

RESEARCH ARTICLE

Resilience of an aquatic macrophyte to an anthropogenically induced environmental stressor in a Ramsar wetland of southern Chile

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Abstract In mid-2004, anthropogenically induced changes in water quality of the Río Cruces wetland, a Ramsar site located in southern Chile (ca. 40°S), enhanced the resuspension of iron-enriched sediments, which were subsequently deposited over the most abundant aquatic macrophyte of the wetland (*Egeria densa* Planch. 1849). This event triggered the formation of brownish, necrotic patches and increased iron contents in the leaves and stems of *E. densa*, which contributed to a significant demise of the plant within the wetland. In this study, we estimate the recovery time as a proxy for resilience of this macrophyte at organismal and population levels. Macro- and micro-optical characteristics, as well as iron contents in tissues of *E. densa*, were documented in four time windows (2004, 2008, 2012, and 2014). In addition, the size of the macrophyte population and its spatial occurrence were monitored from 2008 to 2016 across 36 study sites within the wetland. Our results suggest necrotic patches and high iron contents in *E. densa* persisted at least until 2008. After 2013, a significant increase in the spatial occurrence of *E. densa* was observed within the wetland, reaching full recovery of the population during 2015. The health of plant tissues and iron contents in leaves and stems showed recovery period close to 4 years, while the recovery of the spatial occurrence of *E. densa* took approximately 9 years. While the monitoring of plant health was not performed on a strict annual basis, the recovery rates estimated here are slower than those described for other macrophytes. This finding might reflect the long-lasting effects of the disturbance from 2004 and the interaction with biotic processes, such as foraging by waterbirds recolonizing the Río Cruces wetland. These results show that full recovery of *E. densa* was achieved

through a cascade of effects starting with abiotic factors (water quality) and passing through physiological and individual levels, to finally reach the population level. A key aspect of this response is the invasive nature of the macrophyte, which likely contributed to its recovery as a consequence of improved water quality. Less successful macrophyte species in other systems may not reach the specific population recovery, and become subdominant species instead, or even be eradicated from the wetland either as the result of herbivory or due to competition with other macrophytes.

Keywords Environmental changes · Iron loads in plants · Spatial occurrence of aquatic macrophytes · Wetland

INTRODUCTION

Wetland areas around the world have diverse ecosystem functions and services including the maintenance of native biodiversity, playing key roles in local and global biogeochemical processes and water cycles, as well as providing cultural, recreational, and educational services, ensuring water quality and stabilizing coastlines (Dise 2009). Wetlands are also extremely sensitive habitats and thus, prone to be affected by human pressure and disturbances (Zedler and Kercher 2005). These stress factors might be due to changes in land use (e.g., agriculture, forestal and industrial siting, processes, and wastes) implying cascading impacts on the abiotic properties (e.g., sedimentation, nutrient loads, heavy-metal concentration; Jaramillo et al. 2007) and altering the structure and functionality at upper biodiversity levels (e.g., primary producers and their consumers; Lagos et al. 2008).

Different studies promote the use of active and passive restoration strategies to revert such broad impacts on lake

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and wetland ecosystems (e.g., Morrison and Lindell 2011; Holl and Aide 2011; Spears et al. 2016). Active restoration refers to strategies implying management techniques, such as planting seeds or seedlings, sediment dredging, or efforts for the relocation of species. Alternatively, passive restoration relies on the cease of environmental stressors without taking particular actions. Important differences and tradeoffs in the restoration results have been observed when active strategies are applied to restore different ecosystem components, with individual components and ecosystem-level properties exhibiting variable responses (e.g., Stevens et al. 2001; Spears et al. 2016). On the other hand, passive strategies rely on the ability of natural processes and pathways to restore ecosystem services (Timpane-Padgham et al. 2017), which highlights the importance of ecosystem resilience as the process underlying its recovery. The degree of resilience determines whether ecosystems can maintain their structure and functions in the face of natural or anthropogenic disturbances, or be able to return to previously observed system configurations after a particular disturbance event (Holling 1973, 1996; Ives 1995; Neubert and Caswell 1997; Peterson et al. 1998; Walker et al. 2004). In this context, the recovery time of an ecosystem after a particular disturbance event can be used as a proxy for the degree of resilience (Ives 1995; Neubert and Caswell 1997). The recovery period of wetland ecosystem after an anthropogenic disturbance might have different expressions, pathways, and legacies depending on the nature of the affected components (Spears et al. 2016). Successfully identifying species that drive the resilient responses in wetland ecosystems, as well as the temporal scales of these responses, can provide key insights and information to improve the decision-making process by providing a time frame for passive restoration goals (Naeem and Li 1997).

