



Local and intermediated-intensity soil disturbances increase the colonization and expansion dynamics of an invasive plant in Southern Patagonian rangelands

R.B. Rauber^{1,2,4}, P.A. Cipriotti^{1,3} and M.B. Collantes¹

¹Laboratorio de Ecología de Pastizales, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina– CONICET

²Instituto Nacional de Tecnología Agropecuaria (INTA), Villa Mercedes, San Luis

³Dpto. de Métodos Cuantitativos y Sistemas de Información, IFEVA, Facultad de Agronomía, Universidad de Buenos Aires / CONICET, Buenos Aires, Argentina

⁴Current address corresponding author. Instituto Nacional de Tecnología Agropecuaria (INTA). Ruta 7 y 8. Villa Mercedes (5730). San Luis. Argentina. Phone/Fax: (542657) 423249, E-mail: rauber@sanluis.inta.gov.ar

Keywords: Exotic species, *Hieracium pilosella*, Plant invasion, Plant spread, Sheep grazing.

Abstract: Disturbances are important drivers in natural ecosystems, affecting the vegetation structure and functioning. Invasions of exotic plant species are often associated to disturbances in a complex manner, because they depend on the type, intensity, spatial and temporal arrangement of disturbances, and the particular abiotic and biotic context. Field studies that evaluate the dynamics of plant invasions under different disturbance regimes have a great importance for the understanding of the disturbance effects on invasion spread. In this work we evaluated, through a field manipulative experiment, the early colonization and expansion dynamics of an aggressive invader of grasslands, *Hieracium pilosella* L., under two disturbance types. We used a split-plot experiment by crossing three levels for a local, sporadic, of increasing intensity disturbance [i.e., 1- undisturbed, 2- vegetation mowing, and 3- ploughing], within two levels for an extensive and chronic disturbance (i.e., grazed and ungrazed). In the range of intensities of disturbance evaluated, the intermediate intensity (i.e., mowing) accelerated the colonization when it is grazed and the expansion of *H. pilosella* in ungrazed condition. In contrast, lower and higher intensity disturbances, such as ungrazed and ploughing treatments decelerated both invasion processes. Changes in resource availability, interspecific competition and particular characteristics of the invader, i.e., high light requirements, prostrate growth and the presence of stolons, could explain these early invasion patterns.

Introduction

Disturbances are key drivers in natural ecosystems, because they can and maintain the species diversity by generating spatio-temporal heterogeneity in resources (Hobbs and Huenneke 1992, White and Jentsch 2001). Responses of the biotic community to disturbances may be very variable due in part to the spatial and temporal characteristics of the disturbance events, their intensity and fluctuations (Catford et al. 2012). Disturbances can be characterized by their duration, frequency, intensity, timing and spatial or temporal variability (Hobbs and Huenneke 1992). Among the different types of disturbances on plant communities, the herbivory by domestic ungulates can be considered as a chronic disturbance of relatively low intensity level, especially on well adapted grasslands (Vavra et al. 2007). Domestic grazing, in other way, has very complex effects on vegetation and depends mainly on the stocking rate (Hobbs and Huenneke 1992, Milchunas and Lauenroth 1993, Ferraro and Oesterheld 2002). Grazing can favor low height and prostrate species by grazing avoiding (Milchunas and Lauenroth 1993), and stoloniferous species because in dense and high sward of ungrazed vegetation, the stolons become suspended above the ground, impeding that they reach the soil and rooting (Belsky 1992).

Invasion of exotic plant species are often positively associated to different types of disturbances, such as grazing, fires and flooding (Catford et al. 2012, Hobbs and Huenneke 1992). On one hand, disturbances may favor plant invasions probably by competition reduction, transient increase of nutrients, enhanced secondary seed dispersal (Hobbs 1989, Hobbs and Huenneke 1992, Jesson et al. 2000, White and Jentsch 2001), and by disrupting the original community and trophic structure (McCann 2007). On the other hand, several results suggest that domestic grazing can facilitate exotic invasion by selective feeding behavior, herbivory adaptations (Augustine and McNaughton 1998, McIntyre and Lavorel 1994), trampling, seeds dissemination or changes in fire intensity (Fleischner 1994, Rogstad et al. 2009, Vavra et al. 2007).

