Effects of the invasive plant *Lupinus polyphyllus* on vertical accretion of fine sediment and nutrient availability in bars of the gravel-bed Paloma river[☆]

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A B S T R A C T

Floodplain vegetation is fundamental in fluvial systems, controlling river corridor geomorphology and ecology through a series of hydraulic, sedimentological, and biological processes. Changes caused by introduced plant species can thus result in shifts in river regime, succession trajectories and nutrient availability, affecting native biodiversity. The exotic bigleaf or marsh lupine *Lupinus polyphyllus*, introduced in Patagonia in the last decades, is aggressively invading fluvial corridors. It fills unoccupied ecological niches in southern Chilean rivers, due to its capacity for nitrogen fixation, its perennial habit, and high shoot density and leaf surface area.

We investigated the effects of *L. polyphyllus* on vertical accretion of fine sediment, and soil carbon and nitrogen content, on gravel bars of the Paloma river, Chilean Patagonia, where lupine is believed to have been introduced in 1994. We sampled plot pairs with and without lupine, with each pair located at the same elevation above river stage, and plots distributed over the reach scale. We measured the thickness of the fine soil horizon, grain size distribution, and soil carbon and nitrogen content. We also compared aerial photographs to evaluate changes in spatial coverage of lupine along the study reach.

Presence of lupine was strongly correlated with a thicker layer of finer sediment, in turn characterized by higher organic carbon, carbon to nitrogen ratio, and inorganic carbon content. Contrary to our expectations, we did not find any significant differences in total nitrogen. Aerial photographs did not reveal important differences in coverage between 2007 and 2010, but plant density appears to have increased between the two dates, and invaded gravel bars also appear to be more stable. Lupine dominance of otherwise sparsely vegetated gravel bars in Patagonian rivers appears to have greatest consequences on bar physical structure (increased rates of accretion of fines) and secondary repercussions on soil quality (increase in recalcitrant organic matter), with potential transient effects on nutrient availability (possible increased soil metabolism, followed by carbon mineralization and loss of lupine nitrogen subsidy).

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Introduction

Vegetation is one of the most important controls on geomorphological processes and landforms (Kirkby 1995). Riparian plants affect fluvial landforms through changes in water budgets, soil moisture, resistance to flow, nutrient availability, sediment deposition, bank strength and erosion, channel and floodplain evolution, etc. (Simon et al. 2004). As a rule, river landscapes have been considered to be controlled mostly by hydrogeomorphic processes, the interaction between the flow and sediment regimes. This idea was first challenged by Hickin (1984), who emphasized the effects of vegetation on flow resistance and bar sedimentation, among others. More recently, Gurnell and Petts (2002) and Gurnell et al. (2012) show that vegetation actually plays an active role, particularly in the case of wandering gravel-bed rivers. For example, Tal et al. (2004) confirm the role of riparian vegetation as a primary control on channel form, in the case of multi-thread gravel-bed rivers. Indeed, Paola (2011) argues that the emergence of terrestrial vegetation corresponds in geological time with dramatic global changes in river morphology. Not only does riparian vegetation directly affect many hydrogeomorphic processes, its development depends in turn on those same processes, through positive feedback loops (Gregory et al. 1991; Richards et al. 2002; Francis 2006; Corenblit et al. 2007, 2009; Schnauder and Moggridge 2009).

Primary succession is among the oldest (Cowles 1911) but still evolving concepts in the field of ecology (Connell and Slatyer 1977); in summary, it states that pioneering species establish on bare substrates and then facilitate the colonization by woody species through pedogenesis or other modifications to the micro environment.

The colonization of gravel bars in wandering or braided river systems is a good example of primary succession. Floodplain succession in gravel-bed rivers begins in the active part of the river corridor, the parafluvial zone (sensu Stanford et al. 2005), when plants colonize recently created, bare gravel bars (Braatne et al. 1996; Karrenberg et al. 2002). The initial colonization of gravel bars by pioneering vegetation is a fundamental process underlying floodplain formation and habitat dynamics in alluvial rivers (Gregory et al. 1991; Décamps 1996; Bennett and Simon 2004; Stanford et al. 2005). When covered with vegetation, bars become hydraulically rougher and trap more fine sediment during floods, thus growing by vertical accretion (Hickin 1984; Gurnell and Petts 2002). In a positive feedback loop, deeper and finer soils, located at higher elevations provide a better environment for plant growth, because the frequency of flooding and scouring disturbances is reduced, while water-holding capacity increases (Décamps 1996; Gurnell and Petts 2002; Francis 2006; Corenblit et al. 2007). In time, bare gravel bars become the new floodplain surface, allowing for succession to proceed.

One of the key limiting factors in plant succession on fluvial gravel bars is the restricted availability of soil nutrients, especially nitrogen (Adair and Binkley 2002; Morris and Stanford 2011). Therefore, key characteristics that determine plant succession and soil development in riparian zones include the presence of plants with adaptations to withstand at least temporary nitrogen limitation or else with the capacity for nitrogen fixation, or systems that receive nitrogen subsidies such as from salmon carcasses (Morris and Stanford 2011).