Aquatic macrophytes have been considered to act as ecosystem engineers (Jones et al. 1994). Their presence in wetlands could be linked to the attenuation of available light and water flow, enhancement of sedimentation, oxygenation of the rhizosphere, sequestration of nutrients from the water column, as well as the provision of habitat for zooplankton and fishes (e.g., see Yarrow et al. 2009 and references therein). In addition, macrophytes likely play a key role in determining habitat and food availability for herbivorous water birds in wetland environments (e.g., Corti and Schlatter 2002; Lagos et al. 2008). Thus, direct or indirect anthropogenic impacts affecting macrophytes are expected to induce major transformations of the structure and functions of the wetland ecosystem, requiring a potentially complex recovery. In fact, there are very few studies describing recovery times of macrophytes after the occurrence of natural or anthropogenic disturbances. Those studies showed variable results across ecosystems, ranging from seasonal scales up to 2 years for the recovery of

diversity and abundance patterns (e.g., Weisser et al. 1992; Barrat-Segretain and Amoros 1995; Spears et al. 2016).

In mid-2004, industrial activities of a new wood pulp mill industry located 25 km upstream from the Río Cruces wetland, a Ramsar site in southern Chile, (ca. 40°S, Fig. 1), caused sudden changes in its water quality (UACH 2005; Escaida et al. 2014; Jaramillo et al. 2018). These changes resulted in a dramatic decrease in the population abundance of the aquatic plant *Egeria densa*, which was limited to restricted areas around few tributary rivers of the wetland. Before 2004, this plant was the most common aquatic macrophyte in the wetland (Steubing et al. 1980; San Martín et al. 2000) and the main food for herbivorous water birds, such as the black-necked swan (Corti and Schlatter, 2002; Norambuena and Bozinovic 2009). *E. densa* forms a biological cover filter, demise of which enhanced the suspension of iron-enriched sediments (UACH 2015, 2016) and increased the presence of turbid waters in the wetland. These conditions persisted over the course of several years (see Lagos et al. 2008). In July 2013, a judicial court in Valdivia (southern Chile) confirmed that changes in population abundances of *E. densa* were related to the discharges of waste waters by the pulp mill (see Escaida et al. 2014; Jaramillo et al. 2018 regarding the judicial process).

So far, scientific studies in the Río Cruces wetland mainly focused on the changes in water quality and the assemblage of herbivorous water birds following the anthropogenic impacts (e.g., Lagos et al. 2008; Gonzalez and Fariña 2013). Analyses of the long-term responses of more complex ecological processes, such as the recovery periods of macrophytes in the wetland have not been done so far. Previous studies in this wetland showed no evidence of macrophyte recovery for almost four years after the disturbance (Lagos et al. 2008), suggesting low resilience for this plant compared with other macrophytes (Weisser et al. 1992; Barrat-Segretain and Amoros 1995; Spears et al. 2016).

In this study, we integrate available data of the external conditions (micromorphology) and iron contents of plants, with a long-term monitoring of the population levels of *E. densa* following the anthropogenically induced environmental changes in 2004. The focus of this study on the external conditions and iron contents of plants is based on the trophic relations between *E. densa* and black-necked swans, which were affected during 2014 due to high iron contents in their livers (Jaramillo et al. 2018). We describe the state of the formerly widespread *E. densa* in the wetland, 12 years after the anthropogenically induced environmental changes from 2004. Furthermore, we provide a systematic estimation of the recovery time (as a proxy for resilience) of: (i) the external conditions observed in plants collected from 2014 onward, and (ii) the temporal variability in the spatial distribution of *E. densa* within the wetland since 2004 till 2016.