Studies that deal with the effects of different types of disturbances on invasion success generally evaluate the state of the vegetation – and the invasion – at a certain moment of time after disturbance events. Even though some theoretical models were proposed (Pausas et al. 2006, Spence et al. 2011), the dynamic of invasion through the time after disturbances remains almost unexplored, despite that disturbance effects on native vegetation dynamic have been largely studied in several ecosystems (Jentsch 2001, Łaska 2001, Linderman et al. 2006). There might be thought that the

dynamics of invasion is equivalent to the native vegetation dynamic, because an invasion can be considered a large-scale natural event where any species grows and expands (Higgins and Richardson 1996). Nevertheless, there are evidences that disturbances can favor the abundance and performance of the invasive plant species in a novel environment with respect to its native range by escaping from specific soil pathogens (Hierro et al. 2006), or by a previous better adaptation to anthropogenic disturbances (Kowarik 2008). Furthermore, the success of an invasion event seems to be dependent of a lot of factors interacting in a complex manner, and the invasibility of a site would be a property that fluctuates also along time (Renne et al. 2006). Hence, a comprehensive evaluation of the effects of different types of disturbances on early invasion dynamic considering both the particular traits of the invader and characteristics of the abiotic context (e.g. different types of disturbances), could help to understand the community ecology and the underlying mechanisms behind an invasion event. Even more, there is important an evaluation of how an only one-time disturbance could affect invasive processes, because it would be enough to break the barrier to invaders spread, promoting exotic species establishment (Johnstone 1986), and it is important to avoid those kind of practices that increase invasive invader establishment (West 1993).

Mouse-ear hawkweed (*Hieracium pilosella* L.) is a well-known plant invader. *H. pilosella* is native to northern Eurasia (Bishop and Davy 1994) and aggressively invades different grasslands around the World (Covacevich 2009, Treskonova 1991, Vander Kloet 1978, Winkler and Stöcklin 2002). After colonization, this perennial species gradually forms dense and prostrate mats that exclude other species. It is common in dry, poor and degraded grasslands (Bishop and Davy 1994), but it is very efficient in nutrient pulse capture and use (Fan and Harris 1996). It may also release an allelopathic compound which inhibits the radical growth of other species (Makepeace et al. 1985). It can reproduce by stolons, which are stimulated by grazing (Covacevich 2009), and by sexually or apomictically generated seeds, which are efficiently dispersed by wind (Sheepens 1994). The particular combination of these features confer to this species competitive and stress tolerance characteristics (Grime 1977).

In the Argentinean Fuegian grasslands, where domestic sheep have been grazing for 110 years (Anchorena et al. 2001), high cover of *H. pilosella* (up to 70%) was associated to sporadic disturbances events such as plant removing, ploughing, oil pipelines standing, pasture sowing and fertilizer, and road construction (Cipriotti et al. 2010). Evidences from other studies indicate that *H. pilosella* success is associated to disturbances like fire and overgrazing (Foran et al. 1992, Jesson et al. 2000, O'Connor et al. 1999, Rose et al. 1998, Treskonova 1991), probably because this species grows better in sites with open and short vegetation, with high light availability and nutrient pulses (Bishop and Davy 1994, Köhler et al. 2005). Different field studies and experiments, however, show contradictory results about *H. pilosella* responses to disturbances, in particular, to sheep grazing (Grove et al. 2002, Meurk et al. 2002, Rose et al. 1995, Walker et al. 2005, Wilson 1992).

