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ORIGINAL PAPER

Using assembly rules to measure the resilience of riparian plant communities to beaver invasion in subantarctic forests

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Abstract The present study measures the resilience of riparian herbaceous communities to beaver invasion in subantarctic forests of southern Chile and Argentina. Divergence in community composition and spatial structure was measured comparing beaver-disturbed and undisturbed vegetation assemblages along a sequence of beaver meadow ages; the former by performing a Principal Component Analysis and the later by estimating a co-occurrence index (C-score). Community composition and spatial structure of vegetation showed an increasingly divergent trend from undisturbed sites to older beaver meadows. These results indicated that understory vegetation in deciduous subantarctic forests was not resilient to beaver invasion. Using "assembly rules" as a conceptual framework, we propose a resilience index of host communities to disturbances caused by herbivore invaders that also can be used for subsequent restoration programs to monitor the effectiveness of intervention and mitigation efforts.

Keywords Tierra del Fuego · Ecosystem engineer · Environmental impact · Invasive herbivore · Assembly rules · Temperate forests

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Introduction

The ways in which biological invasions alter community structure is increasingly well understood (Wilkinson 2004; Hobbs et al. 2006; Sax et al. 2007). Invasions and their impacts have important ecological and conservation implications, as they are the source of diverse disturbance regimes that disrupt co-evolved interactions (i.e. as those between specialist predators and prey, or plants and their seed dispersers) thereby changing coexistence patterns and altering ecosystem attributes (Vitousek 1990; Sanders et al. 2003; Dukes and Mooney 2004). To predict if these de novo communities are a transient or persistent response to invasion disturbance, a measure of resilience (i.e. the capacity of a system to absorb changes and recover initial properties after a disturbance pulse, see Holling 1973) for recipient
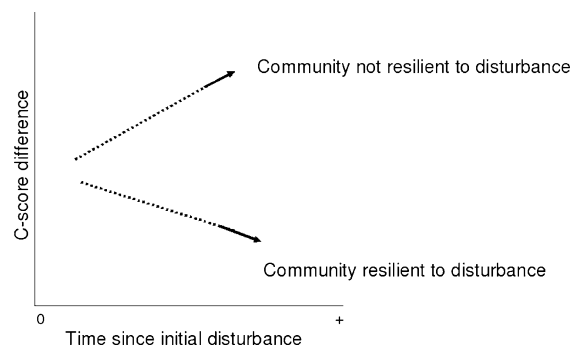
communities is required. Nonetheless such indexes of community resilience are still lacking.

Extensive ecological research on the structure of biotic communities has shown that non-random patterns of species assemblage exist (Weiher and Keddy 1995), and this insight has guided ecologists to search for general principles (i.e. assembly rules) that determine how species come together to form communities. Given a particular pool of species, it is predicted that assembly rules act through resource, environmental, biological and/or spatial dynamics to select subsets of species that can coexist (Keddy 1992; Beleyea and Lancaster 1999). Assembly rules have long been established in the ecological literature (e.g., Keddy 1992; Fox and Brown 1993; Weiher and Keddy 1995; Beleyea and Lancaster 1999; Feeley 2003), and the concept has been used to investigate issues of community invasion susceptibility (Tilman 2004) or to identify potential invader species (Von Holle and Simberloff 2004). However, comparatively little emphasis has been placed on using assembly rules to determine how invader species create novel communities in their alien habitats (Sanders et al. 2003; Holdaway and Sparrow 2006). We propose, in addition, that the conceptual framework provided by assembly rules is particularly useful to develop a quantitative index that estimates the resilience capacity of host communities to invasion disturbance.

Biological communities behave as dynamic systems, which have particular attributes that determine their stability, sensitivity and resilience to disturbance regimes (Holling 1973; Reeves and Fraser 2009) and thus establish their identity and persistence in time and space. As dynamic systems, they exist and display specific patterns resulting from their underlying assembly rules. Community patterns, such as species co-occurrence, are easily measured and represent the visible outcome of the operation of invisible assembly rules. Consequently, co-occurrence patterns may be useful to inform the relative importance of biotic interactions in structuring an assemblage, including demonstrating how a competitively dominant invasive species can disassemble a host community (Sanders et al. 2003). Community organization can be measured using a C-score index (Stone and Roberts 1990) to detect randomness in co-occurrence patterns (Sanders et al. 2003). Here, this index was used to test the resilience of herbaceous communities to the disturbance caused by an invasive