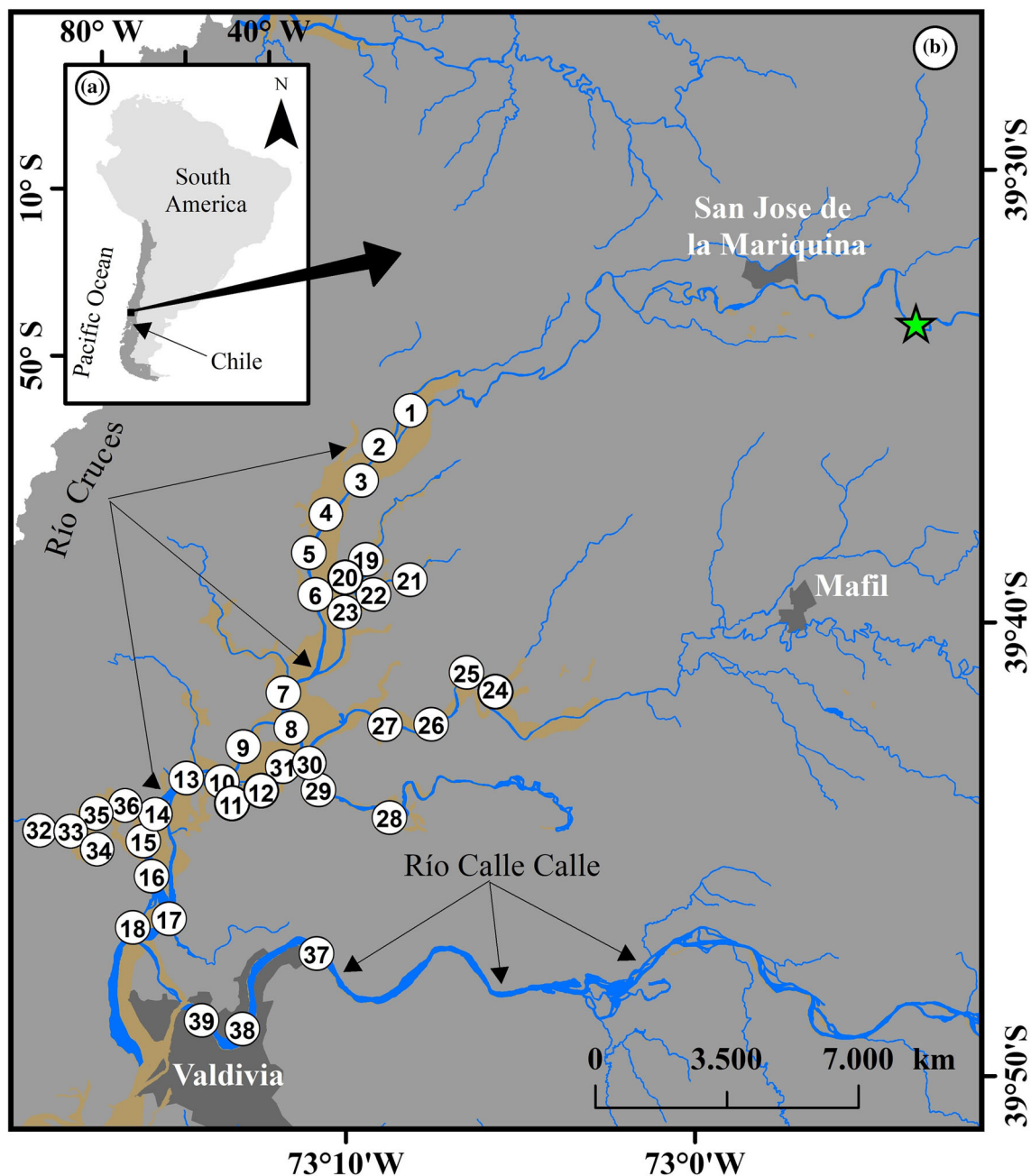


Fig. 1 **a** Location of the Río Cruces wetland in southern Chile. **b** The central area of the wetland, its tributary rivers, and location of sampled sites (1–36) to evaluate the spatial occurrence of *E. densa* during the period 2008–2016. Sampled sites 37–39 were located at Río Calle Calle and were considered as reference sites (see “Materials and Methods”). Light brown corresponds to shallow water areas originated during the earthquake of 1960. The approximate location of the pulp mill is indicated by the green star

MATERIALS AND METHODS

Study area

The Río Cruces wetland is an estuarine ecosystem located north of the city of Valdivia in southern Chile (40°S) (Fig. 1a). The tidal range within the wetland is ~ 50 cm (UCh 2015). The wetland is composed by a main central

area occupied by the rivers Río Cruces and Chorocamayo and seven tributary rivers (Fig. 1). Since June 1981, the central area of the wetland is declared a nature sanctuary and a Ramsar site (see www.ramsar.org). The Río Cruces wetland and its shallow depths originated in May 1960 due to tectonic subsidence (ca. 2.7 m) caused by the Mw 9.5 Valdivia earthquake (Plafker and Savage 1970; Cisternas et al. 2005).

