

Hieracium pilosella invasion in the Tierra del Fuego steppe, Southern Patagonia

P. A. Cipriotti · R. B. Rauber · M. B. Collantes ·
K. Braun · C. Escartín

Received: 13 May 2009 / Accepted: 13 November 2009
© Springer Science+Business Media B.V. 2009

Abstract Biological invasions have important ecological impacts at both local and global levels, affecting biodiversity, ecosystem functioning, and economic sustainability. The study of invasions requires specific methodological approaches to gain rapid insight into the spatial and temporal dynamics of the system. We studied a recent invasion by the exotic herb *Hieracium pilosella* L. (Mouse-ear hawkweed, Asteraceae) in the Argentinean portion of the northern part of Tierra del Fuego Island in Southern Patagonia. To assess the extent of this invasion and the related ecological and land use factors, we performed an extensive field sampling at a regional scale and used a

spatial pattern approach using geostatistical techniques to build a map of the invasion. Our results showed that the invading species is widely distributed across the entire Fuegian steppe, in general with low cover (<2%) and a particular spatial structure having hot spots (10–70%) related to specific land uses. We found regional-latitudinal and also local-community level variability in the frequency, cover and spatial distribution of the invasive species, each of them associated with particular ecological factors, and no association with regular domestic animal grazing. Region-wide invasion may be accounted for by wind dispersal of the seeds and the latitudinal variability of the precipitation; while local-variability was associated with the susceptibility of different plant communities to invasion. Hot spots were found to be related to massive soil disturbances (e.g., road building, shrub removal, physical impacts of long-term and intense domestic animal use, etc.), probably due to the presence of bare soil favoring colonization by the invading species. Scrublands, lawns and grasslands were more invaded than wetlands, heathlands or salt grasslands. Since the invasion is apparently at initial stages due to the low cover values found, we believe that information about the extent and environmental or management factors involved in this exotic plant's expansion should be used to design appropriate control and mitigation tools. In this sense, our results point to management actions focused on reducing the presence of hot spots of invasion by means of quick revegetation of bare soil after a massive disturbance event takes place.

P. A. Cipriotti · R. B. Rauber · M. B. Collantes ·
K. Braun · C. Escartín
Laboratorio de Ecología de Pastizales, Museo Argentino
de Ciencias Naturales, CONICET, Buenos Aires,
Argentina

P. A. Cipriotti
Cátedra de Métodos Cuantitativos Aplicados, Dpto. de
Métodos Cuantitativos y Sistemas de Información,
Facultad de Agronomía, Universidad de Buenos Aires,
Buenos Aires, Argentina

P. A. Cipriotti (✉)
Department Ökologische Systemanalyse, Helmholtz
Zentrum für Umweltforschung, Permoserstraße 15,
04318 Leipzig, Germany
e-mail: pablo.cipriotti@ufz.de; cipriotti@agro.uba.ar

Keywords Autocorrelation · Grasslands · Geostatistics · Hawkweed · Plant invasions · Sheep grazing · Spatial statistics

Introduction

Biological invasions are considered to be the second leading cause of biodiversity loss for native communities after land use changes and habitat destruction (Diaz et al. 2006; Sala et al. 2000) and a key component of global change (Vitousek 1990, 1994; Vitousek et al. 1997). Invasions by alien plant species represent a significant threat to ecosystem function and economic sustainability (Asner and Vitousek 2005; D'Antonio and Vitousek 1992; Levine et al. 2003; Mack et al. 2000). Thus, the study of changes in the abundance and distribution of exotic plants in invaded habitats and identification of land use and environmental factors involved is fundamental to elucidating causes and consequences of invasion (Crawley 1987; Drake et al. 1989). Specifically, the mechanisms involved in the spatial expansion of an exotic species after its arrival to a novel area (Thuiller et al. 2006), and the invasion dynamics at regional scales are poorly understood (Asner et al. 2008; Bruno et al. 2004). Hence, methodological approaches that enable quick assessment at the early stages of an invasion are needed to manage and mitigate the impact of these events.

The success of invasions depends on the specific traits of an invading species and the interaction of biotic and abiotic factors in the environment at different spatial scales (Pysek and Hulme 2005; Pysek et al. 2008; Thuiller et al. 2006). Different factors have been proposed to be determinants of a plant community's susceptibility to invasion, or *invasibility* (Hector et al. 2001). Higher native species diversity, for instance, has been suggested to increase community resistance to plant invasions (Levine and D'Antonio 1999; Lonsdale 1999; Perelman et al. 2007). However, invasibility as determined mainly by species diversity has been challenged by some authors (Chaneton et al. 2002; Davis et al. 2000, 2005; Levine et al. 2004; Shea and Chesson 2002). In fact some of them attribute invasion success to either specific invader plant traits like clonality, seed output, propagule pressure, or to environmental stressors such as human disturbance (Lockwood et al.

2005; Rejmánek and Richardson 1996; Rouget and Richardson 2003; Thuiller et al. 2006).

Changes in land use patterns have often triggered biological invasions in terrestrial ecosystems (Larson et al. 2001; Vitousek et al. 1997). Grasslands, in particular are highly invaded ecosystems as a result of anthropogenic disturbances associated with crop cultivation and livestock grazing (Chaneton et al. 2002; Hobbs and Huenekke 1992; Mack 1989). Grazing can promote the introduction and expansion of exotic plants because of selective feeding behaviors, changes in the balance of biotic interactions among native and exotic species, soil disturbance like trampling, and increases in the dispersal range of plants by herbivores (Bellingham and Coomes 2003; Brown and Archer 1989). Also, grazing management practices such as sown pastures or fertilization may facilitate the establishment of invasive species.

In addition, island ecosystems, are particularly vulnerable to biological invasion because of the relative condition of genetic isolation from the mainland (Drake et al. 1989). In these ecosystems, alien species having biological traits different than the resident species can evolve quickly under particular circumstances, replace the native biota, and modify ecosystem functioning (Vitousek 1990). Some examples are the commonly reported invasions to Mediterranean or Pacific islands by species from different kingdoms (Gimeno et al. 2006; Vitousek et al. 1987; Vitousek and Walker 1989; Traveset et al. 2008).

The herb *Hieracium pilosella* L. (Mouse-ear hawkweed, Asteraceae), has recently (around 15 years ago) invaded the northern Tierra del Fuego rangelands (Livraghi et al. 1998) forming in some cases large patches that replace native flora. *H. pilosella* is a known grassland invader native to Eastern Europe and Western Asia (Bishop and Davy 1994) that rapidly forms mono-specific patches due to vegetative (stolons), sexual and apomictic reproduction (Bishop and Davy 1994), and usually ends up replacing native flora and decreasing palatable forage biomass and secondary productivity (Johnstone et al. 1999; Makepeace et al. 1985; Treskonova 1991). *H. pilosella* is avoided by sheep livestock due to its prostrate growth, highly pubescent leaves (i.e. dense short and long hairs on both leaf's sides) and because it has high foliar concentrations of secondary metabolites (Bishop and Davy 1994; Rose et al.

