Austral
ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2013) **38**, 436–442

Biotic and abiotic constraints to a plant invasion in vegetation communities of Tierra del Fuego

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Abstract The biotic resistance theory relates invader success to species richness, and predicts that, as species richness increases, invasibility decreases. The relationship between invader success and richness, however, seems to be positive at large scales of analysis, determined by abiotic constraints, and it is to be expected that it is negative at small scales, because of biotic interactions. Moreover, the negative relationship at small scales would be stronger within species of the same functional group, because of having similar resource exploitation mechanisms. We studied the relationship between the cover of a worldwide invader of grasslands, *Hieracium pilosella* L., and species richness, species diversity and the cover of different growth forms at two different levels of analysis in 128 sites during the initial invasion process in the Fuegian steppe, Southern Patagonia, Argentina. At regional level, the invader was positively correlated to total ($r = 0.28$, $P = 0.003$), exotic ($r = 0.273$, $P = 0.004$), and native species richness ($r = 0.210$, $P = 0.026$), and to species diversity ($r = 0.193$, $P = 0.041$). At community level, we found only a weak negative correlation between *H. pilosella* and total richness ($r = -0.426$, $P = 0.079$) and diversity ($r = -0.658$, $P = 0.063$). The relationship between the invader and other species of the same growth form was positive both at regional ($r = 0.484$, $P < 0.001$) and community ($r = 0.593$, $P = 0.012$) levels. Consequently, in the period of establishment and initial expansion of this exotic species, our results support the idea that invader success is related to abiotic factors at large scales of analysis. Also, we observed a possible sign of biotic constraint at community level, although this was not related to the abundance of species of the same growth form.

Key words: biological invasion, functional diversity, growth form, *Hieracium pilosella* L, species diversity, species richness.

INTRODUCTION

Biological invasions are one of the major causes of biodiversity loss (Mack *et al.* 2000; Levine *et al.* 2003). Exotic plants can affect ecosystem structure and functioning through changes in fire regimes, hydrology, soil biota, nutrient cycling, etc. (Callaway *et al.* 2004; Liao *et al.* 2008; Firn & Buckley 2010). Moreover, exotic species can cause severe economic losses (Pimentel *et al.* 2001). Many attempts have been made to determine what factors influence invasion (Lonsdale 1999; Kolar & Lodge 2001), knowledge of which would help to predict invasion events.

Biotic resistance theory relates the invasion resistance of a community to its species richness (Tilman 1997; Thiele *et al.* 2010). This theory is based on the idea that, as the amount of species increases, niches are progressively occupied, reducing the probability of a new species entering. Nevertheless, tests have produced controversial results, attributed in part to the scale dependence of this relationship (Shea & Chesson 2002; Knight & Reich 2005). At large observation scales, the relationship between species richness and invasion success would be positive, determined mainly by extrinsic abiotic constraints (Shea & Chesson 2002; Perelman *et al.* 2007), because, as the environment becomes more stressful, it is less propitious to species, both natives and exotics. At small scales, however, in an area where the environment can be considered relatively homogeneous, the relationship would be negative, because of mechanisms such as competition and resource limitation.

Predictions appear to be confirmed at large scales, but results of studies at small scales are contradictory (Lonsdale 1999; Brown & Peet 2003; Knight & Reich 2005; Perelman *et al.* 2007; Thiele *et al.* 2010). These conflicting results may be because of the fact that

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Accepted for publication June 2012.

doi:10.1111/j.1442-9993.2012.02427.x

species richness would not be a good measure of niche occupation because of an overlapping of functional traits (Drenovsky & James 2010). Instead of species richness, a better predictor of biotic resistance would be the functional diversity or functional richness of a community (Díaz & Cabido 2001). Competition, and biological resistance, will be stronger among species belonging to the same functional group, because of their similar nutrient exploitation mechanisms and strategies (Fargione *et al.* 2003). Hence, in addition to the spatial scale or level of analysis, the degree of biological similarity among plant species may matter (Perelman *et al.* 2007).

Studying invasion ecology is relevant to ecological theory, because invasion events can be considered large-scale natural experiments (Higgins & Richardson 1996) that can elucidate mechanisms and processes related to vegetation changes across time. Furthermore, characterizing patterns at different analysis levels (or scales) in an invasion at early stages would enable a comprehensive understanding of processes involved in invasion events and vegetation changes.