Riparian vegetation is a fundamental driver of river ecosystem function (Tabacchi et al. 1998). The Shifting Habitat Mosaic of Stanford et al. (2005) explains the pattern and process of fluvial ecosystems in the case of alluvial rivers with floods. It refers to the complex, heterogeneous, and dynamic distribution of habitat patches within a floodplain, which are used by aquatic and riparian organisms. This mosaic is driven by the flow, sediment, and large woody debris (LWD) regimes, interacting with the floodplain vegetation and materials along a given reach. Plants are a primary control on the biophysical complexity of alluvial ecosystems, partly explaining their structure and functioning (Gregory et al. 1991; Malanson 1993; Naiman and Décamps 1997; Décamps 2005): they provide shade, allochthonous organic matter inputs, filtration of nutrients in shallow groundwater flows and of fine sediments in overland flows, and are a source of LWD to aquatic ecosystems; they modify the microclimate and serve as corridor for movements of both animals and plants, and also as habitat for mammals and birds.

Lupinus polyphyllus Lindl. is an invasive, perennial herbaceous plant in the Fabaceae family. It is native to western North America, but has successfully invaded rivers in many European countries (Fremstad 2010), as well as in New Zealand, Australia, and Argentina (ISSG global invasive species database, http://www.issg.org/database/species/ecology.asp?si=944&fr=1&sts=&lang=EN). Because it produces a considerable number of large seeds, has capacity for nitrogen fixation, is toxic (it produces an alkaloid that may enhance competition with other plants and reduce grazing impacts), and can reproduce vegetatively, it has a high regeneration capacity following disturbances such as scour or fire (Fernández 2007; Quiroz et al. 2009). Lupines were introduced as ornamental plants by the first European settlers to Chilean Patagonia, and *Lupinus* spp. now cover many of its river corridors

and roadside areas. Although the first record for *L. polyphyllus* in the Aysén region (Central Patagonia) of Chile is relatively recent (Rodríguez et al. 2008), general observations suggest that it is already widespread and often an aggressive invader in many river basins in the region. For example, bars dominated by *L. polyphyllus* stands up to 2.0 m in height have been observed on the Palena (Palena river), Aysén (Mañihuales, Simpson, and Paloma rivers) and Baker Catchments (Murta and Baker rivers), a range spanning over 400 km, with possibly hundreds of kilometers of riparian zone invaded in three major watersheds of Chilean Patagonia. This study focuses on the colonization by *L. polyphyllus* of coarse, recently deposited gravel bars. However, the species has also been observed in a wide range of habitats in the region: vegetated wetlands bordering shallow lakes, roadsides, well-drained upland pasture on andisols, in addition to a variety of riparian habitats, from poorly drained depressions, coarse sands, low orthofluvial terraces (mixed with *Holcus*) and on bare gravel and cobble bars.

In this reach-scale investigation, we examine the effects of *L. polyphyllus* on vertical accretion of fine sediment and on nutrient availability (organic carbon and nitrogen) on gravel bars of the Rio Paloma, a wandering gravel-bed river in Chilean Patagonia. We hypothesize that the presence of *L. polyphyllus* increases bed roughness over bars, resulting in slower flow velocities and enhanced deposition of finer sediment. We expect that a subsequent increase in vertical accretion rates, together with litterfall and nitrogen fixation in dense lupine stands, will also alter nutrient availability, specifically with an increase in total soil nitrogen. The lupine invasion in Patagonia, which remains largely undocumented, may be among the most significant alterations in rivers and streams in the region, with potential changes in geomorphological regimes and soil fertility and consequent effects on primary succession, and novel feedbacks between vegetation and river geomorphology.

Methods

Study reach

The field data were collected on bars located along the Paloma river, a 5th order, wandering gravel-bed stream in Chilean Patagonia, located about 60 km south of the city of Coyhaique (Fig. 1). The study reach is about 13 km long, with an average valley slope of 0.33%. The active channel along the reach ranges in width from 80 to about 300 m. Flow regime is mixed, with runoff from over 50% of the catchment regulated by large lakes, but also with significant rainfall-driven runoff events from unregulated tributaries throughout the year, as well as predictable snowmelt floods in spring. The drainage area at the lower end of the study reach is 832 km^2, with a mean annual flow estimated at about 50 m^3 s^{-1}. Lowest flows occur during the winter.