1995). This species has invaded New Zealand (Duncan et al. 1997; Rose et al. 1998; Treskonova 1991), the US (Carson et al. 1995; Vander Kloet 1978; Voss and Böhlke 1978), Switzerland (Winkler and Stöcklin 2002), and Chile (Covacecich 2001). In New Zealand, the invasion experienced an unexpected expansion in 1950–1960 (Connor 1964, 1965, 1992), about 30 years after its arrival to the area (Allan 1924; Webb et al. 1988) and attributed to the presence of degraded pastures and grasslands from overgrazing (Rose et al. 1995). *H. pilosella* invasion in New Zealand has led to severe ecological and economic damage, a problem that has still not been solved today (Meurk et al. 2002).

The recent *H. pilosella* invasion in the Tierra del Fuego rangelands, therefore, is expected to result in substantial ecological and economic damage in a system largely dependent upon natural pastures for economic sustainability (Anchorena et al. 2001). The main ecosystem impact of this invasion may be related to decreases in forage biomass (Meurk et al. 2002; Rose et al. 1998) and changes in nutrient cycling (Boswell and Espie 1998; McIntosh and Allen 1993; McIntosh et al. 1995), since *H. pilosella* is avoided by sheep, has a more labile litter, and a much higher litter decomposition rate than dominant native species in the Fuegian steppe (Braun 2009). We believe that information concerning the current extent of the invasion and the factors involved should be rapidly identified in order to increase the possibility of controlling or eradicating the invasion (Radosevich et al. 2003). In this sense, the early detection and study of an invasive species generally reduces costs and time involved in control and increases the probability of successful eradication (Anderson et al. 1993; Rejmánek and Pitcairn 2002).

The biotic and abiotic constraints of the new habitat and the tradeoffs that the invading species faces (Robinson et al. 2008; Thuiller et al. 2006; Tilman 1988; Zhu et al. 2007) are frequently expressed in the spatial patterns of the invasion (Arim et al. 2006; Duryea et al. 1999; Wu et al. 2006). Available quantitative methods linking spatial patterns with ecological processes at broad spatial scales are powerful tools used in basic ecological research and environmental applications (Cook et al. 2007; Keeling et al. 2004; Nehrbass et al. 2007; Pysek and Hulme 2005; Turner and Gardner 1991), because they can yield fast and sound information (Higgins et al. 2001;

Radosevich et al. 2003; Rouget and Richardson 2003). In this study, we used a spatial pattern approach at a regional scale to elucidate the extent and major mechanisms involved in *H. pilosella* invasion in the northern part of Tierra del Fuego Island (Argentine portion). To this end, first, we investigated the extent of the *H. pilosella* invasion on the steppe of Tierra del Fuego, and we built the first map of the invasion using geostatistical techniques; second, we analyzed the community and land use factors related to the invasion.

Methodology

Study area

The Fuegian steppe covers about 5,000 km² from the Strait of Magellan to approximately 54°S, at the northern end of Tierra del Fuego Island (Fig. 1). It is the southernmost portion of the Magellanic steppe (Hueck and Seibert 1972), a rare example of cold temperate oceanic grasslands in South America. In a regional context, the area can be viewed as a transition between arid Patagonia and humid sub-Antarctic climates.

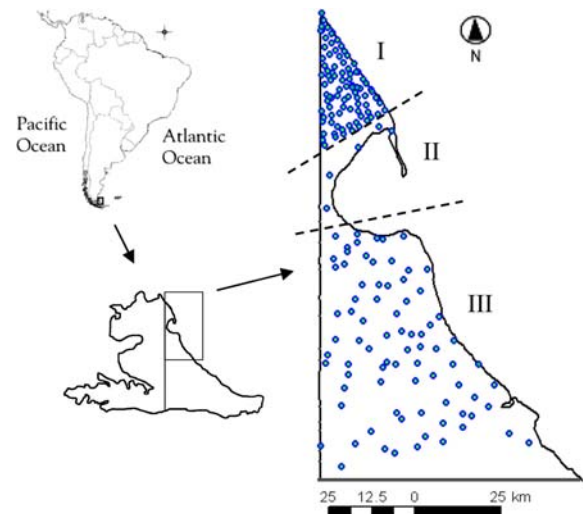


Fig. 1 Study area in the northern Argentine portion of Tierra del Fuego Island. Sampling sites in the Fuegian grasslands are depicted and show the three zones studied: (I) North of San Sebastian Bay, (II) San Sebastian Bay and (III) South of San Sebastian Bay

The climate of the Magellanic steppe is chilly, windy and cloudy. At Río Grande, a city on the Atlantic coast (53°47'27"S, 67°42'46"W), the mean temperature during the coldest month (July) is 0°C and during the warmest month (January) is 10°C. Precipitation is evenly distributed throughout the year and increases from NE to SW away from the Andes range, bringing about a rain shadow. In the northern extreme, Holy Spirit Cape, it rains 260 and 400 mm per year south of Río Grande city (Collantes et al. 1999). Noticeable water balance deficits occur in December and January (Koremlit and Forte Lay 1991).

Vegetation has been classified as a humid grass steppe (León et al. 1998; Collantes et al. 2005). Highlands are covered by a tussock steppe of *Festuca gracillima* Hooker f. that grades into a scrub of *Chiliotrichum diffusum* (Forster f.) O. Kunze or into dwarf shrub heaths of *Empetrum rubrum* Vahl ex Willd (Frederiksen 1988; Moore 1983; Pisano 1977), while lowlands are covered by wetland communities dominated by hygrophilous vegetation. On one hand, highland vegetation is controlled by a soil nutrient gradient, abundance of *E. rubrum* and other cushion shrubs are associated with acidic, poor nutrient soils of coarse texture, while short grazing lawns are indicative of high saturated soils with neutral reactivity (Collantes et al. 1999). On the other hand, wetland vegetation from lowlands is controlled by a moisture gradient (Collantes et al. 2005). After European settlement in the last decade of the nineteenth century, a large investment in sheep farming took place (Martinic 1982). During the last 100 years, the main land use in the region has been extensive sheep breeding to produce wool and meat.

The invader species: *Hieracium pilosella* L.