herbivore. Specifically, we propose that this resilience index can be measured from the temporal change in differences of C-scores between communities that have suffered a disturbance by invaders versus un-invaded communities. Since differences in co-occurrence patterns indicate a shift in mechanisms that produce community assemblage (i.e. increasing patchiness suggests increasing importance of competitive interactions, see Keddy 1992), we can expect that differences in C-scores between invaded and un-invaded communities will indicate an underlying change in these assembly rules. By extension, if the differences between natural and impacted sites increase with time since disturbance, the probability of recovering to the original community structure decreases. Thus, resilient communities would be expected to display decreasing differences of C-scores compared to un-invaded communities with time after removal of the invasion impacts, and the contrary is expected for non-resilient communities (Fig. 1).

The invasion of the North American beaver (*Castor canadensis*) in the Tierra del Fuego Archipelago of southern Chile and Argentina provides an ideal study system to apply and test the utility of this approach. As ecosystem engineers (Jones et al. 1994, 1997; Wright et al. 2002, 2003; Wright and Jones 2004), introduced beavers are expected to have large

Fig. 1 Biotic community structure is expected to respond to a disturbance event by returning to pre-disturbance conditions (resilient) or not (un-resilient). A quantitative C-score index that measures species co-occurrence patterns can also assess the differences between disturbed and un-disturbed sites, thereby demonstrating the magnitude of change between these site categories. When a community is not resilient to a particular disturbance event, this divergence is hypothesized to increase with time from the impact. However, the exact shape the function (*dotted line*) may vary depending on the particular case

impacts on environmental factors and thus on assembly rules of host communities. Further, the subantarctic forests of the Fuegian Archipelago are relatively simple, making it a manageable task to test the effects of invasion on recipient riparian vegetation communities. Beaver engineering activities structure the vegetation communities in forested ecosystems via herbivory, which increases sunlight incidence by removing overstory trees, and impoundments, which increase soil organic matter and nutrient content (Naiman et al. 1988). Both herbivory and flooding, in turn, reduce or destroy seed and sapling banks of riparian vegetation communities (Naiman et al. 1988).

With the present study, we set out to characterize the re-assembly of herbaceous communities by beavers along a time gradient departing from initial habitat modification stages up to 20 years after pond abandonment and meadow formation. This approach allowed us to test the ability of riparian forest ecosystems to regain their initial structure after beaver removal (i.e. resilience to beaver invasion). Specifically, we evaluated the hypothesis that differences in patterns of species segregation between modified and un-modified riparian forests increase with time after site abandonment by beavers, which would indicate that these communities are not resilient to the environmental regime changes (or disturbances) imposed by beaver impacts. Previous works lead to the expectation that native riparian assemblages in the subantarctic archipelago are vulnerable to being permanently altered due to the invasion of this herbivore, as it appears that the beaver meadows' successional pathway diverges from un-modified riparian vegetation (Anderson et al. 2006a; Martínez Pastur et al. 2006; Lencinas et al. 2008).

Methodology

Study system

The Tierra del Fuego Archipelago, located at the southern tip of South America (approximately 52°5′ to 55°0′S), is home to a mosaic of habitats, including Magellanic steppe, moorland and subantarctic forest ecoregions (Moore 1983; Rozzi et al. 2004). The forests are dominated by three broadleaf species of

Nothofagus. Two of them (*N. pumilio* and *N. antarctica*) are deciduous, and one is evergreen (*N. betuloides*). Furthermore, the riparian forest understory vegetation harbors unique plant species and functional groups, making these riparian ecosystems distinctive habitat units within the subantarctic forested landscape (Lencinas et al. 2008).

