”, references the tendency of branches under shear stress of flowing water to break away, which can readily sprout to form new individuals (Karrenberg et al., 2002). According to our observations, *S. fragilis* propagation is most likely vegetative (also observed in eastern Patagonia by Thomas et al., 2012) as we observed neither seedlings nor male flowers, and this reproductive strategy may provide an advantage in active floodplains. Relative to seeds, tree fragments with partially pre-formed shoot or root primordia and a large store of carbohydrate reserves permit more immediate and rapid growth (Karrenberg et al., 2002). In a dynamic fluvial system, rapid initial growth will provide more extensive root systems and better hold fasts on unconsolidated sediments, especially in the face of frequent scouring events (Parolin, 2002). Moreover, larger shoots also safeguard against complete submergence of plant organs during high flood events (Parolin, 2002). In this sense, the slow growth of seedlings and juveniles of native floodplain species (Raffaele et al., 1998) may be a major constraint for the colonization and establishment of areas with more severe, recurring flood disturbance where *S. fragilis* is vigorously taking hold.

Our data further indicate that the rate at which *S. fragilis* populations increase along river margins can be extremely rapid. At De los Ñadis River, we estimated an increase from 2 ind ha⁻¹ to 16 ind ha⁻¹ during 2009–2016, a 4-fold increase in population size compared to the previous seven-year periods. While an upsurge in transplanting by humans is one possible explanation, the timing of the explosive increase at De los Ñadis River also corresponds with glacial lake outburst floods (GLOFs) originating upstream from the Colonia valley since 2008 (Dussailant et al., 2010). These outbursts propagate downstream as heavy flood events at De los Ñadis River (B. Reid pers. obs.) and may represent major dispersal events for *Salix* spp. as branches fragment, drift downstream, and establish on

disturbed river banks. If this is the case, invasive spread of *Salix* spp. may be exacerbated by increasing frequency and intensity of flood-disturbance events that are driven by climate change (Rahel and Olden, 2008).

A striking aspect of the Patagonian woody floodplain community is its lack of phylogenetic diversity – we documented only three native tree species in Patagonian floodplains, all of which were congeneric. The native community, characterized by a presence of relatively few woody species is generally attributed to the region’s small, isolated landmass and severe Pleistocene glaciation history, including nearly complete glaciation during cold periods. In such a phylogenetically restricted pool of species, the specialized traits required to grow and survive in the most severely disturbed and highly flooded riparian sites may not be present in the community. Rather than floodplain specialists, the native species occupying Patagonian rivers tend to be habitat generalists, tolerant to a wide range of regional environmental conditions and habitat types. For example, *Nothofagus dombeyi* and *Nothofagus pumilio* were both scattered within the floodplains, but predominantly beyond our transects, outside the limits of the active flooding zone. The only native tree species we observed to occur at high cover in floodplains was *Nothofagus antarctica*, this species forming the majority of riverine forests (*Chusqueo-Nothofagetum antarcticae*) in the region (Vidal et al., 2011). Even this species, however, might be described as a habitat generalist, demonstrating high phenotypic plasticity, high genetic variability, and diverse habitat associations (Steinke, 2008; Vidal et al., 2011). Along our studied floodplain gradient, niche distributions of the great majority of species overlapped, and compositional differences among sites were due to slight shifts in species abundances, rather than species turnover. The apparent lack of a floodplain specialist may be another contributing factor making Patagonian floodplains vulnerable to invasion, whereby invasive species possessing unique trait values exploit resources previously under occupied by the native community (i.e., ‘vacant niche hypotheses’) (Elton, 1958). The ‘vacant niche hypotheses’ speculates that unused soil resources enable the spread and growth of alien species. Indeed, based on family-level analyses, Rejmánek (2013) previously speculated that temperate regions of the Southern Hemisphere represent ‘open/vacant niches’ for *Salicaceae*. Consistent with this idea, the comparatively faster growth, higher flood-disturbance tolerance, and propensity for vegetative propagation all contribute to the capacity of *S. fragilis* to successfully colonize, survive, grow and reproduce along highly disturbed river margins - a frequently disturbed, successional habitat representing an abundant and relatively unoccupied resource in regional floodplains. The cascade of effects that colonizing *S. fragilis* populations will have on Patagonian riparian ecosystems remains unclear (Pauchard et al., 2004; Quiroz et al., 2009; Speziale et al., 2012). However, we expect increasing density of stems and roots to drive adjustments in river geomorphology by stabilizing sediments and, consequently generating less dynamic, narrower channels. This, in turn, will influence flood regimes. Additionally, increased organic input to river water through larger amounts of leaf fall and litter may also have profound impacts on aquatic nutrient cycles and organic debris. Higher leaf area may increase transpiration loss, reducing water availability in soils and affecting ground water, while increased shading below trees may remove important propagation sites for native plants (Vilà et al., 2011). Navigation may also be affected. In one noteworthy case, *S. fragilis* has congested the main channel of Cochrane River (a moderately-sized river in the Baker River catchment with 10–20 m³ s⁻¹ baseflow) and impedes navigation (B. Reid pers. obs). With this in mind, we view *Salix* spp. as an ecosystem engineer (Gurnell, 2014) and expect it to rapidly alter the local environment as well as processes considered vital to sustaining the local floodplain habitat as we currently understand it.