Woody riparian vegetation on forested islands is mostly composed of lenga (*Nothofagus pumilio*), ñirre (*N. antarctica*), and notro (*Embothrium coccineum*; Chilean fire bush), with some coihue (*N. dombeyi*). Recent bars are sparsely colonized by *Holcus lanatus*, also non-native and widespread in pastures in Chile, with occasional contribution by native bamboos in the genus *Chusquea*. *Holcus* is the most common associate of lupine, and is co-dominant on the orthofluvial zone, when a consistent layer of fines has already accumulated. The colonization sequence and interaction (competition or facilitation) between the two taxa is unknown. In the Paloma valley, which is inhabited by only a handful of families, it is clear that lupine was introduced in 1994, by the owner of a then recently opened fishing lodge. Indeed, its observed distribution within the valley covers from the lodge downstream.
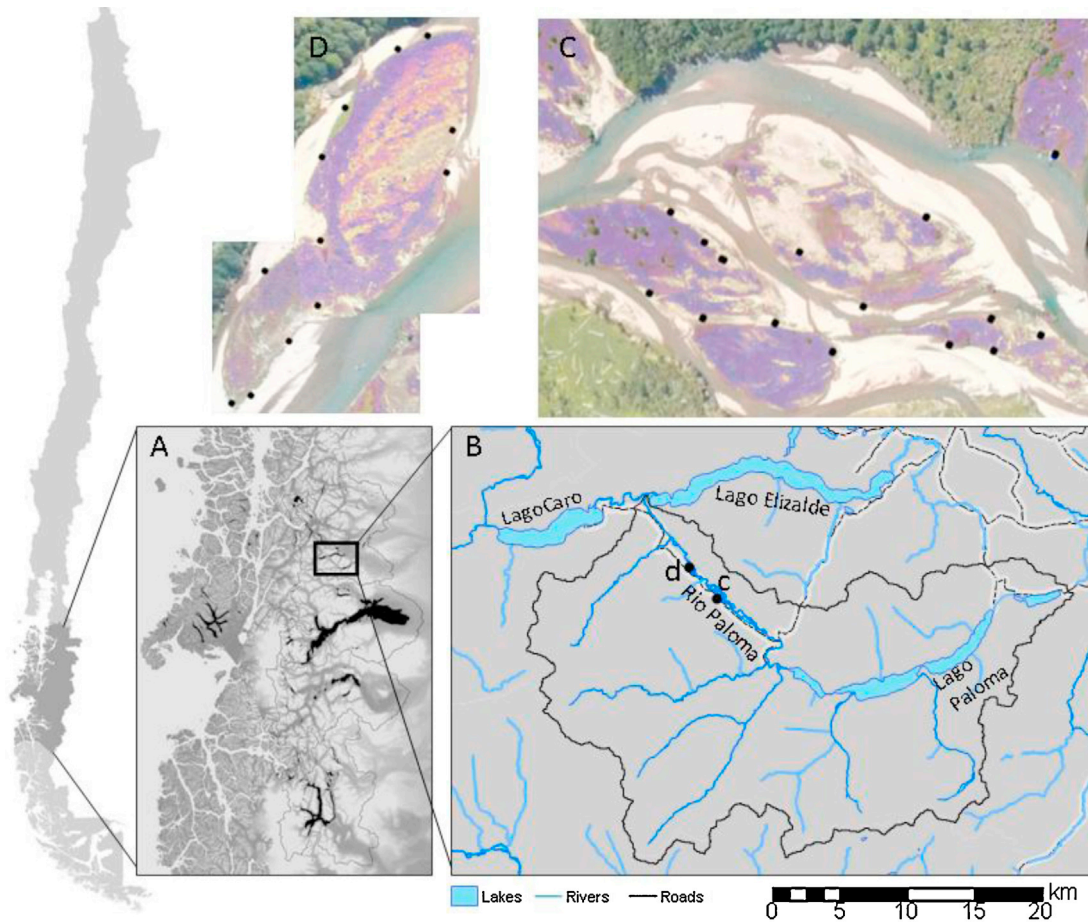
Fig. 1. Location of the study site. (A) The Aysén region of central Chilean Patagonia; (B) The Paloma river basin with the study reach, showing the two bar complexes (C) and (D) with the sampled plots.

Estimation of changes in Lupinus cover

We overlayed unrectified aerial photos from 2007 and 2010, using ArcGis 9.2 and the 2010 images as a base, identifying an 8.3 km reach invaded by *L. polyphyllus*. We then compared relative areal coverage on eight randomly selected bars.

Field work

Data collection in the field was performed in February and March 2011. We randomly chose 30 locations over a reach with two large bar complexes, totaling 3.5 km in length (Fig. 1C and D). We applied a paired-plot sampling design, looking for two plots at each location: one with lupine cover and the other without. Each plot pair was chosen so that: (i) separation distance between plots was 5 m or less, (ii) the area of each plot was at least 4 m^2, and (iii) bar surface at both plots was at the same elevation, in order to control for flooding frequency and vertical distance to the water table or capillary fringe (the driving factors in plant water availability).

At the center of each plot, we laid a 50 cm × 50 cm square, and used a soil auger to collect the fine sediment overlaying the gravel, at five locations (center and four corners of the square). The five soil samples were then pooled for grain size and chemical analyses. We measured the depth of this fine layer at the five locations (to the nearest cm) and then averaged the five readings to obtain the depth of fines, Δz (cm).

Laboratory analyses

The pooled samples of fine material (two per sampling location, for a total of 48, as there were 12 no-lupine sites without a layer of fine soil) were sieved in a Ro-Tap machine in order to obtain the weight proportion in each of the following size classes: gravel (sieve diameter > 2 mm), very coarse sand (between 2000 and 1000 μm), coarse sand (between 1000 and 500 μm), medium sand (between 500 and 250 μm), fine sand (between 250 and 125 μm), very fine sand (between 125 and 63 μm), and silt (<63 μm). Following Meier (2008), we then computed an index of fineness (FI, dimensionless) for each soil sample, as the percentage in weight of the fine material (defined as everything finer than 2.0 mm, i.e. sand and silt) finer than 250 μm. In other words, FI is that proportion of the fines made up of fine sand, very fine sand, and silt:

$$\text{FI} \ (\%) = \frac{\text{material finer than} 250 \ \ \mu\text{m}}{\text{material finer than} 2.0 \ \ \text{mm}} \times 100 \tag{1}$$