The aim of this work was to evaluate the short-term dynamic of an aggressive invader of grasslands at a small spatial scale under the combination of two different types of disturbances that commonly occur in the region: a local and sporadic vs. an extensive and chronic disturbance. For this, we carried out a field manipulative experiment, and as local disturbance we experimentally generated three different disturbances of increasing intensity. The first one corresponded to the control treatment, without any soil or vegetation disturbance. The second one involved vegetation mowing but leaving the soil structure intact, and the third one corresponded to vegetation mowing plus soil ploughing. These disturbances were crossed by two grazing conditions, ungrazed and grazed. The single and the interactive effects of these disturbance types on changes in the invader species frequency and cover were evaluated along five years. We predict an accelerated dynamic of invasion under local and of the highest intensity disturbance in grazed plots, due to the previous field observations and knowledge of the species, this is: a) *H. pilosella* presents a regional pattern of high invasion in sites with drastic soil disturbance history in the Argentinean Fuegian steppe (Cipriotti et al. 2010, Rauber et al. 2012); b) grazing generally favor to prostrate species (Milchunas and Lauenroth 1993); c) asexual reproduction by stolons of *H. pilosella* is stimulated by grazing (Covacevich 2009); and d) invasion of exotic species generally increment as disturbance intensity increment (Duggin and Gentle 1998). Therefore, from the experiment, we expect a greater colonization and cover in ploughed and grazed condition than the other ones after experiment beginning.

Methods

Study area

The experiment was carried out in a Fuegian grassland at the north of Tierra del Fuego province, Argentina (52° 54' 53'' S, 68° 33' 37'' W). The Fuegian grasslands are in the southern portion of the Magellanic steppe, a humid variant of the Patagonian semi-desert (Collantes et al. 2009), covering around 5,000 km² at the north of Tierra del Fuego Island, Argentina. The area has a climatic gradient, with precipitation increasing and temperature decreasing in a northeast-southwest direction. Rains vary from 300 to 450 mm/yr across this gradient, and are evenly distributed along the year, although water balance deficit is greater in summer because of strong W-NW winds (Walter and Box 1983). At landscape scale, most of the area is covered by the tussock grass *Festuca gracillima* Hooker f. The shrub *Chiliotrichum diffusum* (Foster f.) O. Kunze, however, dominates on deeper and moisture soils, *Poa spiciformis* (Steud.) Hauman & Parodi grass lawns on dry, north-facing slopes, and hydrophytic communities occupy valleys and depressions (Collantes et al. 1999, 2009).

Field experiment

The experiment was carried out in a paddock of about 200 ha, where all shrubs were mechanically removed one time and

Table 1. Statistical significance for the fixed single effects of grazing, local disturbance and year, and the double and triple interaction effects among them on the logarithm of the accumulated colonization probability of *H. pilosella*

	D. F.*	F	p-value
Intercept	1	8.13352	0.046
Grazing	1	0.03404	0.862
Local disturbance	2	3.35564	0.047
Year	2	5.53722	0.009
Grazing*Local disturbance	2	3.83021	0.032
Grazing*Year	2	1.68112	0.202
Local disturbance*Year	4	2.33300	0.077
Grazing*Local disturbance*Year	4	0.61425	0.655

*D.F. = Degrees of freedom

exotic species (*Dactylis glomerata* L., *Trifolium repens* L. and *Festuca arundinacea* Schreb) were sown with fertilizer addition many times between 1966 and 1989 (Serra 1990). Currently, cover vegetation is almost 100% and native and sowed species coexist. At the beginning of the experiment, *H. pilosella* cover was 15% in the sowed area. First, we selected six plots of approximately 0.5 ha inside the paddock, all similar in topography and species composition [similarity index higher than 76%, (Sørensen 1948)], and separated by 200 to 2,000 m. Three of these plots were randomly selected for livestock exclusion with 1.4 m high fences. Therefore, there are 6 plots, 3 grazed and 3 ungrazed. Previous to the experiment beginning, all plots had similar grazing management with stocking rates of 0.8 sheep/ha (Anchorena et al. 2001). Grazing treatments in the experiment continued with the same stocking rate. Within each plot, we set 15 subplots of 1 m² without *H. pilosella*, at 25 - 100 cm windward from an already occupied invader patch, resulting in a total of 90 subplots (15 subplots in 6 plots).