Temporal variation of external conditions and iron contents in *E. densa*

Early observations indicated the occurrence of brown necrotic patches on leaves and stems, as well as high iron contents in tissues of *E. densa* plants collected within the wetland. These characteristics were not observed outside the wetland (Pinochet et al. 2004). Necrotic patches appear to be a typical condition of aquatic macrophytes affected by iron excess (Lucassen et al. 2000). We therefore analyzed the external appearance and iron contents in plants and established two categories: (1) discolored plants with dark brownish necrotic areas and crusts of diatom frustules and sediments on their leaves and stems, and (2) greenish, clean plants without necrotic spots and crusts. Leaves and stems of plants were cleaned with distilled water, mounted on carbon object holders, and analyzed in a Zeiss Leo 420 scanning electron microscope (SEM) to get detailed images of their external appearance. The energy used for image acquisition was set to a 15 keV tension. The iron content of another set of samples was analyzed with an ICP-MS 2502 PT05-IT08. A two-way ANOVA (factors: areas within and outside the wetland and years 2004, 2008, 2012, 2014) and Tukey as a posteriori test were used to identify which area or year show significant differences in iron concentrations. Prior to the analyses, data were $\log_{10}(x + 1)$ transformed to meet ANOVA assumptions.

Plant samples were collected from randomly selected sites located within the wetland during the austral summer (February–March) of the years 2004, 2008, 2012, and 2014. These months were selected for sampling, because of the low water levels, and therefore easier identification of submerged plants such as *E. densa*. Plants along Río Calle Calle which is located nearly four kilometers outside the wetland (Fig. 1b) were also collected for comparative analyses (see Table S1 for location of sampling sites).

Temporal variation in spatial occurrence of *E. densa*

A monitoring program of the spatial occurrence of *E. densa* was launched in 2008, when the first evidences of isolated patches of plants recolonizing the wetland were observed. Thirty-six sites were annually sampled in late March and early April between 2008 and 2016 to analyze the annual variability in spatial occurrence of this macrophyte (Fig. 1b; Table S1). We also visited three sites along Río Calle Calle (37–39; Fig. 1b; Table S1). Those sites were used for reference because the spatial occurrence of *E. densa* has remained stable along this river since 2004 (Jaramillo et al. 2007). That is probably due to the fact that wetland waters moving downstream to the sea during low tides never reach those sites. The spatial occurrence of the macrophyte was measured as the percent of sites with

presence of plants from the total number of sites monitored.

The spatial dynamics of *E. densa* (presence–absence data) within the wetland and reference sites were evaluated by fitting a logistic regression model to account for the occurrence in percentage as a function of time. This was done by fitting a generalized linear model with a binomial error distribution and a logit link (Crawley 2012). In this analysis, the response variable was the proportion of occupied sites, while time was the independent variable, measured in years. We also fitted a linear regression model using the stats library in the R program (R Development Core Team 2014). Both the logistic and linear regression models were ranked according to their Bayesian information criterion (BIC or Schwarz criterion; Schwarz 1978). Once fitted, the model with the minimum BIC was selected (i.e., low BIC values are indicative of better model; Schwarz 1978). Pairwise Tukey comparisons between sampling years were carried out with the R package multcomp and using a two-sided alternative hypothesis (Hothorn et al. 2008; Bretz et al. 2011).

RESULTS

The macro- and microscopic external conditions of the leaves and stems of *Egeria densa* within the Río Cruces wetland showed dramatic temporal changes, as compared with plants from reference sites along Río Calle Calle (Fig. S1). The 2004 and 2008 optical microscope images of *E. densa* plant remnants from the wetland indicated brown necrotic patches—a condition that was not observed in samples from Río Calle Calle (Fig. S1a and S1b). Moreover, SEM images of wetland plants collected in 2004 and 2008 revealed a crust of diatom frustules (periphyton) and sediments attached to the external surface of their leaves and stems (Fig. S1c), while outside the wetland the plant surfaces were clean (Fig. S1d). From 2012 onward, the collected wetland plants are green, and exhibit clean surface areas without any crust material (Fig. S1c and S1d), similar to plants collected in 2012 and 2014 along Río Calle Calle (Fig. S1).