H. pilosella (Mouse-ear hawkweed) is a small yellow-flowered herb belonging to the *Asteraceae* family (tribe *Lactucaceae*), native to Europe and western Asia. It is a hispid perennial plant, with a basal rosette of leaves, and glandular hairs covering all vegetative organs. The flowering stem sprouts from the center of the basal rosette, and the flowerheads are born singly onto the scape. *H. pilosella* grows in dense patches, excluding other vegetation. It produces stolons that generate a new rosette at their extremity, and can develop into a new clone forming dense mats in the open space. This species may also

be apomictic (Bishop and Davy 1994; Jenkins 1992; Krahulcova and Krahulec 1999), and its seeds, sexual or asexually generated, are mostly dispersed by wind. It is also a known allelopathic plant (Makepeace et al. 1985), with substances inhibiting root growth and generating in some circumstances a halo of bare soil surrounding its patches (Scott et al. 2001). *H. pilosella* is a known grassland invader in North American, New Zealand (Bishop and Davy 1994) and Chilean grazing ecosystems. In New Zealand, it has appeared in the short tussock grassland previously dominated by fescue tussock (Makepeace et al. 1985). In England, growth in nitrogen deficient soils occurs in areas of low rainfall with well-drained, sandy soils of low soil water potential in summer (Bishop and Davy 1994).

Sampling design and field studies

Based on previous vegetation and soil maps (Anchorena et al. 2001; Collantes et al. 1999) and recent satellite images (Landsat 7 ETM+, February 2002) of the Fuegian steppe, we defined three major zones associated with regional, environmental and vegetative community variability: (1) North of San Sebastian Bay, (2) San Sebastian Bay, and (3) South of San Sebastian Bay (Fig. 1).

The area north of San Sebastian Bay is mainly dominated by *F. gracillima*, *C. diffusum* scrublands, and by *E. rubrum* heathland communities. San Sebastian Bay is mostly dominated by *Puccinellia* spp. salt grasslands, *Sarcocornia perennis* salt marshes and *Lepidophyllum cupressiforme* scrublands. This zone has frequent flooding, and it is under tidal influence. Region south of San Sebastian Bay is dominated by *F. gracillima* grasslands and lawns of short grasses (*Poa spiciformis*, *Hordeum pubiflorum*, *Rytidosperma virescens*, and *Carex andina*), with less extensive *C. diffusum* scrublands and *E. rubrum* heathlands.

In the three defined zones, we superimposed a grid with ca. 162 sampling sites across the whole region, at different spatial resolution scales according to site accessibility and previous information on plant invasions (Fig. 1). North of San Sebastian Bay, the average distance between the two closest sampling sites was less than 1.7 km and resulted in a total of 82 sampling sites, while the Southern sites averaged about 7 km apart and included 80 sampling locations.

At each sampling site, we measured *H. pilosella* cover, characterized the vegetation community and the land use of the site, and estimated current grazing intensity. To calculate the cover of *H. pilosella*, we recorded all individual plants or mono-specific patches of *H. pilosella*, and measured their size using two orthogonal diameters from the maximum dimension within a plot of 50 × 50 m (¼ ha).

To characterize the vegetation community we measured the plant species and bare soil cover using the line intercept method along a 20 m transect randomly placed inside the ¼ ha. plot. All vegetation and bare soil intercepting the line was recorded. Vegetation was classified according to Collantes et al. (2005) and Cingolani et al. (2005) (e.g., shrubs, tussock grasses, short grasses, dwarf shrubs, forbs).

To characterize land use, we recorded information at each site related to shrub removal, sown pastures, road sides, livestock pathways, gas or oil pipeline locations, areas with long-term intense domestic animal use (i.e. physical impacts of grazing), and abandoned fields. To estimate short-term grazing intensity, we performed the recorded the following as indirect grazing indicators (Collantes et al. 2005; Stoffella 2003): measuring the total bare soil and litter cover along a 20 m transect randomly placed inside the ¼ ha plot, the frequency of feces in one hundred 0.5 × 0.5 m quadrants randomly distributed inside and around the study plot, and measured the resistance of soil penetration (impedance) in kg/cm² with a Proctor soil penetrometer (20 measures per site) (Black 1965; Klute 1986).

Data analyses

To study the spatial pattern of *H. pilosella* invasion, we employed geostatistical techniques. Geostatistical methods were developed to deal with autocorrelated spatial processes (Goovaerts 1997; Rossi et al. 1992). Sampling of spatially explicit processes, like those in our case or studies on species distribution, violate the main assumption of independence of observations and preclude the use of standard generalized linear models (e.g., *logit* models; Wood 2006; Zuur et al. 2009). Positive spatial auto-correlation (i.e. the most common situation of correlation structure) violates the usual assumption of independence between data points and leads to an underestimation of standard errors, and can elevate type I errors if not accounted

for (Legendre 1993). Hence, we decided to present the first description of the invasion pattern using two well-known geostatistic tools (i.e. the variogram and interpolation by kriging). The San Sebastian Zone (II) was excluded from the analysis because the invasive species was not found in this area. First, we evaluated the distributional assumptions (stationary and continuity) of *H. pilosella* cover at each zone. The major constraint for applying normal distribution assumptions to the applied geostatistics was the presence of areas with zero abundance data. To overcome this problem, we randomly removed some of the sampling sites having zero cover of *H. pilosella* (ca. 10% for each zone) and performed a logarithmic transformation of the original data ($\log[x]$), generating an invasion scenario that is possibly worse than reality. Once the distributional problems were solved, we found a trend (first order process) for both zones through exploratory studies, and removed this by applying first order polynomials to meet the stationary assumption. When the assumptions were met, we built the experimental semivariogram for each zone. First, we calculated all pair-wise distances between sampling sites for different lag-distances between 500 and 16,000 m for the Northern zone and lag-distances between 6,000 and 84,000 m for the Southern zone, always assuring that at least 20 pairs had cover data. Second, we calculated the omnidirectional semivariance for each lag-distance using the classical estimator (Cressie 1991),

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=h}^{N(h)} (z_i - z_{i+\Delta h})^2$$

where $\gamma(h)$ represent the semivariance calculated for a specific spatial distance h , and z represents the random variable. In this case the *H. pilosella* cover, measured at site i , $i + \Delta h$, and $N(h)$ is the number of all pairs of sites separated by distance h .

After we obtained the two empirical omnidirectional semivariograms for each zone, we fitted different models (i.e. exponential, spherical and Gaussian) and chose the best model according to the residual square sum and a generalization of the standard determination coefficient (R^2). Then, using both spatial models of semivariograms characterizing the particular spatial structure of each zone, we interpolated the models using the universal kriging technique in a new grid finer than the original (ca.

half of the spatial resolution employed in the original sampling design). To calculate the empirical semi-variograms, fit the models, and apply the interpolation techniques, we used the *geoR* (Ribeiro and Diggle 2001) and *gstat* packages (Pebesma 2004) in the R environment (R Development Core Team 2008). To compare the invading species frequency in the different zones or vegetation communities, we performed Chi-square tests from the respective log-linear models (Everitt 1977). To study the relationships between vegetation and *H. pilosella* cover, we used two approaches. First, to compare *H. pilosella* cover among the different vegetation communities we used a one-way ANOVA with the vegetation community as the main discrete factor. Second, we performed multiple step-wise regressions between the cover of the plant invader and using other plant species as a continuous factor.