Our aim was to study the constraints to *Hieracium pilosella* L. invasion in Tierra del Fuego plant communities. For this, we evaluated correlations between the invader cover and richness, diversity and growth form cover of resident plant communities at an early stage of the invasion process. We worked at two levels closely related to two spatial scales, region (large scale) and vegetation community (small scale), and considered the growth form classification as a functional classification (Cornelissen *et al.* 2003). Our hypotheses were that (i) *H. pilosella* cover is positively correlated to species richness and diversity at the regional level, but negatively correlated to them at the community level; and that (ii) the negative correlation at community level is stronger when the relationship between *H. pilosella* cover and the cover of plant species belonging to the same growth form (i.e. forbs) is evaluated.

METHODS

Study site

The Fuegian steppe is the southern portion of the Magellanic steppe, a humid variant of the Patagonian semi-desert (Collantes *et al.* 2009), that covers around 5000 km^2 in the north of the Argentinean side of the Tierra del Fuego Island. The area presents a climatic gradient, with precipitation increasing (300–450 mm) and temperature decreasing in a northeast–southwest direction. The area has been grazed by sheep for more than 100 years (Anchorena *et al.* 2001).

At the regional level, upland vegetation is controlled by climate and lithology (Collantes *et al.* 1999). Tussock grasslands of *Festuca gracillima* Hooker f. dominate the area. Towards the south, soils increase their acidity, because of higher leaching and lower temperature, promoting the acidic variants of the steppe, characterized by dwarf shrubs such as *Empetrum rubrum* Vahl ex Willd. This pattern is altered by lithology. Landscapes on tertiary rocks have finer and richer soils, resulting in species-rich variants of the steppe. In contrast, landscapes on Quaternary deposits have coarser soils, and more acidic vegetation, that develops into *Empetrum* heathlands on the more leached substrates. At the landscape level, topographic moisture determines a gradient towards scrubs of *Chiliotrichum diffusum* (Foster f.) O. Kunze on the deeper soils, and towards *Poa spiciformis* (Steud.) Hauman & Parodi grass lawns on dry, north-facing slopes. Extensive eroded heathlands, as well as most grass lawns, are attributed to heavy sheep grazing and trampling of former tussock grasslands, shrub-steppes and scrubs (Collantes *et al.* 1999; Anchorena *et al.* 2001, 2011).

The invader species

Hieracium pilosella L. (*Asteraceae*) is native to Eurasia (Bishop & Davy 1994). It is common in sites with low precipitation, short vegetation and bare soil (Bishop & Davy 1994), which are probably degraded by overgrazing (Treskonova 1991). *H. pilosella* tolerates drought and frost and is present in a large range of soil types and pH values (Bishop & Davy 1994). It forms dense, large and prostrate patches, displacing native vegetation and reducing forage resources (Treskonova 1991).

Hieracium pilosella is a known invader of grasslands in many countries, like New Zealand (Treskonova 1991), the UAS (Vander Kloet 1978), Switzerland (Winkler & Stöcklin 2002) and Chile (Covacevich 2009). In New Zealand, it has caused severe ecologic and economic damage, and it is a problem that has not yet been solved (Meurk *et al.* 2002). The species was reported in southern Chile in 1951 (Domínguez 2004), and, at present, it covers many hectares in sites with good soils. It is becoming abundant in tussock grasslands of the Chilean sector of the Fuegian steppe (Covacevich 2009). In Argentina, the first report of *H. pilosella* in the steppe of Tierra del Fuego was in 1993 (Livraghi *et al.* 1998). In previous regional vegetation censuses (between 1985 and 1989), the exotic species was not detected (Collantes *et al.* 1999). Currently, the species occurs in the entire steppe region (5000 km^2, approximately) with a frequency of 66%, a mean cover lesser than 2% and a clear aggregated spatial pattern (Cipriotti *et al.* 2010). These results suggest that the species is in an initial stage of invasion in the Argentinean side of the Fuegian steppe.

Sampling and vegetation censuses

We imposed a regular grid on a previous vegetation map (1:200 000, Collantes *et al.* 1985) and located a sampling site at every line intersection, with a mean distance of about 4.5 km between sites, resulting in a set of 128 points for the whole region. In the field the points were located via GPS, and once the plant community, represented in the map, was

doi:10.1111/j.1442-9993.2012.02427.x

detected, we carried out a floristic census in a homogeneous area of 50 × 50 m. We estimated species abundance through the modified Braun-Blanquet scale (Westhoff & van der Maarel 1978), and recorded *H. pilosella* cover in the same 50 × 50 m area. We estimated the cover of *H. pilosella* patches as $\pi \times a \times b$, where a and b are the two orthogonal patch radii. Its per cent cover was calculated as the quotient of the patches cover and the area evaluated (50 × 50 m).