Twenty-five mating pairs of beavers were released in the Claro River area of Tierra del Fuego Island in 1946 (Anderson et al. 2009). Current estimates of the beaver population size range between 60,000 and 90,000 individuals (Skewes et al. 2006). The invasion has expanded across the archipelago to occupy multiple islands with the colonization of the Brunswick Peninsula on the Chilean mainland beginning by the 1990s. The near absence of natural predators and the suitable habitat and food resources explain this successful invasion event (Wallem et al. 2007; Anderson et al. 2009). As invasive herbivores in the subantarctic ecoregion, beavers are known to change the riparian vegetation community toward greater understory species richness and biomass (Anderson et al. 2006a; Martínez Pastur et al. 2006). Also, a large number of the plant species found in beaver-modified assemblages do not grow in primary riparian forests, but rather naturally inhabit non-forested, adjacent associated environments such as grasslands, peat bogs or *Nothofagus antarctica* forests (Martínez Pastur et al. 2006).

Field methods

With the aim of characterizing differences in co-occurrence patterns of herbaceous assemblages in habitats with different stages of beaver modification, we used a database that included two separate field surveys conducted from 2002 to 2006 of riparian vegetation communities along four streams, one in Argentina and three in Chile (Table 1). Initial habitat modification stages where characterized by the surveys of three Chilean streams. For each stream a recently disturbed site (i.e. an active beaver pond formed within the past 3 years, given the rotting state of cut stems surrounding the pond) and an un-disturbed site (i.e. mature riparian forest) were surveyed within 1 km distance of each other. Advanced stages of habitat succession after removal of invasion impact where characterized at the Argentine stream, along which a total of five sites were surveyed: one undisturbed and

Table 1 Summary of field methodologies utilized in the present analysis with their respective references

Site category	Field methodology	Location	Reference
Recently modified and un-modified sites, located in Chile	Twelve 1 m² plots randomly placed along transects parallel to pond margin at 5 and 25 m distance	Escondido Lake, Karukinka Natural Park, Tierra del fuego Island, Chile (54°22′S; 68°44′W)	Wallem (2009)
1, 5, 6, 9 and 20 year old beaver meadows, and un-modified sites, located in Argentina	Thirty-two 0.25 m² sub-plots placed within a 8 larger sampling plots	Tierra del Fuego National Park, Tierra del Fuego Island, Argentina (54°50′S; 68°32′W)	Martínez Pastur et al. (2006)

Both surveys were conducted considering two sites categories: beaver disturbed sites along a variable time gradient from 0 to 20 years post-beaver pond abandonment, and mature un-disturbed riparian forests

four beaver disturbed sites that have been abandoned for one, five, six, nine and 20 years. History and age of beaver impacts in the Argentine study area were well known, since the site was within Tierra del Fuego National Park and monitored by the National Parks Administration and the *Centro Austral de Investigaciones Científicas*. Un-disturbed assemblages among streams were shown to be highly homogeneous, therefore, differences observed between disturbed and un-disturbed communities were attributed to beaver engineering impacts.

To quantify community assemblage responses to beaver habitat alteration, the herbaceous layer (<1 m height) was surveyed. Two general methodologies were used: (1) at the Chilean sites, twelve plots of 1 m² were placed along transects parallel to the water body at each surveyed site, and (2) at the Argentinean site, eight plots were randomly located within each surveyed area. Every plot included four subplots of 0.25 m² set 5 m apart from a central point (Table 1).

In the present analysis, the smallest unit of measure at each survey site (1 m² plot and 0.25 m²) was considered as the replicate unit for statistical analyses. Specimens were determined to the genus or species level following Moore (1983) and Correa (1969–1998).

Quantifying species co-occurrence

For each survey site, data were organized into a presence–absence matrix that contained all replicate units. Unique species, defined as those observed in only one plot, were eliminated from the analysis as these do not contribute information on segregation patterns. To compare co-occurrence patterns between un-modified and modified assemblages, separate matrices were created for each site category at each location. Checkerboardness of each occurrence matrix was calculated using the C-score index, a quantitative measure of community organization (Stone and Roberts 1990). C-scores quantify the number of checkerboard units that can be found for each species pair. A checkerboard unit is a 2×2 sub-matrix of the form 01/10 or 10/01. For each species pair, the number of checkerboard units is (R_i–S) (R_j–S), where R_i is the number of occurrences for species I; R_j is the number of occurrences for species j; and S is the number of sample plots in which both species occur. The C-score is the average number of checkerboard units for each unique species pair. Large index values indicate spatial segregation and small values denote spatial aggregation of species.