To analyze the relationships between short-term domestic grazing intensity and *H. pilosella* cover, we performed a multiple regression analysis. We regressed the invader cover against grazing intensity indicators such as bare soil and litter cover, feces frequency, and soil impedance (Anchorena et al. 2001; Cingolani et al. 2005; Posse et al. 2000). For all regression analyses, we performed a logarithmic transformation with the response variable (*H. pilosella* cover) to achieve a normal distribution, and previous multiplication by a constant k ($\log[k \cdot x]$) to avoid working with small numbers (<0.001). Finally, we used a Chi-square test to assess the effects of land use history (i.e. shrub removals, sown pastures, physical impacts of grazing at long-term, etc.) on the plant invasion. Statistical analyses other than geostatistical studies were performed using the Statistica[®] v8 software package.

Results

Invasion extent

At a regional level, *H. pilosella* was distributed throughout the entire study region with a high mean frequency ($66 \pm 4\%$; mean \pm SE), but a low mean cover (less than 2%) and high variability (CV = 200%). *H. pilosella* distribution and cover were affected by latitude, occurring as the most frequent species ($\chi^2_1 = 27.8127.81, P < 0.001$; Fig. 2a) and having four

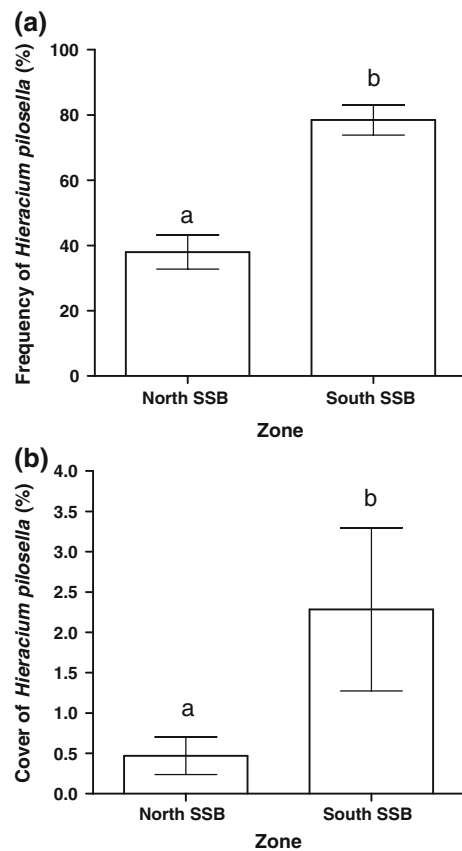


Fig. 2 **a** Frequency and **b** cover of *Hieracium pilosella* North and South of San Sebastian Bay (SSB). Bars indicate means \pm SE. Different letters indicate significant differences ($\alpha = 5\%$)

times higher or more variable cover in the South compared to the North (mean = 2.3%, SD = 9.04% vs. mean = 0.5%, SD = 2.11%, Welch-corrected $t_{86} = 2.027, P = 0.04$) (Fig. 2b).

Invasion pattern

According to the omnidirectional variograms, each zone had a different spatial structure (Fig. 3; Table 1). In fact, the spatial variability of Northern and Southern zones represented 92 and 61% of the total variability (sill), respectively. Also, the nugget, the sill, and the range parameters presented marked differences according to the adjusted exponential and Gaussian models (Table 1). The nugget effect was tenfold higher in the Southern zone versus the Northern zone. This remnant spatial variation at a micro-scale could possibly be related to the differences

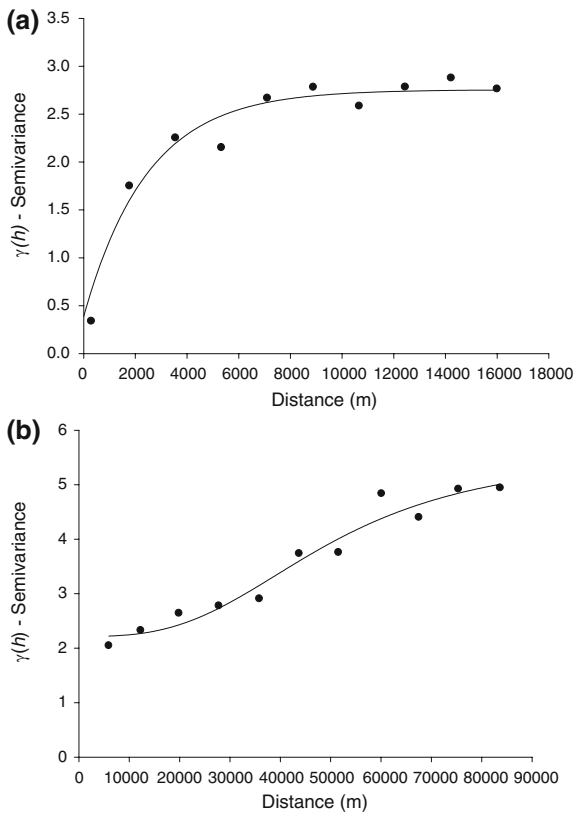


Fig. 3 Omnidirectional semivariograms of *Hieracium pilosella* cover for both zones of the Fuegian steppe: **a** North and **b** South of San Sebastian Bay. *Dots* represent the experimental semivariogram, and *lines* the respective fitted models from both zones

occurring at the finest spatial resolution for each zone. On the other hand, the range for positive autocorrelation was higher in the South with respect to the North. From the anisotropy studies, we were not able to determine a dominant direction of the invasion across the region. With each model using omnidirectional variograms, we applied the universal kriging technique to generate an invasion map for each zone. Despite differences across zones, both maps show a clear invasion process with major foci (Fig. 4).

Table 1 Fitted models for the experimental variograms from each zone

Zone	Model	Nugget (Co)	Sill (S)	Range	[S-Co]/S	R ²	RSS
North-SSB	Exponential	0.19	2.56	2150	0.92	0.97	0.186
South-SSB	Gaussian	2.09	5.35	55300	0.61	0.96	0.494

Estimators for main parameters (nugget, sill, and range), ratios between spatial and total variability ([S-Co]/S), and adjusting criteria (R² and RSS) for each model

Ecological factors related to the invasion

Vegetation communities exhibited different invasibility by *H. pilosella* as shown by the species frequency ($\chi^2_5 = 33.37, P < 0.001$; Fig. 5a) and cover ($F_{4,124} = 2.97, P = 0.024$; Fig 5b). *H. pilosella* species was absent in wetlands and had the lowest cover and frequency in *E. rubrum* heathlands, followed by *F. gracillima* grasslands, and by lawns; while it was more frequent and had the highest cover in open scrublands of *C. diffusum* (Fig. 5). Also, the cover of shrubs and forbs (dicotyledonous herbs) was associated in a quadratic fashion to *H. pilosella* cover at regional scales (Fig. 6; Table 2).