We measured the cover of each growth form along a 20-m transect randomly placed inside the 50 × 50 m area, where all growth forms and bare soil intercepting the line were recorded. We classified the growth forms as shrubs, dwarf shrubs, cushion shrubs, tussock, sedges-rushes, soft grasses and forbs, according to Collantes *et al.* (1999). Botanical nomenclature followed Moore (1983) and Correa (1969–1998), taking into account Zuloaga and Morrone (1996, 1999) for nomenclature updating of vascular plants.

Data analysis

Sites with intensive soil disturbances were excluded because they are extremely altered environments. Sites in wetlands and saline environments were also excluded, because the invader was absent in them. This left 117 sampling sites. We investigated floristic gradients and the relationship of *H. pilosella* with them using a Detrended Correspondence Analysis (DCA, PCOrd v 5.0 program, MjMSoftware). We classified community types with Two-Way Indicator Species Analysis (TWINSPAN, Kent & Coker 1994) using PCOrd v 5.0. Mid-point transformations of the Braun-Blanquet cover scale were used. Pseudospecies cut level values were: 0.5; 1.0; 2.5; 5.0; 7.5; 12.5; 17.5; 37.5 and 87.5, and we considered three division levels. The resulting community types were compared with Collantes *et al.*'s (1999) regional classification into communities. We used two parameters to characterize the abundance of *H. pilosella* within each community type. The first parameter, constancy, corresponded to the quotient between the number of sites where the species was present and the total number of sites visited. The second parameter, mean cover, was calculated considering only those sites where the species was present, as a measure of the suitability of sites. We compared the mean cover among community types with a Kruskal–Wallis test.

To characterize the different community types in relation to species diversity and richness, we calculated the total diversity (1-D Simpson index complement), total richness, native richness and exotic richness values, averaged within each community type, and compared among community types by using the Least Significant Difference Fisher test.

We used the complete data set to make the regional level analyses, whereas, at community level, we took into account only the censuses corresponding to each respective community type. Spearman correlation tests were calculated to evaluate relationships between *H. pilosella* cover and total richness, exotic richness, native richness, species diversity and growth forms cover. We tested all data sets for normality (modified Shapiro–Wilks test, Infostat v.2009) and homogeneity of variances (Levene test).

To interpret results in relation to habitat characteristics, classified communities were assimilated to community types previously defined by Collantes *et al.* (1999), who also determined soil parameters for each community type.

RESULTS

From the floristic gradients characterization, DCA axis I (15.43% of explained variance) represented a soil fertility gradient (Fig. 1) because of acidophilous species, especially the cushion or prostrate shrubs *Empetrum rubrum* and *Bolax gummifera* (Lam.) Spreng, at the negative extreme (left) *vs.* the absence of acidophilous species at the positive extreme (right). On the other hand, axis II (6.65% of explained variance) represented a humidity gradient, where the most hygrophytic species of the studied communities, *C. diffusum*, was in the negative extreme, and the xerophilous species, *Poa spiciformis*, in the positive extreme. Within the axis I gradient, *H. pilosella* was located in the high fertility area, and it was in the most humid sector of axis II (Fig. 1, Table 1).

Seven groups emerged from the TWINSPAN analysis (Figs 1,2, Appendix S1). Although *H. pilosella* was present in all of them, its cover was higher in group V, where it also reached a high constancy (Table 2). Group V was a mixture of two communities described by Collantes *et al.* (1999), neutrophilous (non-acidic) *C. diffusum* scrubs and neutrophilous *Festuca-Poa* grasslands. Within group V, positive correlations were found among *H. pilosella* and *C. diffusum* ($r = 0.57$, $P = 0.04$), but no correlations were found among