While understanding these processes is a critical goal of future research, our results suggest that *S. fragilis* will continue to vigorously colonize relatively non-vegetated and disturbed sites near river channels, a course that will fundamentally alter ecosystem functioning and biotic interaction in the region’s riparian environments.

Author contributions

AL conceived research, performed field work, designed data analysis, analysed data, and wrote the manuscript; GE conceived and designed research, performed field work and interpreted data; BR interpreted data and wrote the manuscript; AChB wrote the manuscript; VGG designed data analysis, analysed data and wrote the manuscript; EH analysed data and wrote the manuscript; all authors contributed to data interpretation and approve the final manuscript.

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Supplementary Material

Table S1. Growth functions of woody species, for height growth and basal diameter growth for different age range subsets. The corresponding functions, number of samples (N), R-squared (R²) and goodness-of-fit (*p*-value) are given.

Species	Age range	Height growth (m)			Basal diameter growth (cm)				
		Functions	N	R ²	<i>p</i> -value	Functions	N	R ²	<i>p</i> -value
<i>Salix fragilis</i>	2 - 27	$y = 0.3466 x$	27	0.941	< 0.001	$y = 0.6764 x$	27	0.931	< 0.001
	2 - 5	$y = 0.4272 x$	19	0.854	< 0.001	$y = 0.4941 x$	19	0.829	< 0.001
<i>Nothofagus antarctica</i>	3 - 50	$y = 0.2704 x$	47	0.927	< 0.001	$y = 0.7837 x$	47	0.881	< 0.001
	3 - 5	$y = 0.2042 x$	8	0.922	< 0.001	$y = 0.2094 x$	8	0.959	< 0.001
<i>Nothofagus dombeyi</i>	3 - 64	$y = 0.3075 x$	12	0.930	< 0.001	$y = 0.6719 x$	12	0.849	< 0.001
	3 - 7	$y = 0.0889 x$	3	0.870	0.067	$y = 0.1798 x$	3	0.781	0.116
<i>Escallonia virgata</i>	2 - 47	$y = 1.098 \ln(x) - 0.759$	20	0.902	< 0.001	$y = 0.1861 x$	20	0.915	< 0.001
	2 - 5	$y = 0.1723 x$	7	0.810	0.002	$y = 0.1609 x$	7	0.916	< 0.001
<i>Discaria chacaya</i>	2 - 47	$y = 1.372 \ln(x) - 1.177$	25	0.743	< 0.001	$y = 0.2821 x$	25	0.834	< 0.001
	2 - 5	$y = 0.1604 x$	7	0.843	0.001	$y = 0.2301x$	7	0.786	0.003
<i>Baccharis obovata</i>	2 - 6	$y = 0.667 \ln(x) - 0.187$	35	0.270	0.001	$y = 1.114 \ln(x) - 0.572$	35	0.430	< 0.001
	2 - 4	$y = 0.2053 x$	29	0.784	< 0.001	$y = 0.2262 x$	29	0.783	< 0.001
<i>Berberis empetrifolia</i>	1 - 16	$y = 0.412 \ln(x) + 0.0946$	15	0.579	< 0.001	$y = 0.1577 x$	15	0.898	< 0.001
	1 - 5	$y = 0.1604 x$	10	0.873	< 0.001	$y = 0.1474 x$	10	0.824	< 0.001