No relationship between the cover of *H. pilosella* and the indirect short-term sheep grazing variables was detected. However, sites having a very high cover of *H. pilosella* or “hot spots” (see Fig. 4) were associated with massive soil disturbances produced by shrub removal, sown pastures, road sides, livestock pathways, gas or oil pipelines, and intense domestic animal use in small paddocks (Table 3).

Discussion

H. pilosella invasion is widespread throughout northern Tierra del Fuego, a region known as the Fuegian steppe, with a high frequency, low mean cover, and a clear spatial pattern that suggest that the plant invasion is at an initial phase (Radosevich et al. 2003). The invasion exhibited an association with land use and spatial variability at different levels ranging from regional to local scales, and accounting for various processes occurring simultaneously at different spatial scales with each having their own related spread mechanism and environmental constraint (Pysek and Hulme 2005).

At a regional-level, wind dispersal of seeds may have spread the invading species across the whole region from the current source populations (i.e. foci),

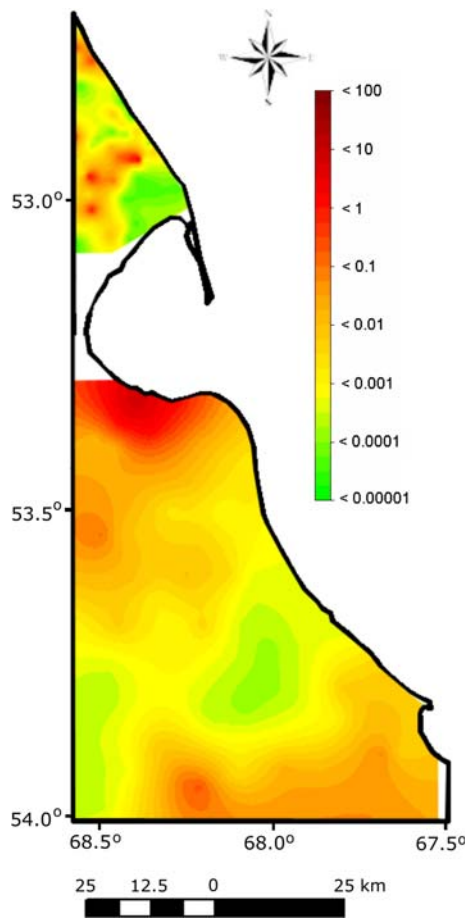
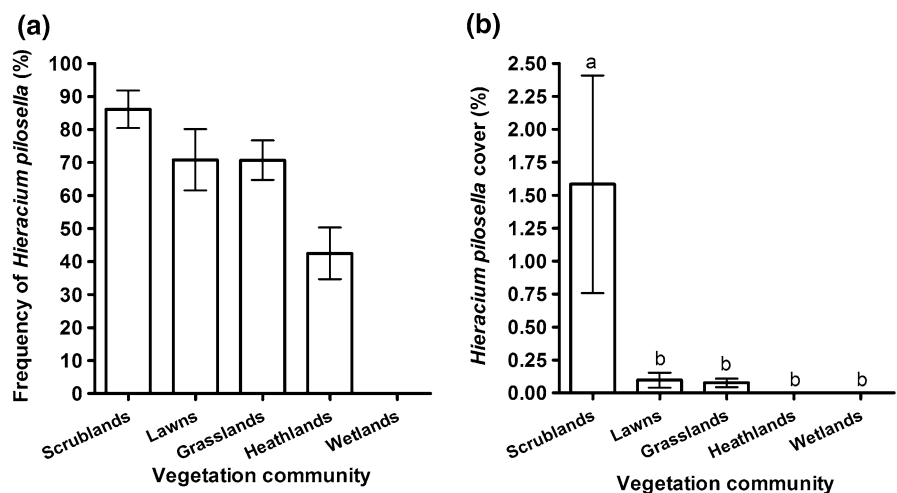


Fig. 4 Predicted invasion map of *Hieracium pilosella* cover (%) using the universal kriging technique for both zones of the Fuegian steppe, North and South of San Sebastian Bay

and may account for the high consistency observed in this study. However, the higher autocorrelation range of the variogram in the Southern zone could indicate a faster rate of plant spread or an older invasion than is present in the North. Further establishment success of the invading species in this region may be affected by the latitudinal rainfall gradient, ranging from 260 mm of mean annual precipitation in the North East to 400 mm in the South West. This gradient may also account for the higher frequency and cover of the invader in the Southern zone, as observed in similar ecosystems (i.e. New Zealand, Duncan et al. 1997; Rose et al. 1998).

At local levels, invader success was associated with the heterogeneity of vegetation communities. In fact, vegetation communities exhibited different invasibility with respect to *H. pilosella*. Wetland and heathland communities had the lowest cover and frequency of weed invasion, probably related to the ecological constraints to *H. pilosella* establishment. This is especially true in stands from those communities with similar propagule pressure (e.g., highly infested paddocks). Flooding and water-saturated soils during the winter and early spring (Anchorena et al. 2001; Collantes et al. 2005) may impair the invasive species' establishment in the wetlands; while soil acidity (pH < 5.4) may constrain nutrient uptake and growth in the heathlands (Collantes et al. 1999). Also, the higher invasibility of the scrubland communities compared to the lawns and grasslands may be accounted for by the higher soil water content, as

Fig. 5 a Frequency and **b** cover of *Hieracium pilosella* for each major vegetation community. Bars indicate means \pm SE. Different letters in panel "b" indicate significant differences based on post-hoc Tukey tests ($\alpha = 5\%$)



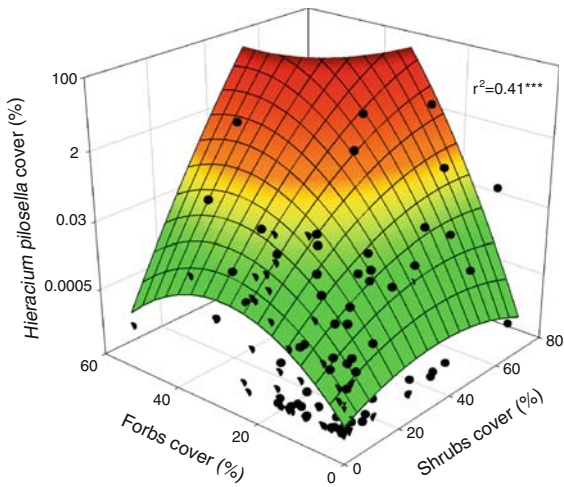


Fig. 6 Multiple quadratic regression between *Hieracium pilosella* cover and forbs and shrubs cover. The scale for the Z-axis is depicted using the untransformed variable as a percentage

was reported for similar ecosystems (Duncan et al. 1997). Scrublands occupy sites having lower incidences of sun and lower maximum temperatures at ground level compared to fescue grasslands and lawns (Braun 2009), factors that may also result in wetter sites. Hence, open scrublands (20–35% shrub cover) result in an appropriate environment for *H. pilosella* establishment because there is a balance between soil moisture and sun incidence, especially in a water-constrained ecosystem. Otherwise, in closed scrublands (>70% shrub cover; <5% scrubland censuses) and wetlands, the weed cover and

occurrence is constrained by low light incidence at ground level in areas with high shrub cover and high moisture in wetlands. This seems to be the physiological trade-off between moisture and sun incidence that invading species face, and can be seen in the quadratic form of the regression between the invader cover and the forbs and shrubs cover. Negative relationships between woody and forbs cover were also reported for other ecosystems (Sax 2002).