Iron concentration recorded in leaves and stems of *E. densa* also varied significantly between areas (Río Cruces wetland vs. Río Calle Calle) and sampling periods (Fig. 2, Table S2). During the years 2004 and 2008, the iron contents in *E. densa* were significantly higher in plants collected within the wetland compared to those outside the wetland ($p < 0.001$). In 2012 and 2014, the iron contents in wetland plants decreased and returned to similar levels in both areas ($p > 0.05$) (Fig. 2, Table S2). Since 2012, the iron contents of leaves and stems and the external appearances of *E. densa* were similar for plants collected

within and outside the wetland (Fig. 2, Table S2). Together, these results indicate that at the organismal level, the health recovery of *E. densa*, as evidenced by the macro- and microscopically assessed external patterns, as well as iron contents, was close to 4 years.

At the population level, the spatial occurrence of *E. densa* showed contrasting temporal patterns when comparing sites within and outside the wetland (Fig. 3). Sampling sites at Río Calle Calle indicate constant spatial occurrence of *E. densa* for the period from 2008 to 2016 (Fig. 3).

The contrasting spatial occurrence of *E. densa* within the wetland observed shortly after the environmental changes in 2004 vs. 2016 is displayed in Fig. S2. While vast areas of the wetland lacked the cover of *E. densa* during the spring of 2004, during the summer of 2016 and in the present, those areas are almost fully covered. The increase in spatial occurrence of *E. densa* in the Río Cruces wetland presents a sigmoidal pattern ($\beta = 0.8937$, SE $\beta = 0.1158$, $p = 1.20e-14$, BIC = 185.2057) (Fig. 3). While the linear regression model may also describe this gradual increment in spatial occurrence within the wetland ($\beta_1 = 0.13081$, SE $\beta_1 = 0.00871$, $p < 2e-16 < 2e-16$, BIC = 189.456), the logistic model is favored due to its lower BIC value. Pairwise comparisons among years revealed that the spatial occurrence of *E. densa* observed in 2012 became significantly higher compared to that in 2008 (see Table S3). By 2015, *E. densa* appeared to have reached 100% coverage inside the wetland, and therefore 100% of its original spatial occurrence (Fig. 3, see Table S3). Thus, at the population level, *E. densa* needed approximately 9 years of recovery in order to reach the spatial occurrence observed across the wetland prior to

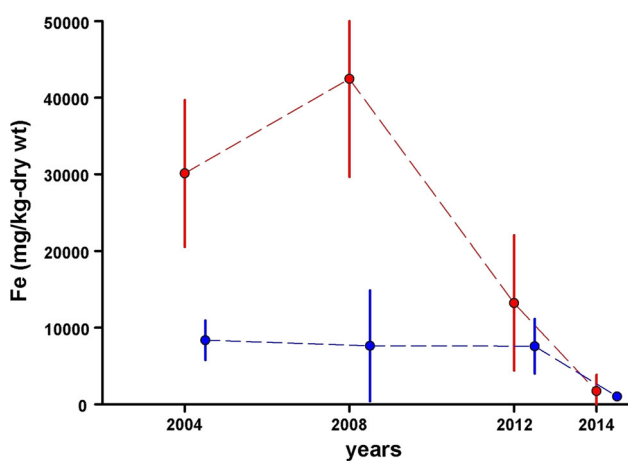


Fig. 2 Iron contents in plants of *E. densa* (mg kg⁻¹-dry wt). The figure shows mean values $\pm 1\sigma$ (standard deviation). Plants were collected within the Río Cruces wetland (red dots and red dashed lines) and outside that area (blue dots and blue dashed lines; Río Calle Calle) (cf. Table S1)