Data analyses

Given the different field methodologies employed in the accumulation of the dataset (Table 1), subsequent comparisons were performed exclusively within each study location, rather than between locations. We evaluated both composition and spatial structure of herbaceous communities. The distinctiveness of species composition in modified riparian herbaceous communities was compared to un-modified assemblages by Principal Component Analysis (PCA), using abundance matrices. This allowed the characterization of divergence in species assemblage in modified riparian herbaceous communities at different stages of abandonment compared with un-modified assemblages. Only mean values of dissimilarities for each site category with their respective confidence intervals were represented.

To quantify direction of the changes in the spatial organization between modified and un-modified sites along a time gradient, differences of standardized C-scores between site categories were calculated (i.e. each C-score was divided by the largest possible score obtained for a given matrix). Statistical significance of these differences was determined by bootstrap analysis with 1000 repetitions, whereby replication units were randomly assigned to un-modified or modified habitats without replacement (Manly 1997). All analyses were performed using R language for statistical computing (R Development Core Team 2006).

Results

Community composition

A total of 58 plant species were identified during field surveys and used for this analysis (37 dicots, sixteen monocots and five ferns/lower plants). Among these, five exotic taxa (four dicots, one monocot) were identified ("Appendix"). Beavers affected the species richness of this community, but the response over time was not statistically significant (Spearman Rank Correlation = 0.6, $P = 0.08$). However, a general trend was observed; immediately after pond abandonment richness was reduced, but quickly recuperated and ultimately exceeded pre-invasion levels (Table 2).

With regards to taxa identity, though, various species disappeared from beaver-impacted zones. One species to disappear was *Chodonorchis lesonii*, which was consistently absent in all beaver-impacted

sites from the initial invasion (i.e. active beaver ponds and meadows). In later stages of habitat modification by beavers, a total of thirteen species were extirpated, not being found at all in any older meadows. On the other hand, species that appeared principally or only in beaver meadows included various exotics, which were nearly absent from pristine sites ("Appendix").

Species composition of survey plots also showed significant differences between beaver-disturbed and un-disturbed sites for all beaver meadow age classes. A clear trend was detected, as well, with increasing dissimilarity between beaver-impacted and pristine sites over time (Fig. 2a, b). The first component of this gradient (i.e. from negative to positive loadings) responded principally to the presence of the shade intolerant grass *Carex curta* and the shade tolerant fern *Blechnum penna-marina*. The second component (i.e. gradient from negative to positive loadings) was explained by the presence (at the negative end) or absence (at the positive end) of both *B. penna-marina* and *Nothofagus pumilio* seedlings.
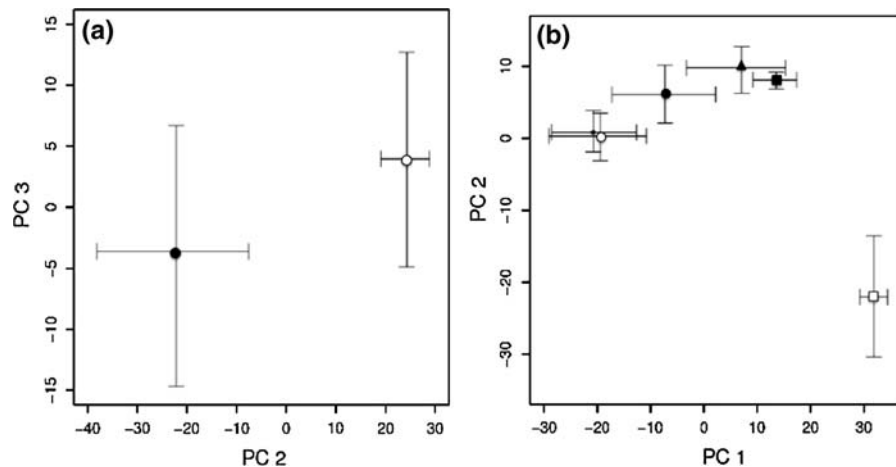
Spatial structure of herbaceous assemblages