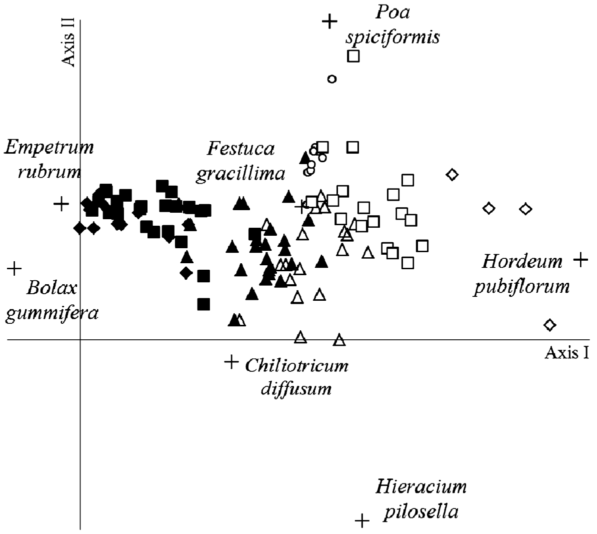

Fig. 1. Detrended Correspondence Analysis (DCA). Symbols represent different TWINSPAN groups associated with vegetation community types: ▲, I; ■, II; ●, III; △, IV; ○, V; □, VI; ◇, VII. Filled symbols indicate community types with high *Empetrum* abundance. Species with major correlation with axes are included. Axis I explain 15.43% of the variability, and Axis II, 6.65%.

H. pilosella and *F. gracillima* (r = –0.30, *P* = 0.19). Group V, in particular, had high richness and diversity values (Table 2).

At the regional level, we observed positive correlations between *H. pilosella* cover and total species richness and diversity (Table 3). Similar results were obtained when correlations between invader cover and native and exotic species richness were evaluated. At the community level, we found only marginally significant negative correlations (0.05 < *P*-value < 0.10) between invader cover and total richness (group V).

Table 1. Correlations between the fist two DCA (Detrended Correspondence Analysis) axes and the main species of the different community types

	Axis I	Axis II
Empetrum rubrum	–0.882***	0.112
Chiliotrichum diffusum	–0.022	–0.665***
Festuca gracillima	0.291**	–0.012
Poa spiciformis	0.213*	0.541***
Hordeum pubiflorum	0.477***	–0.124
Bolax gummifera	–0.329***	–0.016
Hieracium pilosella	0.083	–0.376***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

When we evaluated the relationships between invader cover and the cover of each growth form at the regional level, positive correlations were observed for shrubs, grasses, forbs and sedges-rushes, while a negative correlation was seen for dwarf shrubs (Table 4). At the community level, the invader was positively correlated with forbs in community groups I, III and V, and with sedge-rushes in community group V. In contrast, the invader was negatively correlated with dwarf shrubs in community group III.

DISCUSSION

Through this study we determined that, at an early stage of a plant invasion, *H. pilosella* is associated

Table 2. Invader constancy (%), mean invader cover (%), maximum invader cover (%), average richness and diversity values for each community type

Community	*n*	*Hieracium pilosella* constancy	*H. pilosella* cover (%)*	Max. *H. pilosella* cover (%)	Total diversity**	Total richness**	Native richness**	Exotic richness**
I	11	27.3	0.75a	1.00	0.69ab	16.82a	15.33ab	2.18ab
II	28	10.7	0.67a	1.00	0.64a	16.57a	15.50ab	1.67a
III	26	38.5	1.05a	2.50	0.76bc	20.73bc	17.81c	2.78bc
IV	10	50	0.88a	1.00	0.73bc	20.40bc	17.22bc	2.78bc
V	20	40	10.69b	37.50	0.77c	23.00c	19.75c	3.26c
VI	18	33.3	0.83a	1.00	0.79c	20.00b	17.33bc	2.59b
VII	4	25	1.0ab	1.00	0.83c	14.75a	12.00a	3.00bc

*Kruskal–Wallis test, $P = 0.05$. **Least Significant Difference Fisher test, $P < 0.001$. Different letters indicate differences of invader cover, richness or diversity among communities.