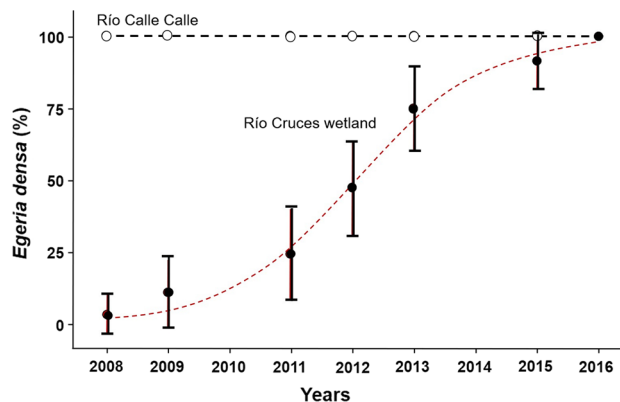


Fig. 3 Temporal dynamics of the spatial occurrence of *E. densa* (mean %-values) within the Río Cruces wetland (filled circles) and outside that area (Río Calle Calle, open circles). Error bars show 95% confidence intervals for the wetland data. The occurrence of *E. densa* in Río Calle Calle remained constant across all sites and sampling years (100%), and thus, confidence intervals for this area are not shown. The dashed red line shows the logistic regression function fitted to data from the Río Cruces wetland. The dashed blue line shows the lowest regression fitted to data from Río Calle Calle

2004 when its distribution spanned all the wetland area (San Martín et al. 2000).

DISCUSSION

Resilience should be measured relative to a specific system attribute and scale, as well as relative to a specific disturbance (whether natural or artificial) or management action (Carpenter et al. 2001). Evaluating the resilience of a system might either focus on measuring its ability to withstand perturbations by remaining in one of multiple alternate stable states, or by estimating its efficiency to return to the original state of equilibrium following a disturbance event (Gunderson 2000; Walker et al. 2004). The present study is based on the second approach estimating recovery times (as a proxy for resilience) after a particular disturbance event (Ives 1995; Neubert and Caswell 1997).

Our results suggest the necrotic brownish patches on leaves and stems in *E. densa* were indicators of conditions induced by the anthropogenic impact of the pulp mill located upstream the wetland (Jaramillo et al. 2007; Escada et al. 2014). These pathological macroscopic characteristics as well as high iron contents persisted at least until 2008. After that year, the improvement in the macroscopic characteristics and reduction in iron content were concomitant with a significant increase in spatial occurrence of *E. densa* within the wetland, reaching 100% of plant coverage during the period of 2015–2016. Thus, the recovery time for the studied indicators was variable and dependent on the measured attribute. At the organismal

level, the macro and micro-optical assessment of plant health as well as iron contents indicates recovery times of nearly 4 years (2004–2008). On the other hand, the recovery time at the population level was close to 9 years (2004–2013).

The first restoration process observed in *E. densa* was the absence of brown and necrotic patches and periphyton on the leaves and stem surfaces 4 years after the disturbance. The presence of these crust of periphyton was considered detrimental to the macrophytes, as it reduces the amount of photosynthetically available radiation (PAR) reaching the plant surface (e.g., Jaramillo et al. 2007). In addition, early studies suggested macrophytes, collected within the wetland during 2004 and 2008 and exhibiting these dark brown necrotic patches, might be affected by iron toxicity (e.g., Pinochet et al. 2004; Woelfl et al. 2006). The improvement of macrophyte's health is likely associated with the quality of the waste waters discharged by the pulp mill after a significant improvement of the industrial processes to standards sustained until the present (Escaida et al. 2014). The specific causes for high loads of iron deposited on the wetland plants of *E. densa* during mid-2004 are unclear. Nevertheless, a pulse discharge of industrial waste waters during the autumn of 2004 likely killed most of the plants within the wetland, leaving vast areas of shallow banks devoid of the natural sediment anchor otherwise provided by this macrophyte (Escaida et al. 2014). When water level dropped during the dry season of 2004–2005, tidal currents mobilized the iron-enriched sediments in the estuarine ecosystem. The interaction between flooding and ebbing tides likely enhanced the deposition of sediment particles on the leaves and stems of *E. densa*, leading to a decrease of this macrophyte within the Río Cruces wetland, which lasted at least until 2008 (UACH 2016).