Herbaceous assemblages from beaver-disturbed sites presented a distinctive spatial structure compared to un-disturbed forested communities. Understory plant communities in invaded sites had consistently larger C-score than un-disturbed sites, thereby demonstrating that the species segregation pattern was systematically greater in disturbed sites irrespective of the survey plot scale used (Fig. 3). Differences in C-scores between un-disturbed sites and disturbed ones were always positive and had an increasing trend with time after pond abandonment and subsequent meadow formation. Significance of these differences increased at older beaver meadows, indicating an ever larger effect on the change in spatial structure with time elapsed after disturbance.
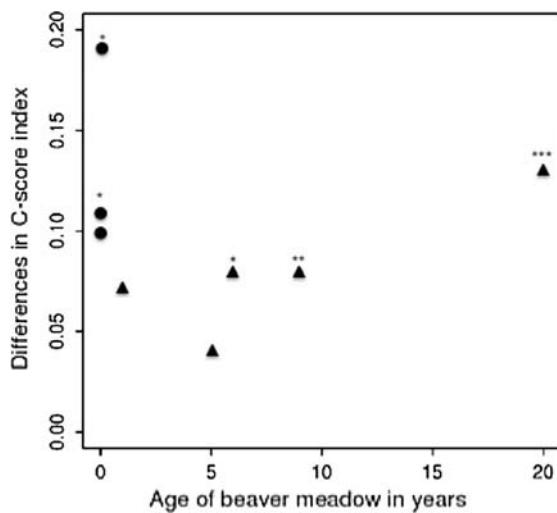
Discussion

Understanding the impacts of biological invasions is an important topic of inquiry for ecologists and conservation managers. However, too often we do not have the long-term data and simple methods that allow us to detect the ultimate consequences of

Table 2 Total number of species that constitute the herbaceous riparian plant community of un-disturbed and beaver-disturbed sites at different stages of meadow succession

Disturbance stage	Total site species richness	Total site exotic species richness
Un-disturbed mature forest	21	1
Active beaver pond	21	1
1 year-old meadow	10	1
5 year-old meadow	26	2
6 year-old meadow	25	4
9 year-old meadow	26	5
20 year-old meadow	24	5

Fig. 2 Mean values of principal component scores (±95% confidence intervals) showed compositional dissimilarities between un-impacted and beaver-impacted riparian forest herbaceous plant communities at all stages of succession: (1) comparison between assemblages from active beaver ponds (*filled circle*) and un-disturbed sites (*open circle*); and (2) comparison between one (*filled square*), five (*filled triangle*), six (*filled circle*), nine (*point*) and twenty (*open circle*) years-old meadows and un-disturbed sites (*open square*)

Fig. 3 Magnitude of the divergence in spatial structure between beaver-impacted and pristine riparian herbaceous communities. Values reflect differences in *C*-score indexes between modified and un-modified communities along an increasing time span since initial disturbance. Circles correspond to recently impacted streams surveyed in Chile (Wallem 2009), while triangles represent sites surveyed in Argentina (Martínez Pastur et al. 2006). Significance is displayed as follows: $P = 0.05*$, $0.01**$ and $0.001***$

introduced species in recipient ecosystems and the resulting novel biotic communities. Previous reports on the impacts of North American beavers in the Fuegian Archipelago have demonstrated the large impacts this invasion is causing to riparian plant assemblages compared to natural conditions (Anderson et al. 2006b; Martínez Pastur et al. 2006), which has led to the question of whether these communities indeed have the capacity to recuperate or instead will attain a new, alternative stable state (Anderson et al. 2009). Here, we used of a quantitative and relatively simple index to assess how invasive beavers reassemble subantarctic riparian plant communities and to evaluate the resilience of these assemblages to this disturbance.

Our results for the trends in *C*-scores conformed with the theoretical expectations (Fig. 1) of an assemblage that was not resilient to beaver invasion. It was apparent instead that the beaver-impacted communities were not only different than undisturbed areas, but became increasingly divergent from natural forest conditions over time. This result held true for both compositional and spatial patterns. Furthermore, the utility of our combined method, which included a novel application of the *C*-score index, proved valuable to answer this type of question, compared to other simple measures such as species richness. In addition to quantifying impacts, this approach allowed us to detect an increasing trend in divergence of these communities over time. It also permitted inferences to be made about underlying mechanisms that explained the ultimate consequences of this invasion on the identity of species in the community.

By changing the assembly rules of these communities over the long-term, beavers essentially were found to affect the capacity of the biota to return to pre-invasion conditions within the time span and under the dynamics that are natural for the regeneration of *Nothofagus* forests.