Once established, agamic regeneration of *H. pilosella* by stolons may be the main factor attributed to local growth at the patch level, and may result in lower spread rates compared to the regional scales reached by wind-driven seed dispersal mechanisms. However, the competitive ability and allelopathic metabolites (Makepeace et al. 1985) produced by *H. pilosella* may result in an efficient and quick invasion (Bishop and Davy 1994; Scott et al. 2001), as observed during the sudden growth of this species in New Zealand (Lamoureux et al. 2003; Rose et al. 1995).

H. pilosella invasion in northern Tierra del Fuego was not associated with moderate soil disturbance caused by regular domestic grazing (i.e. extensive grazing in large paddocks), as has been reported in other temperate grasslands (Chytrý et al. 2008; Stohlgren et al. 1999). However, invasion hot-spots (i.e. large patches) seem to be related, regardless of latitude or plant community, to massive soil disturbances and probably favor seed germination and recruitment (Rose et al. 1998). In general, those disturbances are a result of shrub removal and/or sown pastures (which may have also been responsible

Table 2 Summary of ANOVA from the multiple quadratic regression between *Hieracium pilosella* cover (analysis was performed with transformed variable) and shrubs and forbs cover. Bold letters indicate *P*-values less than 5%

Variation source	Parameters		Square sum	df	Mean square	<i>F</i>	<i>P</i> -value
	Estimate	SE					
Model			655.39	5	131.08	17.46	<0.0001
Intercept	2.08	0.4827	150.34	1	150.34	20.02	<0.0001
Shrubs cover	0.0837	0.0515	20.85	1	20.85	2.77	0.106
Shrubs cover ²	−0.0012	0.0009	13.71	1	13.71	1.83	0.201
Forbs cover	0.297	0.0642	155.2	1	155.2	20.66	<0.0001
Forbs cover ²	−0.0053	0.0017	69.54	1	69.54	9.26	0.0025
Shrubs x Forbs	0.0051	0.0017	66.98	1	66.98	8.92	0.0035
Error			915.84	122	7.51		

Table 3 Summary of the Yates corrected Chi square test for the association between considerable invaded sites (*Hieracium pilosella* cover >10%) and massive soil disturbance (i.e. shrub removal; sown pastures). Bold letters indicate *P*-values less than 1%

Invader focus	Disturbance history	
	Yes	No
No	5	143
Yes	9	5
	$\chi^2_1 = 52.63$	<i>P</i> < 0.0001

for the initial introduction of the invasive species to this area as contaminated seed in the '70 and the '80), road building, the physical impacts of long-term intense domestic animal use (i.e. small paddocks and high stocking rates) and oil industry-related activities such as pipeline construction.

From previous vegetation data (1986–1988; Serra 1990) of specific paddocks in the Northern zone with currently high levels of alien species cover (10–20%), we can deduce that the probable time of the invaders' arrival was around 18 years ago, even before the first report for this area (1993; Livraghi pers.com.). Using the estimated range (2,150 m) from the Northern zone variogram of the invasive species cover and relating it to the probable arrival date (18 years ago), we can estimate a bulk spread rate ca. 120 m y⁻¹. This spread rate may represent an intermediate value for local dispersal events according to a recent meta-analysis of plant invasions (2–370 m y⁻¹; Pysek and Hulme 2005). Considering that our approach does not account for possible long-distance dispersal events, *H. pilosella* invasion may be taking place relatively quickly.

Finally, this study provided a rapid methodological approach and gave insights into the extent and patterns of the invasion, along with the identification of related ecological and land use factors. Although this is a recent plant invasion (i.e. low average invader species cover) and may not represent a severe rangeland problem at present, the great dissemination of this species across the region, its known success in similar ecosystems, and its probable ecosystem impact presents challenges to management regimes and suggests that quick action is needed to control the invasion and prevent a broader ecological impact. In this sense, our results point to management actions focused on reducing the presence of bare soil provoked by massive soil disturbances (i.e. road

building, oil pipe line construction, soil sowing, intense domestic animal use) by means of quick revegetation techniques, in order to constrain the propagule colonization of the invading species and prevent weed spread.

Acknowledgments We thank to E. Livraghi, R. Cerezani, V. Canalis, M. Jacob, H. Pico, C. García Sampedro and M.E. Gallego for the logistic and technical assistance during the project; Mr. José Bonilla for fieldwork assistance; and Brandon E. Lang Morris and one anonymous referee for useful comments on our manuscript. We also thank the ranchers of Tierra del Fuego, especially Mr. Errol O'Byrne from Cullen Ranch. O. Bruzzone and A. Sosa made valuable suggestions at early stages of this project. 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 CFI. R.B.R. and C.E. were supported by a doctoral fellowship from CONICET. K.B. was supported by a doctoral fellowship from the Agencia Nacional de Promoción Científica y Tecnológica, BID-PICT 14198.

References

- Allan HH (1924) Notes of the occurrence of certain exotic plants in New Zealand. *N Z J Agric* 29:311–315
- Anchorena J, Cingolani A, Livraghi E, Collantes M, Stoffella S (2001) Manejo del pastoreo de ovejas en Tierra del Fuego. EDIPUBLI S.A., Buenos Aires, ISBN 987-99049-2-3
- Anderson GL, Everitt JH, Richardson AJ, Escobar DE (1993) Using satellite data to map false broom weed (*Ericameria austrotexana*) infestation on South Texas Rangelands. *Weed Technol* 7:865–871
- Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. *PNAS* 103:374–378
- Asner GP, Vitousek PM (2005) Remote analysis of biological invasion and biogeochemical change. *PNAS* 102:4383–4386
- Asner GP, Knapp DE, Kennedy-Bowdoin T, Jones MO, Martin RE, Boardman J, Hughes RF (2008) Invasive species detection in Hawaiian rainforests using airborne imaging spectroscopy and LiDAR. *Remote Sens Environ* 112:1942–1955
- Bellingham PJ, Coomes DA (2003) Grazing and community structure as determinants of invasion success by scotch broom in a New Zealand montane shrubland. *Divers Distrib* 9:19–28
- Bishop GF, Davy AJ (1994) *Hieracium pilosella* L. (*Pilosella officinarum* F. Schultz and Schultz-Bip.). *J Ecol* 82:195–210
- Black CA (1965) Methods of soil analysis. Part 2. Chemical and microbiological properties. American Society of Agronomy, Madison
- Boswell CC, Espie PR (1998) Uptake of moisture and nutrients by *Hieracium pilosella* and effects on soil in a sub-humid grassland. *N Z J Agric Res* 41:251–261