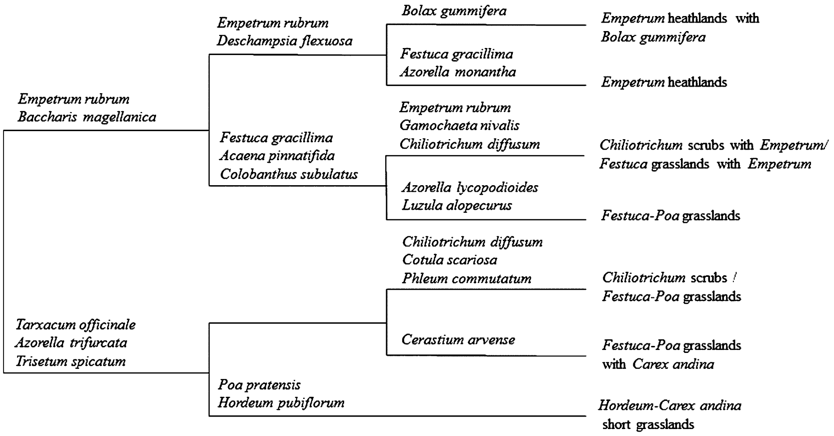

Fig. 2. Community types obtained from the TWINSPAN analysis. TWINSPAN groups are indicated by roman numbers and community type names correspond to comparisons with descriptions of Collantes *et al.* (1999). Indicator species for each division are shown.

doi:10.1111/j.1442-9993.2012.02427.x

Table 3. Correlation analysis (Spearman coefficient) between *Hieracium pilosella* cover (%) and richness or diversity

Analysis level	Variables	*n*	Correlation coefficient	*P*
Regional	Total richness	117	**0.28**	**0.003**
Regional	Exotic richness	117	**0.273**	**0.004**
Regional	Native richness	117	**0.210**	**0.026**
Regional	Diversity	117	**0.193**	**0.041**
Community (V)	Total richness	20	–0.426	0.079
Community (IV)	Diversity	10	–0.658	0.063

Analysis was carried out at the regional level (with the whole data set) and at the community level (within each TWINSPAN group, in brackets). *P*-values smaller than 0.05 are in bold and *P*-values greater than 0.1 are not included.

Table 4. Correlation analysis (Spearman coefficient) between *Hieracium pilosella* cover (%) and growth forms cover (%)

Analysis level	Variables	*n*	Correlation coefficient	*P*
Regional	Forbs	117	**0.484**	**<0.001**
Regional	Soft grasses	117	**0.287**	**0.002**
Regional	Shrubs	117	**0.295**	**0.002**
Regional	Dwarf shrubs	117	**–0.277**	**0.003**
Regional	Sedges and rushes	117	**0.283**	**0.003**
Community (I)	Forbs	11	**0.762**	**0.011**
Community (V)	Forbs	20	**0.593**	**0.012**
Community (III)	Dwarf shrubs	26	**–0.415**	**0.034**
Community (I)	Sedges and rushes	11	0.561	0.063

Analysis was carried out at the regional level (with the whole data set) and at the community level (within each TWINSPAN group, in brackets). *P*-values smaller than 0.05 are in bold and *P*-values greater than 0.1 are not included.

mainly with communities having *C. diffusum* shrubs (Fig 1, Table 1). Within group V, the invader reaches maximum cover values of almost 38%, with a mean cover of 10.69% (Table 2). So, further evaluations at community level will be focused on group V. The percentage of variability explanation seen in DCA axis I and II was low (less that 23%, Fig. 1). It is possible that there are other variation factors that are not considered in this analysis. The fact that group V is composed of both the *C. diffusum* scrubs and *F. gracillima* grasslands having scattered *Chiliotrichum* shrubs suggests that the latter could be an altered variant of the former, as reported by Stoffella (2003). Stoffella (2003) found that historical grazing has caused the opening of closed scrubs and that there is a strong correlation between soil compaction and decreased shrub cover. This would suggest that *H. pilosella* invasion has been facilitated by historical sheep disturbance of the original dense scrubs. However, within community type V, we did not find a correlation between invader cover and either frequency of feces or soil impedance (data not shown), two variables used to estimate the grazing pressure.

Our results are consistent with the idea that environmental stress is a determinant of both native and exotic species success along the environmental gradients. *H. pilosella* occurs in communities of high soil nutrient and water content, as suggested by its position along environmental gradients (Fig. 1, Table 1) and by its negative correlation with dwarf shrubs, indicators of highly acidic and/or xeric habitats (Table 4). We found a positive relationship between *H. pilosella* cover and total species richness and diversity at a regional level (Table 3), in line with the predictions (Shea & Chesson 2002; Fridley *et al.* 2007; Perelman *et al.* 2007). Coincidently, *H. pilosella* cover was positively correlated to native and exotic richness at a regional level (Table 3). Moreover, the high richness and diversity of group V (*Chiliotrichum* scrubs and *Festuca-Poa* grasslands) suggests that this community has fertility conditions favourable for plant growth. Soils beneath *C. diffusum* scrub have a relatively fine texture and a high organic matter, nutrients and water content (Collantes *et al.* 1999), and they have the highest species richness (total, native and exotic) and diversity (Table 2). Other upland communities, with lower species richness and *Hieracium* cover (Table 2), have either poorer soils (groups I–IV), drier soils (group VI) or excessively compacted and eroded soils (group VII) (Collantes *et al.* 1999).