After homogenizing each pooled soil sample, a small subsample was introduced into a previously weighed silver capsule, oven-dried at 70 °C until constant weight, followed by acid fumigation for 12 h (Harris et al. 2001). Soil carbonates (C_{inorg}, g kg^{-1} of sediment) were estimated by mass loss from fumigation. Acidified samples were analyzed for organic carbon (C_{org}, g kg^{-1} of sediment) and total nitrogen (N_{total}, g kg^{-1} of sediment) using a LECO Truspec CHN Analyzer. Carbon to nitrogen ratio, C:N, was calculated based on the molar ratio of organic carbon to total nitrogen.

Table 1
Correlation coefficients for all variables, pooled across all plots ($n = 36$, values in bold are significant at $p < 0.05$).

	C_{inorg}	N_{total}	C_{org}	C:N	Δz	FI
C_{inorg} (g kg^{-1})		**0.36**	**0.36**	0.20	−0.20	−0.10
N_{total} (g kg^{-1})	**0.36**		**0.73**	−0.20	−0.09	0.10
C_{org} (g kg^{-1})	**0.36**	**0.73**		**0.42**	−0.23	**−0.33**
C:N	0.20	−0.20	**0.42**		−0.25	**−0.66**
Δz (cm)	−0.20	−0.09	−0.23	−0.25		0.39
FI	−0.10	0.10	**−0.33**	**−0.66**	0.39	

Statistical analyses

In order to explain the effects of a lupine cover on sedimentation and soil fertility, we tested for differences in Δz, FI, C_{inorg}, C_{org}, N_{total}, and C:N across paired plots with and without lupine, using Wilcoxon's matched paired tests. Where differences were marginally or not significant we also evaluated the correlations between C_{org}, and N_{total}, C:N ratio for data pooled across all sites. Co-variation across variables was evaluated using Pearson product-moment correlation. All statistical analysis was conducted with Statistica 6.0, Statsoft Inc.

Results

The comparison of lupine cover on eight different bars showed no startling differences between 2007 and 2010. On the other hand, it was easy to notice on the images that plant density was noticeably higher in 2010, even though both sets of photographs were taken approximately around the same date (late February, end of summer), in two years with similarly wet spring and summer seasons. The photographs for 2010 suggest a higher density of lupine, and the colonized bars seem to be more stable than those without vegetation.

Analysis of plot pairs showed that fine sediment depth Δz and index of fines FI were significantly greater for sites with lupine (Wilcoxon Matched Pairs, $n = 30$, $p < 0.001$). Soil thickness ranged from 7 to 72 cm at locations with lupine cover (mean 27.6 cm $\pm$ s.d. 18.6 cm). Values were notoriously lower at locations without lupine, ranging from 0 to 33 cm (9.0 $\pm$ 11.2 cm). Similarly, the fineness index FI was higher at locations with lupine plants, ranging from 17.7 to 80.1% (59.3 $\pm$ 16.6%), while for locations without lupine, it ranged from 0 to 41.6% (12.5 $\pm$ 14.4%).

Total nitrogen content (Fig. 2) was similar between lupine stands (0.44 g kg^{-1} $\pm$ 0.34 s.d.) and plots without lupine (0.40 g kg^{-1} $\pm$ 0.16 s.d.), and the differences were not significant for paired plots (Wilcoxon matched pairs, $n = 18$, $p = 0.98$) or pooled plots (Mann Whitney U-test, $p = 0.97$). Soil carbonates were slightly higher for lupine stands (19.8 $\pm$ 10.3 g kg^{-1}) compared to plots without lupine (13.9 $\pm$ 16.5 g kg^{-1}), not quite significant for plot pairs ($p = 0.10$) but significantly higher for pooled plot data ($p = 0.04$). Organic carbon content was significantly higher for lupine stands (9.7 $\pm$ 7.2 g kg^{-1}) than plots without lupine (2.5 $\pm$ 2.3 g kg^{-1}) based on analysis of both plot pairs ($p = 0.002$) and pooled data ($p < 0.001$). C:N ratio of sediment organic matter was also significantly higher in lupine stands (24.9 $\pm$ 7.1) compared to bare plots (7.8 $\pm$ 7.3) for both the plot pairs and pooled data ($p < 0.001$).

Pearson correlation coefficients between all possible pairs of variables (Table 1) show significant correlations between FI and the depth of fines, organic carbon, and C:N ratio, with the latter showing the strongest, negative relation (a high index of fines corresponded with lower organic matter quality, $r = -0.66$). A second cluster of correlations occurred between soil carbonates, total nitrogen, and organic carbon, with the nitrogen and carbon showing the strongest positive relation ($r = 0.73$).

Discussion

Lupine stands along the Paloma river correspond with a thicker layer of finer superficial sediment. Its perennial habit, thick foliage and dense cover makes it very efficient at trapping fine sediment during flood events; this increased vertical accretion is probably a direct effect of dense lupine stands on gravel bar roughness. Similar results have been previously found by Piégay (1995), Elliott (2000), and Corenblit et al. (2009) for herbaceous vegetation on bars within the active channel.