Three treatments of different types of local disturbances were randomly assigned to the subplots in a completely randomized split-plot design. The treatments were: 1- undisturbed (U); 2- mowed (M), in which all aboveground plant organs were removed with scissors at the soil surface level, but without soil disturbance; and 3- ploughed (P) in which the upper 15 cm soil layer was disturbed with a hoe, and all the underground organs were removed. The treatments were applied in the spring of 2005.

H. pilosella colonization and expansion

The early dynamic of the invader species was evaluated by considering two processes of plant spread, colonization and expansion, at the first, second and fifth year after the experiment beginning. The colonization was estimated as the percentage of subplots with the occurrence of *H. pilosella* over the total initially empty subplots and the expansion was estimated as the cover percentage of the invader inside the subplots along time.

To calculate *H. pilosella* cover, we measured two orthogonal diameters for each rosette or continuous patch, and then we estimated the patch area as $\pi \times a \times b$, where *a* and *b* are the two patch radii. The sum of all patch areas was divided by the area of subplots (1 m²), resulting in the cover estimation.

Data analysis

We carried out mixed models for a completely randomized split-plot design. As a measure of colonization, we estimated the logarithm of the accumulated frequency of the number of subplots with presence of the invasive species across treatments and years and we estimated the effects from a linear mixed model (local disturbance type \times grazing \times year), considering the plot as a random effect (Højsgaard et al. 2006, Zuur et al. 2009). On the other hand, to assess expansion dynamic, we used a generalized mixed model with a biased distribution to take into account zero-inflated data for continuous variables (Tweedie models), and we estimated the single and interactive fixed effects from the model (local disturbance type \times grazing condition \times year), with the plot as a random effect (El Shaarawi et al. 2011). For both response variables, we conducted post-hoc Tukey tests (alpha=5%) to contrast means only for significant single or interactive effects in respective ANOVAs. Statistical analyses were performed with the R environment, packages lme4 (Pinheiro et al. 2009), multcomp (Hothorn et al. 2008),phia (De Rosario-Martinez 2013), tweedie (Dunn 2013) and software Infostat (Di Rienzo et al. 2008) and Statistica.

Results

Colonization

The accumulated probability of invader occurrence increased through the time after the experiment beginning (Table 1; Fig. 1a). Under the mowed and grazed treatment, *H. pilosella* colonization was accelerated and its colonization probability was higher than for any other treatment. In contrast, the undisturbed and ungrazed treatment showed the lowest colonization. The other treatments had similar colonization probabilities (50-65%, Fig. 1b).

Expansion

The mean percentage of the invader cover also increased significantly over the years (Table 2; Fig. 2a). But, *H. pilosella* presented the highest cover (8.8%) under the mowed treatment in ungrazed condition, and no differences were seen among the other treatments (1.5-3.7%, Fig. 2b).

Table 2 Statistical significance for the fixed single effects of grazing, local disturbance and year, and the double and triple interaction effects among them on the invader mean cover of *H. pilosella*

	D.F.*	Chi-square	p-value
Intercept	1		
Grazing	1	17.6710	<0.001
Local disturbance	2	8.8215	0.012
Year	2	320.0026	<0.001
Grazing*Local disturbance	2	12.6837	0.002
Grazing *Year	2	0.4112	0.814
Local disturbance *Year	4	9.4332	0.051
Grazing *Local disturbance *Year	4	1.2343	0.872