Accordingly, macrophytes studied during the spring of 2004 yielded iron concentrations nearly 17 times higher than those reported for healthy plants of *E. densa* in Brazil (Pinochet et al. 2004; Correa et al. 2003). Woelfl et al. (2006) analyzed wetland plants with total reflection X-ray spectrometry and compared their results with literature data for *E. densa* and similar aquatic macrophytes (*Elodea canadensis*), also confirming particularly high iron concentrations in plants collected at the Río Cruces wetland. Several studies discussing the impact of iron toxicity on aquatic macrophytes suggest that high iron contents promote increased formation of reactive oxygen species. These in turn induce damages to the cellular membranes, proteins, pigments, and nucleic acids through lipid peroxidation and decreasing antioxidants (e.g., Yamagushi 1989; Snowden and Wheeler 1993, 1995; Lucassen et al. 2000; Yarrow et al. 2009), which in turn would result in reduced plant growth or even death. These results are consistent

with the leaf dieback and the formation of necrotic spots on leaves and stems observed in *E. densa* and other macrophytes in the Río Cruces wetland (Pinochet et al. 2004, Jaramillo et al. 2007, Yarrow et al. 2009).

Sustained improvement of the water quality after 2004 and until the present (e.g., Escaida et al. 2014), likely allowed the initiation of restoration at individual and population levels of *E. densa*. These processes are reflected by the reduction of iron contents in leaves and stems of the plant, and by the gradual increase in spatial occurrence of the species across the wetland. Several studies suggest variable rates of recovery of macrophytes at population levels depending on the magnitude and persistence of the disturbances (Weisser et al. 1992; Barrat-Segretain and Amoros 1995, Spears et al. 2016). For instance, macrophytes subjected to experimental disturbances creating denuded patches, showed fast recovery times on a seasonal scale. Notably, the impact of the disturbances varied also according to the phenology of the plants, where macrophytes appear as particularly sensitive (Barrat-Segretain and Amoros 1995). Sudden natural or anthropogenic disturbances that cause the development of periphyton on the leaf surfaces, apparently contribute to a decline of submerged macrophytes requiring 2 years for the recovery of density and diversity (Weisser et al. 1992). Furthermore, the responses of aquatic macrophytes varied significantly under active restoration strategies, including the application of La-bentonite that contributes to general improvement in water quality and restoration of the macrophyte community within 2 years (Spears et al. 2016). Our results indicate that the recovery periods of *E. densa* macrophytes also vary between studied attributes. Generally, we observe that both individual and population level attributes are characterized by slower rates of recovery, as compared to previous studies. The slow recovery of *E. densa* is particularly interesting, given the well-established high invasiveness of this macrophyte on temperate wetlands and lakes (Wells and Clayton 1991), due its high growth rates under warmer environmental conditions (Tanner et al. 1990). The comparatively slow recovery rates of *E. densa* recorded in this study are of particular interest as they might reflect a spontaneous restoration process occurring under the gradual improvement of water quality in the Río Cruces wetland. The observed recovery process might furthermore constrain the long-term effects of anthropogenically induced environmental changes on propagule availability and growth of macrophytes (e.g., Bakker et al. 2013). Furthermore, species interaction with herbivores could have additionally reduced the recovery rates of *E. densa*. This macrophyte forms the principal food for black-necked swans (*Cygnus melancoryphus*)—large herbivorous water birds that emigrated from the wetland during 2004, when *E. densa* was very scarce or absent from

several areas of the Río Cruces wetland (Lagos et al. 2008). However, as the spatial occurrence of the macrophyte started to recover, the abundance and foraging impact of these water birds also increased and might have impacted the plant population.

The observed response of the ecosystem to the pulse disturbance in water quality demonstrates that full recovery of *E. densa* was achieved through a series of restoration effects starting at the abiotic level (water quality), passing through the physiological and individual levels, to finally affect the population. In turn, the presence of press and ramp disturbances, or generally any repeated disturbance of water quality associated with waste water discharges, might not have allowed the gradual recovery at the physiological and individual levels, forestalling any population recovery in this wetland ecosystem. Notably, the engineering role of invasive species in this ecosystem likely permitted the sound restoration of the population after individuals recovered under improved water quality conditions. Less successful macrophytes in other systems may not exhibit the specific population response, and may well become subdominant species or even be eradicated from the wetland because of herbivory or competitive interactions with other macrophytes.

Thus, we would recommend that future management actions in the wetland should take into consideration the monitoring of the spatio-temporal variability of this particular macrophyte. Our results confirm its resilience as a relevant tool for the passive restoration of wetland ecosystems in temperate regions of southern Chile.

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