Davies-Colley (1997) describes how pioneering herbaceous vegetation colonizes and stabilizes gravel bars, narrowing the channel because of the increased cohesion from roots (Simon and Collison 2002; Wynn et al. 2004) and the higher shear resistance along banks (Micheli and Kirchner 2002). Wilson et al. (2003) conclude that herbaceous species with leaves, such as *Lupinus*, create a large drag, slowing flow velocities. The presence of leaves decreases turbulent mixing, resulting in a slow moving layer of water through the vegetation, fostering fine sediment deposition. We suspect that invasive woody plants may also be producing the same effects in Patagonian rivers. Most likely, the effects of lupine, willow and other invasive riparian species will be relatively more severe in Patagonia because of the resulting high plant densities, as compared to the typically barren parafluvial zones of un-invaded river systems.

Invasive plants do not only alter nutrient availability (Ehrenfeld 2003), but may also exploit novel or otherwise poorly understood mechanisms of nutrient acquisition and soil nutrient cycling (Weidenhamer and Callaway 2010). In the case of non-native nitrogen fixers, various authors have demonstrated clear effects on soil nutrient status. For example, Pickart et al. (1998) documented fertilization effects of an invasive lupine in similarly barren dune soils in California (USA); *Myrica faya* was responsible for fixing large amounts of nitrogen in recent volcanic soils in Hawaii, where no N-fixing plants were present pre-invasion (Vitousek and Walker 1989). Invasion of riparian nitrogen fixers may even affect water chemistry, biogeochemical cycling and ecosystem efficiency in streams (Mineau et al. 2011, 2012).

In contrast to our prospects, though, lupine stands on Rio Paloma do not appear to have higher soil nitrogen content, as expected from previous work on other invasive nitrogen fixing plants. Nevertheless, lupine were associated with a different soil quality, including significantly higher organic carbon and C:N ratios, and somewhat higher inorganic carbon (the difference was not quite significant among paired plots, but was significant for data pooled across all sites). This suggests a strong initial effect on riparian soils via litter fall, followed by decomposition and carbon mineralization. Lupine may potentially fertilize soils by a pulse of nitrogen, but only the latter effects were evident in this study: N fertilization might still be observed through higher frequency sampling, along a time series, or with isotopic tracers, or else, more time may be necessary for observable changes in soil fertility to occur (our stands were a dominant feature on the Paloma since at least 2007, but the previous dynamics of lupine stands are unknown). Alternatively, higher organic carbon content on gravel bars covered with lupine may be a result of increased trapping of fine sediment and suspended organic matter during spates. However the correlations among sediment variables (Table 1), together with the observations on soil nutrient status do not correspond with previous results from alluvial gravel deposits (Meier, 2008), showing a strong correlation between finer particle sizes and higher nutrient availability. The moderate negative correlation between FI and organic carbon and the more strongly negative correlation with C:N ratio implies that the loading of particulate organic matter from the river is low (this could be easily verified using grab samples, and is expected due to the strong contribution of lakes in the catchment, see Fig. 1), and soil organic matter simply becomes diluted by the
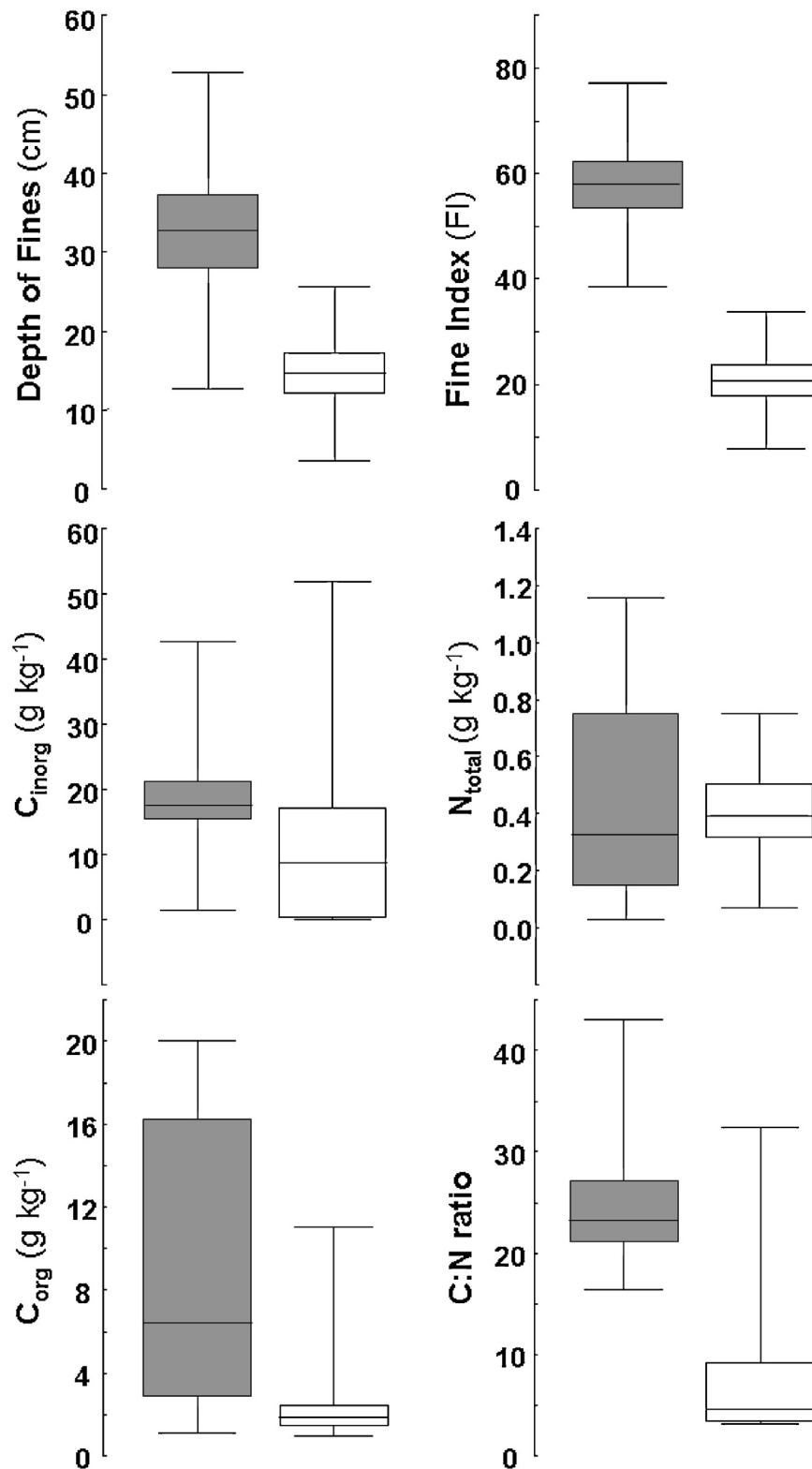
Fig. 2. Box plots of environmental variables, showing mean, se and s.d. (sediment variables) and median, 75% and range (soil nutrient data). In each case, the left (shaded) plot is that for lupine, whilst the right corresponds to the case without lupine.