* D.F. = degrees of freedom

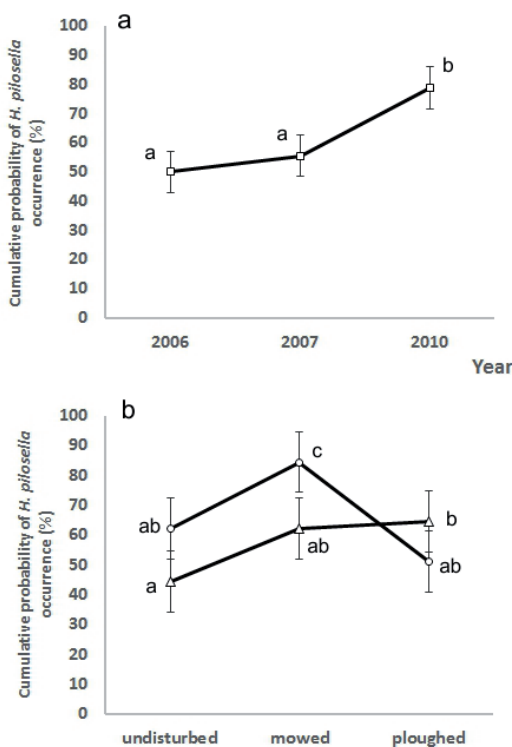


Fig. 1 a) Cumulative probability of *H. pilosella* occurrence through time across all treatments; b) Cumulative probability of *H. pilosella* occurrence for grazing and local disturbance treatments across all years. Triangles: ungrazed, circles: grazed. Hated bars represent the standard error, and different letters represent significant differences among mean values through the post-hoc Tukey test ($\alpha=0.05$).

Discussion

Our results show that, even in the absence of local disturbances under grazing (i.e., the typical conditions of these rangelands), there are possibilities to the invader colonization. Hence, local disturbances are not a key pre-requisite for successful invasion, but *H. pilosella* invasion seems to be accelerated by the mowing treatment. Invasive species colonization presented a higher response to mowing and grazed treatment with respect to the other treatments (Fig. 1b). Short-term heavy defoliation, simulated by the mowing

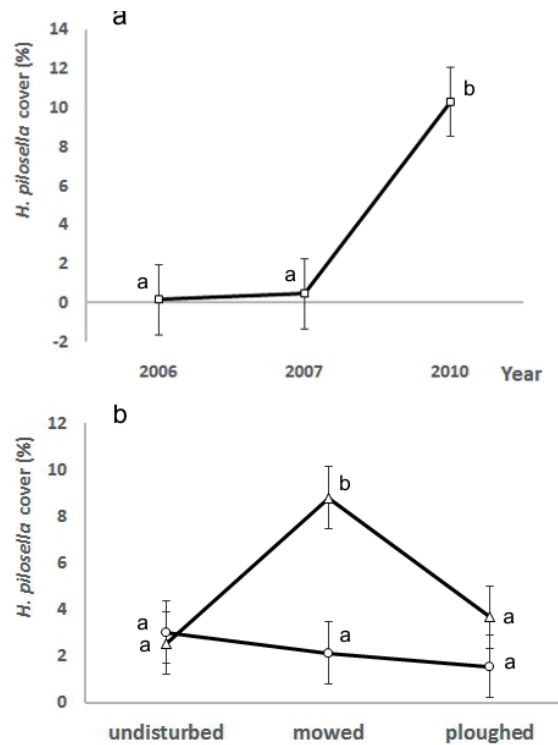


Fig. 2 a) Weighted mean cover of *H. pilosella* through time across all treatments; b) Weighted mean cover of *H. pilosella* for grazing and local disturbance treatments across all years. Triangles: ungrazed, circles: grazed. Hated bars represent the standard error, and different letters represent significant differences among mean values through the post-hoc Tukey test ($\alpha=0.05$).

treatment, strongly affects canopy structure, but not generates great fluctuation over soil chemical properties (Guo et al. 2012). In contrast, short-term heavy defoliation plus soil structure destruction, generated by the ploughing treatment, could increase the availability of both light and soil resources. Therefore, the invasion acceleration after mowed and grazed treatment could not be explained by a transient soil resource increase or variation, but may be explained by a decrease of interspecific competition for light, combined to particular seed and plant characteristics of the invader species. Aboveground biomass elimination favors stoloniferous

expansion (Belsky 1992) and diminishes light competition. The deceleration of colonization in undisturbed and ungrazed condition also could be explained in part by the light limitation for germination (Köhler et al. 2005).