Studies in South American temperate forests have shown that introduced mammalian herbivores affect understory community structure and composition by directly grazing and trampling and/or by indirectly altering species interactions. However, the question of how these impacts influence forest dynamics and regeneration is still relatively unexplored (Vazquez 2002). On the other hand, browsing by large herbivores can produce important floristic and structural changes in forest ecosystems by shifting the dominance of a tree-species through the alteration of the regeneration dynamics and by influencing plant productivity and species diversity (Cavieres and Fajardo 2005). On Tierra del Fuego Island, native guanaco (*Lama guanicoe*), which are large, generalist herbivores, can impact most of the understory plant species as well as forest regeneration (Pulido et al. 2000). Nevertheless, guanacos prefer open areas, such as moist steppe, alpine vegetation zones and the forest-steppe and forest-peatland ecotones, where they feed mainly on grasses and shrubs (Raedeke 1982; Cavieres and Fajardo 2005). Thus, the types of riparian habitats being occupied by beaver herbivores, as well as their flooding impacts, have no precedent in the archipelago.

We have found that riparian vegetation communities are not resilient to beaver invasion, which is altering long-term forest succession. The cause of this change in successional pathways is likely the destruction of *Nothofagus* seed and sapling banks, and due to the ecophysiological tolerances of these tree species to the impacted soil conditions (Anderson et al. 2006b; Martínez Pastur et al. 2007; Peri et al. 2009). Research also has shown that the natural successional pathway of *Nothofagus* forests is related to site conditions and disturbance regimes at different scales. Some species of the genus *Nothofagus,* such as *N. pumilio,* are medium shade-tolerant (Donoso 1993; Martínez Pastur et al. 2007) and therefore, must pass through gap regeneration cycles (Veblen 1989). Forests located at lower elevations and under milder climate conditions, where shade tolerant rain forest species dominate (e.g., coastal forests of Tierra del Fuego), coarse-scale disturbances may be necessary for *Nothofagus* regeneration (Promis et al. 2008), which is due to the existence of a dense cover of understory species and high richness of other woody vegetation that out-compete the *Nothofagus* saplings. On the other hand, at sub-optimal sites with lower species richness, *Nothofagus* regeneration is not as dependent on coarse-scale disturbance (Pollmann and Veblen 2004). However, previous studies have documented that these forests in general have problems regenerating under systematic disturbances, such as those caused by grazing (Raedake 1980; Pulido et al. 2000; Kitzberger et al. 2005).

In the beaver's native habitat, after ponds drain, plant community succession can follow multiple pathways, influenced by surrounding vegetation, hydrology, geomorphology and herbivory. Generally, former beaver ponds become grass and sedge-dominated meadows (Naiman et al. 1988; Johnston et al. 1995; Terwilliger and Pastor 1999). Compared to un-impacted sites, these meadows have distinct ecosystem processes, due to changes in nutrient cycles, decomposition dynamics, physical structure (i.e. canopy removal, soil erosion or flooding), which result from beaver engineering activities (Naiman and Melillo 1984; Naiman et al. 1988; Johnston et al. 1995; Wright et al. 2002).

As introduced herbivores, beaver modify succession and thereby create a novel herbaceous community (Anderson et al. 2006b; Martínez Pastur et al. 2006). Indeed, at least thirteen forest riparian plant species do not return to the assemblage, even after 20 years of succession. A large number of new plant species settle abandoned ponds, however, and many of them do not grow in the primary forests (Martínez Pastur et al. 2006). In addition, environment modifications provide an advantage for introduced plant species, making it evident that invasive habitat modifiers can facilitate further invasions (Simberloff and Von Holle 1999). The occurrence of introduced species is scarce in the primary *Nothofagus* forests, but they settle abundantly after any impact (e.g., after harvesting, Martínez Pastur et al. 2002). Nevertheless, not only do beaver modify understory richness, but they also significantly change cover, biomass, frequency and abundance within the new communities compared to the original assemblages in old-growth forests (Martínez Pastur et al. 2006).