- Braun K (2009) Efectos del pastoreo, el ambiente y las invasiones sobre procesos de la estepa fueguina. Dissertation. Ph.D. Thesis, University of Buenos Aires
- Brown JR, Archer SR (1989) Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80:19–26
- Bruno JF, Kennedy CW, Rand TA, Grant MB (2004) Landscape-scale patterns of biological invasions in shoreline plant communities. *Oikos* 107:531–540
- Carson HW, Lass LW, Callihan RH (1995) Detection of Yellow Hawkweed (*Hieracium pratense*) with high resolution multispectral digital imagery. 1995. *Weed Technol* 9:477–483
- Chaneton EJ, Perelman SB, Omacini M, León RJC (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate pampa grasslands. *Biol Invasions* 4:7–24
- Chytrý M, Jarosik V, Pysek P, Hajek O, Knollova I, Tichy L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541–1553
- Cingolani A, Posse G, Collantes MB (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Tierra del Fuego steppes (Patagonia, Argentina). *J Appl Ecol* 42:50–59
- Collantes MB, Anchorena J, Cingolani AM (1999) The steppes of Tierra del Fuego: floristic and growth-form patterns controlled by soil fertility and moisture. *Plant Ecol* 140:61–75
- Collantes MB, Braun K, Escartín C, Cingolani AM, Anchorena J (2005) Patrones de cambio de la vegetación de la estepa fueguina en relación al pastoreo. In: Oesterheld M, Aguiar MR, Ghersa C, Paruelo JM (eds) *La heterogeneidad de la vegetación de los agroecosistemas*. Ed. Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires
- Connor HE (1964) Tussock grassland communities in the Mackenzie Country, South Canterbury, New Zealand. *N Z J Bot* 2:325–351
- Connor HE (1965) Tussock grassland in the middle Rakaia Valley, Canterbury, New Zealand. *N Z J Bot* 3:261–276
- Connor HE (1992) Hawkweeds, *Hieracium* spp. In tussock grassland of Canterbury, New Zealand in 1960s. *N Z J Bot* 30:247–261
- Cook A, Marion G, Butler A, Gibson G (2007) Bayesian inference for the spatio-temporal invasion of alien species. *Bull Math Biol* 69:2005–2025
- Covacecich C (2001) *Pilosella* en Magallanes: acciones realizadas, recomendaciones y propuestas de estudios. Informe técnico. INIA-XII Región
- Crawley MJ (1987) What makes a community invisable? In: Gray AJ, Crawley MJ, Edwards PJ (eds) *Colonization, succession, and stability*. Blackwell Scientific Publications, Boston, pp 429–453
- Cressie N (1991) *Statistics for spatial data*. (Wiley series in probability and statistics). Wiley, New York, p 920
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology* 86:1602–1610
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- Diaz S, Fargione J, Chapin FS, Tilman D (2006) Biodiversity loss threatens human well-being. *PLOS Biol* 4:1300–1305
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (1989) *Biological invasions: a global perspective*. Wiley, New York
- Duncan RP, Colhoun KM, Foran BD (1997) The distribution and abundance of *Hieracium* species (hawkweeds) in the dry grasslands of Canterbury and Otago. *N Z J Ecol* 21:51–62
- Duryea M, Caraco T, Gardner G, Maniatty W, Szymanski BK (1999) Population dispersion and equilibrium infection frequency in a spatial epidemic. *Physica D* 132:511–519
- Everitt BS (1977) *The analysis of contingency tables*. Chapman and Hall, London
- Frederiksen P (1988) Soils of Tierra del Fuego. A satellite-based land survey approach. *Folia Geogr Danica* 18:1–159
- Gimeno I, Vila M, Hulme PE (2006) Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* L. in the western Mediterranean. *J Biogeogr* 23:1559–1565
- Goovaerts P (1997) *Geostatistics for natural resources evaluation*. Applied geostatistics series. Oxford University Press, Oxford
- Hector A, Minns A, Bazeley-Whiteand E, Lawton JH (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol Res* 16:819–831
- Higgins SI, Richardson DM, Cowling RM (2001) Validation of a spatial simulation model of a spreading alien plant population. *J Appl Ecol* 38:571–584
- Hobbs RJ, Huenekke LF (1992) Disturbance, diversity and invasion: implication for conservation. *Conserv Biol* 6:324–337
- Hueck K, Seibert P (1972) *Vegetationskarte von Südamerika*. Stuttgart, N. York. Aufl. 1981
- Jenkins TA (1992) A review of characteristics of mouse-ear hawkweed (*Hieracium pilosella*). In: Hunter GG, Mason CR, Robertson DM (eds) *Vegetation change in tussock grasslands, with emphasis on hawkweeds*. Occasional Publication No. 2, New Zealand Ecological Society, Christchurch, pp 15–26
- Johnstone PD, Wilson JB, Bremner AG (1999) Change in *Hieracium* populations in Eastern Otago over the period 1982–1992. *N Z J Ecol* 23:31–38
- Keeling MJ, Brooks SP, Gilligan CA (2004) Using conservation of pattern to estimate spatial parameters from a single snapshot. *PNAS* 101:9155–9160
- Klute A (1986) *Methods of soil analysis*. Part 1. Physical and mineralogical methods. American Society of Agronomy, Madison
- Korembli G, Forte Lay JA (1991) Contribución al estudio agroclimático del norte de Tierra del Fuego (Argentina). *Ans Ins Pat Ser Cs Nts* 20:125–134
- Krahulcova A, Krahulec F (1999) Chromosome numbers and reproductive systems in selected representatives of *Hieracium* subgen. *Pilosella* in the Krkonose Mts (the Sudeten Mts). *Preslia* 71:217–234