deposition of fine riverine mineral sediments. The strong correlation between total nitrogen and organic carbon is probably an indication of a single organic matter end member, most likely originating from the nearly monospecific lupine stands (either through litter fall, root material or exudates). More interesting is the correlation between soil carbonates and carbon and nitrogen content. This observation corresponds with the possibility, mentioned below, that the carbonates are biogenic in origin, resulting from mineralization of organic matter, most likely originating from lupine. These speculations could be further evaluated using stable isotope tracers, the end member for biogenic carbon being particularly distinct.

Two invasion trends are evidently emerging within Patagonian riparian zones. The first is the dominance of woody invasive plants such as willow, where early colonizing woody plants do not exist (there are no native *Populus* sp. or *Alnus* sp. in the region). Introduced species of willow (*Salix* spp.) occupy river corridors well south of the range of the native South American willow *S. humboldtiana* (Hauenstein et al., 2005) in both Chile and Argentina, including a genotype of the *S. alba–S. fragilis* complex forming immense clonal stands, dominating nearly 800 km of a river corridor in the Argentine pampas (Budde et al., 2011). Saltcedar (*Tamarix* spp.) and autumn olive (*Eleagnus angustifolia*) are also introduced invaders in riparian zones in Argentinean Patagonia (Natale et al., 2008; Klich, 2000).

The second trend is the invasion of perennial herbaceous taxa, such as the lupine reported herein. Herbaceous invaders could be expected a priori to affect fluvial geomorphological processes less than woody vegetation, but as we observed in this study their effects on bar accretion and sediment profiles may be significant, in addition to potential consequences on soil fertility and pedogenesis (the latter because of nitrogen fixation). These effects might be particularly significant in the Southern Hemisphere, in land masses that have very limited atmospheric nitrogen deposition and streams with unusually low inorganic nitrogen concentrations (Perakis and Hedin, 2002; Reay et al., 2008). Invasion of an N-fixing plant may therefore be particularly significant in areas where such functional traits did not previously exist. In Southern Patagonia the only significant N-fixing plant in riparian zones, *Gunnera* sp. is infrequent, limited to wetter streamsides and backwaters. Interestingly *Gunnera* is considered invasive in the Northern Hemisphere, the symbiosis with the cyanobacteria *Nostoc* being a mechanism unique to its native southern range (Osborne et al., 1991). Both of these invasion trends could be characterized as the filling of vacant niches (*sensu* Elton, 1958) in Patagonian river corridors: the lack of rapidly colonizing woody plants and the scarcity of nitrogen fixing species, respectively.

Although the soil fertilization effects of the lupine invasion were not as we hypothesized, we believe that there are no native herbaceous species competing for the niche that *L. polyphyllus* is currently exploiting, as suggested by the aggressive coverage of large tracts of the active channel in less than 20 years since its introduction to the valley. As a consequence of this invasion, we saw clear differences in sediment structure and quality: sites invaded with lupine had a thicker layer of finer sediments, higher organic matter concentrations, with lower quality (lower C:N ratios), and possibly higher rates of carbon mineralization (inorganic carbon), the latter suggesting higher soil respiration rates. Taken together, the effects on sediment dynamics and soil development may ultimately drive a series of ecological and morphological changes in the fluvial corridor, e.g. sending succession into new, different trajectories, narrowing and deepening river channels, decreasing braiding, increasing nutrient availability, etc. It remains to be seen whether this trend will result in altered or faster vegetation succession on gravel bars, or these will remain in a stable state dominated by lupine. Unfortunately, the characterization of successional chronosequences in Patagonian rivers is a topic that remains largely unstudied, thus limiting our ability to generalize the potential impacts of lupine or other invasive plants in riparian zones.