Table S2. Mean browsing damage exerted by cows and wildlife grazers on each woody species in the three studied rivers. Three browsing damage classes were defined for each height species class and along each transect as follows: 0=none, no browsing damage can be observed / 1 = medium browsing damage, bitten-into branches / 2 = highly damaged branches. Missing values (-) mean that the species was not observed.

Mean browsing damage	De los Ñadis River	Murta River	Paloma River
<i>Salix fragilis</i>	1.54	-	0.00
<i>Nothofagus antarctica</i>	0.67	1.29	1.64
<i>Nothofagus dombeyi</i>	0.67	0.20	-
<i>Nothofagus pumilio</i>	-	-	1.17
<i>Escallonia virgata</i>	1.13	1.48	-
<i>Discaria chacaya</i>	1.20	1.00	-
<i>Baccharis obovata</i>	1.08	1.72	1.14
<i>Berberis empetrifolia</i>	-	1.00	0.33

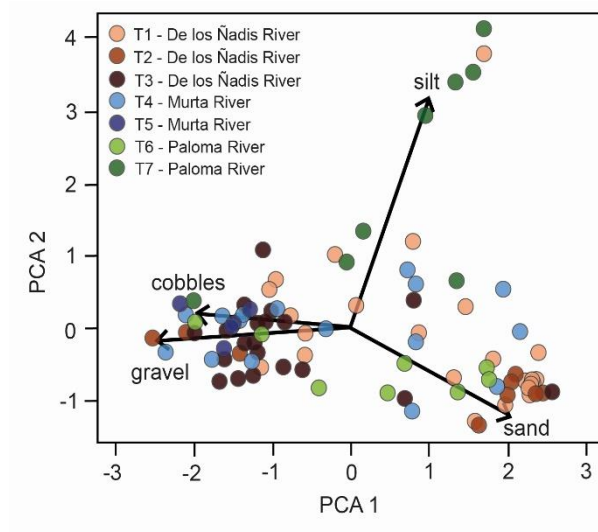


Figure S1. A biplot of grain size distribution (percentage surface cover of cobbles, gravel, sand and silt) for each sampling site. The eight transects are coloured differently. The plot demonstrates how transects encompassed a wide gradient in substrate textures.

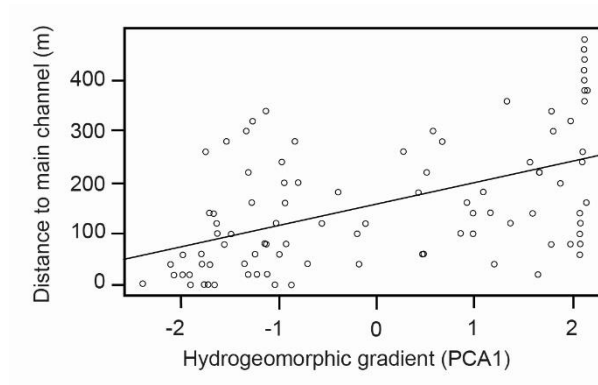


Figure S2. Relationship between first PCA-axis (hydrogeomorphic gradient from highly disturbed to low disturbance) and distance to the main channel of the river (R -squared = 0.26). Each point represents a plot within a transect.