Considering the importance of fine-scale disturbance for explaining forest structure, we know that these *Nothofagus* forests depend on natural gap formations caused by wind blow downs (Veblen 1989; Promis et al. 2008). Even though beaver disturbance also influences canopy cover in a manner that is similar to natural events, it also concomitantly affects soil properties in a way that is unprecedented for these ecosystems (Anderson et al. 2009). Consequently, we suggest that the seemingly permanent divergence in succession results from the inundation of soils and high sediment accumulation, which destroys the seed and sapling banks of *Nothofagus* that have been shown to be the main source of their regeneration (Cuevas 2002). Therefore, by changing these major environmental filters (e.g., soil properties), beaver influence the assembly rules that determine not only the species composition at a particular time, but also the long-term dynamics of the communities' succession (Beleyea and Lancaster 1999).

Conclusions

The understory plant communities in deciduous, riparian forests of the Fuegian Archipelago were not resilient to beaver invasion. Underlying assembly rules are being affected that alter both the composition and succession of herbaceous communities. These differences between beaver-disturbed and undisturbed assemblages are likely related to changes in soil properties, such as moisture and organic matter content, which are know to be affected by beaver impoundments (Naiman et al. 1988). Invaded sites with these conditions, therefore, harbored vegetation adapted to environmental filters that were not present in undisturbed sites. Community composition changes proved to be long-term and included the facilitation of the invasion by exotic plant species. The index developed to display the spatial structure of the species assemblage demonstrated that these modifications became greater over time, indicating a lack of resilience of these communities to the beaver's invasion. Consequently, current efforts to control and/or eradicate beavers from the subantarctic ecoregion must take into account this lack of resilience on the part of invaded communities. Realistic expectations regarding subsequent restoration of the natural riparian forest ecosystems should keep in mind that these areas may have attained a new alternative stable state, and natural regeneration dynamics may be impossible, thereby requiring active restoration and mitigation programs (Anderson et al. 2009).

Appendix

See Table 3

Table 3 Species list of the riparian herbaceous-layer plants found in mature *Nothofagus pumilio* forests and areas impacted by beavers, indicating in which habitat the taxa were found: *M* meadow, *F* forest

Species	Exotic	Dicotyledoneae	Monocotyledoneae	Lower plants
Acaena magellanica		M–F		
Acaena ovalifolia		M–F		
Acaena tenera		M–F		
Adenocaulon chilense		M–F		
Agrostis uliginosa			M	
Alopecurus pratensis	M		M	

Table 3 continued

Species	Exotic	Dicotyledoneae	Monocotyledoneae	Lower plants
Asplenium dareoides				M–F
Berberis buxifolia		M		
Berberis ilicifolia		M		
Blechnum penna-marina				M–F
Bromus araucana			F	
Cardamine glacialis		M–F		
Carex curta			M–F	
Carex decidua			M	
Carex magellanica			M	
Cerastium fontanum	M	M		
Chiliotrichum diffusum		M		
Codonorchis lessonii			F	
Cystopteris fragilis				F
Deschampsia kingii			M	
Dysopsis glechomoides		M–F		
Epilobium ciliatum		M		
Galium aparine		M		
Gamochaeta spiciformis		M		
Gavilea lutea			F	
Geum magellanicum		M–F		
Gunnera magellanica		M–F		
Liverworts				M–F
Hypochoeris radicata	M	M		
Juncus scheuchzerioides			M	
Lagenifera hariotii		M–F		
Macrachaenium gracile		M		
Marsippospermum grandiflorum			M	
Maytenus disticha		M		
Mosses				M–F
Nothofagus antarctica		M		
Nothofagus betuloides		M		
Nothofagus pumilio		F		
Osmorhiza chilensis		F		
Oxalis magellanica		M		
Pernettya pumila		M		
Phleum alpinum			M	
Phleum pratense	M		M	
Poa pratensis	M–F		M–F	
Ranunculus biternatus		M–F		
Ranunculus hydrophilus		M–F		
Ranunculus maclovianus		M–F		
Ranunculus peduncularis		M–F		
Rubus geoides		M–F		
Sagina procumbens	M	M		
Stellaria media	M–F	M–F		

Table 3 continued

Species	Exotic	Dicotyledoneae	Monocotyledoneae	Lower plants
Taraxacum gilliesii		M		
Taraxacum officinale	M	M		
Trisetum spicatum			M	
Uncinia lechleriana			F	
Veronica serpyllifolia	M	M		
Viola magellanica		M–F		

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