We concur with Budde et al. (2011), who commented on the vulnerability of rivers to woody plant invasions in the treeless Patagonian steppe: the relatively bare gravel bars of Patagonian rivers may be particularly vulnerable to plant invasions. Alternatively, Patagonian ecosystems may not be more susceptible to invaders (the converse of the idea that certain regions are more prone to supply them, an idea debunked by Jeschke and Strayer, 2005). The region may simply be on the rising limb of intercontinental invasion, following the same trajectories already played out, first in North America and then in Europe.

Acknowledgements

References

Adair, E.C., Binkley, D., 2002. Co-limitation of first year Fremont cottonwood seedlings by nitrogen and water. Wetlands 22, 425–429.

Bennett, S.J., Simon, A., 2004. Riparian Vegetation and Fluvial Geomorphology, Water Science and Application Series, vol. 8. American Geophysical Union, Washington, DC.

Braatne, J.H., Rood, S.B., Heilman, P.E., 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. In: Stettler, R.F., Bradshaw, H.D., Heilman, P.E., Hinckley, T.M. (Eds.), Biology of Populus and its Implications for Management and Conservation. NRC Research Press/National Research Council of Canada, Ottawa, pp. 57–85.

Budde, K.B., Gallo, L., Marchelli, P., Mosner, E., Leipelt, S., Ziegenhagen, B., Leyer, I., 2011. Wide spread invasion without sexual reproduction? A case study on European willows in Patagonia, Argentina. Biol. Invasions 13, 45–54.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.

Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M., 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. Earth Sci. Rev. 84, 56–86.

Corenblit, D., Steiger, J., Gurnell, A.M., Tabacchi, E., Roques, L., 2009. Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. Earth Surf. Proc. Land. 34, 1790–1810.

Cowles, H.C., 1911. The causes of vegetational cycles. Ann. Assoc. Am. Geographers 1, 3–20.

Davies-Colley, R., 1997. Stream channels are narrower in pasture than in forest. N.Z. J. Mar. Fresh. 31, 99–608.

Décamps, H., 1996. The renewal of floodplain forests along rivers: a landscape perspective. Verh. Int. Verein. Limnol. 26, 35–59.

Décamps, H., 2005. The 'why?' and the 'so what?' of riverine landscapes. In: Wiens, J.A., Moss, M.R. (Eds.), Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge, pp. 248–256.

Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503–523.

Elliott, A.H., 2000. Settling of fine sediment in a channel with emergent vegetation. J. Hydraul. Eng. ASCE 126 (8), 570–577.

Elton, C.C., 1958. The Ecology of Invasions by Animals and Plants. Methuen and Co. Ltd., London.

Fernández, N., 2007. Plantas Exóticas Invasoras de los Parques Nacionales de Patagonia. In: Delegación Regional Patagonia (APN), Universidad Nacional del Comahue (UNC), Buenos Aires, Neuquén, Argentina.

Francis, R.A., 2006. Allogenic and autogenic influences upon riparian vegetation dynamics. Area 38, 453–464.

Fremstad, E., 2010. Invasive Alien Species Fact Sheet—Lupinus polyphyllus. Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS. http://www.nobanis.org

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

Gurnell, A.M., Petts, G.E., 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biol. 47, 581–600.

Gurnell, A.M., Bertoldi, W., Corenblit, D., 2012. Changing river channels: the roles of hydrological processes, plants and pioneer fluvial landforms in humid, temperate, mixed load, gravel bed rivers. Earth Sci. Rev. 111, 129–141.

Harris, D., Horwath, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. Soil Sci. Soc. Am. J. 65, 1853–1856.

Hauenstein, E., Peña-Cortés, F., González, M., Schlatter, R., 2005. New distribution range limits of Salix humboldtiana Willd., Salicaceae, in Chile. Gayana Bot. 62 (1), 44–46.

Hickin, E.J., 1984. Vegetation and river channel dynamics. Can. Geogr. – Geogr. Can. 28 (2), 111–126.

Jeschke, J.M., Strayer, D.L., 2005. Invasion success of vertebrates in Europe and North America. Proc. Natl. Acad. Sci. USA 102, 7198–7202.

Karrenberg, S., Edwards, P.J., Kollmann, J., 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biol. 47, 733–748.

Kirkby, M., 1995. Modelling the links between vegetation and landforms. Geomorphology 13, 319–335.

Klich, M., 2000. Leaf variations in *Eleagnus angustifolia* related to environmental heterogeneity. Environ. Exp. Bot. 44, 171–183.

Malanson, G.P., 1993. Riparian Landscapes. Cambridge University Press, Cambridge.

Meier, C.I., 2008. Cottonwood establishment in a gravel-bed river. The University of Montana, Missoula, Montana (Ph.D. dissertation).