Of course, the differences in *H. pilosella* cover among communities could be because of differences in residence time of the different invasive populations, which would allow more time for plant growth and more time to increase propagule pressure in stands of communities that happened to be invaded earlier. We have no information on the residence time of *H. pilosella* in

doi:10.1111/j.1442-9993.2012.02427.x

each community. Nevertheless, the scattered distribution of vegetation types, which follows geomorphologic and topographic patterns, has given them all similar probabilities of receiving seed from both the much invaded Chilean region (Covacevich 2009) and the high foci in the Argentinean region (Cipriotti *et al.* 2010). In addition, reports from previous vegetation censuses in the same region, or in the same paddocks for specific cases, did not detect the exotic species (Serra 1990; Collantes *et al.* 1999). These evidences support the hypothesis that the distribution pattern of the weed responds to abiotic factors.

Evidence from other studies indicates that most biotic interactions operate principally in later invasion stages, constraining spread and impact, and less so during colonization and establishment (Levine *et al.* 2004). In this case, the marginal relationships observed at community level could be a trend which would become stronger at later invasion stages. Studies in later stages of invasion would help to determine if there is a relationship and to understand the invasion process involved. In more stressful communities (much eroded or on nutrient-poor soils), no relationship was found either among invader cover and species richness and diversity or among invader cover and native or exotic richness. This result is consistent with the idea that, in more stressful habitats, biotic interaction mechanisms might become relatively less important in limiting exotic species establishment (Perelman *et al.* 2007).

No evidence was found in relation to biotic constraints when we evaluated relationships between the invader and the other species of the same growth form at this invasion stage. Correlations among *H. pilosella* cover and the other forb species were positive at both regional and community levels (Table 4). Moreover, there was no evidence of competitive displacement (Thiele *et al.* 2010), either in richer community types or in more stressful habitats, because of the positive relationship between the invader cover and other species of the same growth form. It is likely that functional classification based on growth forms is not the most appropriate classification in this context. A previous study demonstrated that *H. pilosella* tissues have higher nitrogen content than native vegetation of invaded sites and that its decomposition rate is higher than are those of other native species (Braun 2009). It is also possible that abiotic characteristics influence the invader success even at small scales of analysis. New studies that both consider a functional classification more specifically related to resource exploitation, capture and allocation and evaluate variations of abiotic factors at a small scale may help to deal with the biotic–abiotic constraint concern at this scale of analysis.

Although correlation analyses based on observational studies are very useful in ecological studies, they present some limitations. Significant correlations only indicate that two variables are related in a systematic way, but do not test causation. There might be other covariates not considered in the study that could be the cause of the pattern observed. Only with experimental studies is it possible to determine causes and effects and rule out other covariate effects (Shipley 2000).

In conclusion, in the period of establishment and initial expansion of this exotic species, our results are consistent with the community ecology theory at the regional level, because of the positive invasion–diversity and invasion–richness relationships at this level. At the community level, a weak negative relationship between richness and invader cover was seen. When functional identity was considered, we did not find any evidence of biotic constraint, because of the positive relationship between invader cover and the other forbs at the community level. These results could be considered as an example of the patterns of establishment and expansion of any species, regardless of their origin. Further evaluations will have to be carried out to determine the course and patterns that exist in later stages of this invasion process and to establish more precisely the functional identity of involved species for more specific competition evaluations.

ACKNOWLEDGEMENTS

We thank to the ranchers of Tierra del Fuego, especially Mr Errol O'Byrne from Cullen Ranch for his hospitality. We also are very grateful to Dr Scott Wilson for a friendly review of the manuscript and a critical reading of the English version, and to two anonymous reviewers, who contributed valuable comments that helped to improve the manuscript. The studies reported in this manuscript comply with the ethics guidelines and current laws of the Republic of Argentina. This work was supported by a grant from the Consejo Federal de Inversiones and by a doctoral fellowship from Consejo Nacional de Investigaciones Científicas y Técnicas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean cover values and constancy of main species in each TWINSPAN group.

doi:10.1111/j.1442-9993.2012.02427.x