- Lamoureaux SL, Kelly D, Barlow ND (2003) Population dynamics in mature stands of *Hieracium pilosella* in New Zealand. *Plant Ecol* 166:263–273
- Larson DL, Anderson PJ, Newton W (2001) Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecol Appl* 11:128–141
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- León RJC, Bran D, Collantes MB, Paruelo JM, Soriano A (1998) Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral* 8:125–144
- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26
- Levine JM, Vilá M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc Lond B* 270:775–781
- Levine JM, Adler PB, Yelenik SG (2004) A metaanalysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7:975–989
- Livraghi E, Cabeza S, Kofalt R, Humano G, Mascó M, Montes L (1998) Documento de trabajo sobre *Hieracium pilosella* L. Informe Técnico INTA
- Lockwood JL, Cassey P, Blackburn TM (2005) The role of propagule pressure in explaining species invasion. *Trends Ecol Evol* 20:223–228
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Mack RN (1989) Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson W (eds) *Biological invasions: a global perspective*. Wiley, Brisbane, pp 155–179
- Mack MC, Simberloff WM, Lonsdale H, Evans M, Clout FA, Bazzaz SD (2000) Biotic Invasion: Causes, Epidemiology, Global Consequences and Control. *Issues Ecol* 5:1–19
- Makepeace W, Dobson AT, Scott D (1985) Interference phenomena due to mouse-ear and king-devil hawkweed. *N Z J Bot* 23:79–90
- Martinić BM (1982) La Tierra de los Fuegos. Municip. De Porvenir. Chile
- McIntosh PD, Allen RB (1993) Soil pH declines and organic carbon increases under hawkweed (*Hieracium pilosella*). *N Z J Ecol* 17:59–60
- McIntosh PD, Loeseke M, Bechler K (1995) Soil changes under mouse-ear hawkweed (*Hieracium pilosella*). *N Z J Ecol* 19:29–34
- Meurk CD, Walker S, Gibson RS, Espie P (2002) Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990–2000. *N Z J Ecol* 26:95–106
- Moore DM (1983) Flora of Tierra del Fuego. Ed. Missouri Botanical Garden, p 396
- Nehrbass N, Winkler E, Mullerova J, Pergl J, Pysek P, Perglova I (2007) A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. *Biol Invasions* 9:383–395
- Pebesma EJ (2004) Multivariable geostatistics in S: the gstat package. *Comput Geosci* 30:683–691
- Perelman SB, Chaneton EJ, Batista WB, Burkart SE, León RJC (2007) Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *J Ecol* 95:662–673
- Pisano E (1977) Fitogeografía de Fuego-Patagonia Chilena. I Comunidades vegetales entre las latitudes 52 y 56 S. *Ans Ins Pat Ser Cs Nts* 8:121–250
- Posse G, Anchorena J, Collantes MB (2000) Spatial micro-patterns in the steppe of Tierra del Fuego induced by sheep grazing. *J Veg Sci* 11:43–50
- Pysek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience* 12:302–315
- Pysek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends Ecol Evol* 23:237–244
- Radoševich SR, Stubbs MM, Ghera CM (2003) Plant invasions—processes and patterns. *Weed Sci* 51:254–259
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rejmánek M, Pitcairn MJ (2002) When is eradication of exotic pest plants a realistic goal? In: Veitch CR, Clout MN (eds) *Proceedings of the international conference on eradication of islands invasives. Turning the tide: the eradication of invasive species*. Gland, Switzerland: IUCN SSC Invasive Species Specialist Group. pp 249–253
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655–1661
- Ribeiro PJ, Diggle PJ (2001) geoR: a package for geostatistical analysis. *R-NEWS* 1:15–18
- Robinson TP, van Klinken RD, Metternicht G (2008) Spatial and temporal rates and patterns of mesquite (*Prosopis species*) invasion in Western Australia. *J Arid Environ* 72:175–188
- Rose AB, Platt KH, Frampton CM (1995) Vegetation change over 25 years in a New Zealand short-tussock grassland: Effects of sheep grazing and exotic invasions. *N Z J Ecol* 19:163–174
- Rose AB, Basher LR, Wiser SK, Platt HK, Lynn LH (1998) Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. *N Z J Ecol* 22:121–140
- Rossi RE, Mulla DJ, Journel AG, Franz EH (1992) Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecol Monogr* 62:277–314
- Rouget M, Richardson DM (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist* 162:713–724
- Sala OE, Chapin FS, Armesto JJ (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Sax DF (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Divers Distrib* 8:193–210
- Scott NA, Saggat S, McIntosh PD (2001) Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. *Ecol Appl* 11:1311–1322
- Serra J (1990) Relevamiento de pasturas implantadas en Tierra del Fuego. Informe técnico CFI
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176

- Stoffella SL (2003) Efecto de la compactación del suelo sobre la estructura del matorral de mata negra *Chilodactylopusium diffusum* en Tierra del Fuego. Dissertation. M.Sc. Thesis, University of Buenos Aires
- Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hot spots of native plant diversity. *Ecol Monogr* 69:25–46
- Thuiller W, Richardson DM, Rouget M, Procheş Ş, Wilson JRU (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology* 87:1755–1769
- Tilman D (1988) Plant strategies and the dynamics and structures of plant communities. Monographs in population biology N°26. Princeton University Press, Princeton, p 360
- Traveset A, Moragues E, Valladares F (2008) Spreading of the invasive *Carpobrotus* aff. *acinaciformis* in Mediterranean ecosystems: The advantage of performing in different light environments. *Appl Veg Sci* 11:45–54
- Treskonova M (1991) Changes in the structure of tall tussock grasslands and infestation by specie of *Hieracium* in the Mackenzie country, New Zealand. *N Z J Ecol* 15:65–78
- Turner MG, Gardner RH (1991) Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity. Springer, New York, p 535
- Vander Kloet SP (1978) Biogeography of *Hieracium pilosella* L. in North America with special reference to Nova Scotia. *Proc N S Inst Sci* 28:127–134
- Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861–1876
- Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, and ecosystem effects. *Ecol Monogr* 59:247–265
- Vitousek PM, Walker L, Whiteaker L, Mueller-Dombois D, Matson P (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–804
- Vitousek PM, D'Antonio CM, Loope LL, Reimánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *N Z J Ecol* 21:1–16
- Voss EG, Böhlke MW (1978) The status of certain hawkweeds (*Hieracium subgenus Pilosella*) in Michigan. *Michigan Bot* 17:35–47
- Webb CJ, Sykes WR, Arnock-Jones PJ (1988) Flora of New Zealand volume IV. Naturalised pteridophytes, gymnosperms, dicotyledons, botany division. DSIR, Christchurch
- Winkler E, Stöcklin J (2002) Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Annals Bot* 89:525–536
- Wood S (2006) Generalized additive models: an introduction with R (texts in statistical science). Chapman & Hall, London
- Wu Y, Rutchey K, Wang N, Godin J (2006) The spatial pattern and dispersion of *Lygodium microphyllum* in the Everglades wetland ecosystem. *Biol Invasions* 8:1483–1493
- Zhu L, Sun OJ, Sang WG, Li ZY, Ma KP (2007) Predicting the spatial distribution of an invasive plant species (*Eupatorium adenophorum*) in China. *Landscape Ecol* 22:1143–1154
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA (2009) Mixed effects models and extensions in ecology with R (statistics for biology and health). Springer, Berlin