Micheli, E.R., Kirchner, J.W., 2002. Effects of west meadow riparian vegetation on streambank erosion. 2. Measurements of vegetated bank strength and consequences for failure mechanics. Earth Surf. Proc. Land. 27, 687–697.

Mineau, M.M., Baxter, C.V., Marcarelli, A.M., 2011. A non-native riparian tree (*Elaeagnus angustifolia*) changes nutrient dynamics in streams. Ecosystems 14, 353–365.

Mineau, M.M., Baxter, C.V., Marcarelli, A.M., Minshall, G.W., 2012. Invasive riparian tree reduces stream ecosystem efficiency via a recalcitrant organic matter subsidy. Ecology 93, 1501–1508.

Morris, M.R., Stanford, J.A., 2011. Floodplain succession and soil nitrogen accumulation on a salmon river in southwestern Kamchatka. Ecol. Monogr. 81 (1), 43–61.

Naiman, R.J., Décamps, H., 1997. The ecology of interfaces—riparian zones. Annu. Rev. Ecol. Evol. Systematics 28, 621–658.

Natale, E., Gaskin, J., Zalba, S., Ceballos, M., Reinoso, H., 2008. Especies del género *Tamarix* (Tamaricaceae) invadiendo ambientes naturales y seminaturales en Argentina. Bol. Soc. Argent. Bot. 43, 137–145.

Osborne, B., Doris, F., Cullen, A., McDonald, R., Campbell, G., Steer, M., 1991. *Gunnera tinctoria*: an unusual nitrogen-fixing invader. Bioscience 41, 224–234.

Paola, C., 2011. Co-evolution of rivers and plants. Nat. Geosci. 4, 583–584.

Perakis, S., Hedin, L., 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. Nature 415, 416–419.

Pickart, A.J., Miller, L.M., Duebendorfer, T.E., 1998. Yellow bush lupine invasion in Northern California coastal dunes: I. Ecological impacts and manual restoration techniques. Restor. Ecol. 6, 59–68.

Piégay, H., 1995. Dynamique et Gestion de la Forêt Alluviale de Cinq Cours d'Eau à Charge Grossière du Bassin du Rhône: l'Ain, l'Ardèche, le Giffre, l'Ouvèze et l'Ubaye (XIXe-XXe siècles). Sorbonne University IV, Paris (PhD thesis).

Quiroz, C., Pauchard, A., Marticorena, A., Cavieres, L., 2009. Manual de Plantas Invasoras del Centro-Sur de Chile. Laboratorio de Invasiones Biológicas (LIB), Instituto de Ecología y Biodiversidad (IEB), Universidad de Concepción, Concepción, Chile.

Reay, D.S., Dentener, F., Smith, P., Grace, J., Feely, R.A., 2008. Global nitrogen deposition and carbon sinks. Nat. Geosci. 1, 430–437.

Richards, K., Brasington, J., Hughes, F., 2002. Geomorphic dynamics of floodplains: ecological implications and a potential modeling strategy. Freshwater Biol. 47, 559–579.

Rodríguez, R., Marticorena, A., Teneb, E., 2008. Vascular plants of the Baker and Pascua Rivers, Region of Aysén, Chile. Gayana Bot. 65, 39–70.

Schnauder, I., Moggridge, H.L., 2009. Vegetation and hydraulic–morphological interactions at the individual plant, patch and channel scale. Aquat. Sci. 71, 318–330.

Simon, A., Bennett, S.J., Neary, V.S., 2004. Riparian vegetation and fluvial geomorphology: problems and opportunities. In: Bennett, S.J., Simon, A. (Eds.), Riparian Vegetation and Fluvial Geomorphology, Water Science and Application Series No. 8. American Geophysical Union, Washington, DC, pp. 1–10.

Simon, A., Collison, A.J.C., 2002. Quantifying the mechanical and hydrologic effects of riparian vegetation on streambank stability. Earth Surf. Proc. Land. 27, 527–546.

Stanford, J.A., Lorang, M.S., Hauer, F.R., 2005. The shifting habitat mosaic of river ecosystems. Verh. Int. Verein. Limnol. 29, 123–136.

Tabacchi, E., Correll, D.L., Hauer, F.R., Pinay, G., Planty-Tabacchi, A.M., Wissmar, R.C., 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biol. 40, 497–516.

Tal, M., Gran, K., Murray, A.B., Paola, C., Hicks, D.M., 2004. Riparian vegetation as a primary control on channel characteristics in multi-thread rivers. In: Bennett, S.J., Simon, A. (Eds.), Riparian Vegetation and Fluvial Geomorphology, Water Science and Application Series No. 8. American Geophysical Union, Washington, DC, pp. 43–58.

Vitousek, P.M., Walker, L.R., 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecol. Monogr. 59, 247–265.

Weidenhamer, J.D., Callaway, R.M., 2010. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. J. Chem. Ecol. 36, 59–69.

Wilson, C.A.M.E., Stoesser, T., Bates, P.D., Batemann Pinzen, A., 2003. Open channel flow trough different forms of submerged flexible vegetation. J. Hydraul. Eng. ASCE 129 (11), 847–853.

Wynn, T.M., Mostaghimi, S., Burger, J.A., Harpold, A.A., Henderson, M.B., Henry, L., 2004. Variation in root density along stream banks. J. Environ. Qual. 33, 2030–2039.