The results of colonization dynamic did not support our original hypothesis since we expected more accelerated invader colonization under ploughed and grazed treatment, which represents the most highly disturbed condition. However, our results can be interpreted under the intermediate disturbance hypothesis framework (Catford et al. 2012). The combination of competitive and stress tolerant characteristics of *H. pilosella* make it adapted to the intermediate successional state generated by the intermediate disturbance intensity. This idea is supported by the fact that in the most intense disturbance situation (i.e. ploughed), we verified a fast colonization of ruderal species, principally *Rumex acetosella* L. (data not show), which is an early colonizer of disturbed environment in the whole Patagonia. Therefore, ruderal species seems to be favored under intense disturbance and it is possible that in a lower intensity disturbance scenario (undisturbed and grazed), the most competitive species dominate.

The invader colonization under ploughed conditions could also be disfavored by changes occurring in the soil microbial activity (Gros et al. 2004) in the uppermost soil layer. In addition, the increased bare soil area caused by ploughing can diminish *H. pilosella* seed retention in windy environments like these Fuegian steppes in comparison to vegetated treatments, delaying the invader colonization (Rotundo and Aguiar 2005, Schurr et al. 2005). At long-term, it is possible that the invader colonization also has been disfavored by decreasing soil organic matter, C and N as a result of ploughing (López-Fando and Pardo 2009, Stockfisch et al. 1999).

With respect to the expansion dynamic, global pattern seems to be exponential (Fig. 2a), although there are differences in invader cover among treatments (Fig 2b). Despite the higher colonization in the mowed and grazed conditions, the mean cover was higher in the mowed but ungrazed condition. Dissemination of the species would be by seeds (Chapman et al 2000, Jenkins 1992, Koltunow et al 1998), and once it has established, reproduction and expansion would occur asexually through stolons (Stöcklin and Winkler 2004, Winkler and Stöcklin 2002). It is possible that under mowing and grazing the expansion be limited by accidental herbivory on stolons and soil compaction, whereas under mowing and ungrazed, stoloniferous expansion occurs without restrictions. The low expansion rate of this species could be attributed to the stressful environment, because in this site, annually precipitations are lightly below 300 mm. Hence, the community modification by the one-time mowing treatment favors invader expansion, even without grazing. Another study indicates that *H. pilosella* does not generate a permanent soil seed bank in this region (Raubert 2011), which coincide to studies made in other countries like the UK and New Zealand (Jenkins 1992); so, disturbance effects would not be acting through this mechanism.

It can be considered that the disturbances applied in this experiment are different kinds of disturbances and not

a simple intensity gradient. However, taking into account the disturbance as “process removing or damaging biomass” (Grime 1979), as “any relative discrete event in time that disrupt ecosystem, community or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett 1985), or as “an event which alters the niche opportunities available to the species in a system” (Shea et al. 2004), our experimental application of disturbances would correspond to an increasing disturbance intensity (undisturbed, mowing, and ploughing), because increasingly remove and destroy biomass, disrupt the system, changes resources, substrate and physical environment, and alters niche opportunities available.

A shortcoming of our study that provided uncertainties over the results interpretation was the inability of completely exclude colonization by stolons at sub-plot level, and we must to assume that colonization was through seeds, according to precedent studies about strategies of reproduction of this invasive species. For another hand, a factor that could increment the variability source was the incapacity of measure the propagule availability in each subplot. A more controlled experiment in which each subplot receives the same propagule pressure could improve this aspect.

In conclusion, invader response to disturbance intensity seems to be dependent to particular characteristics of the species related to use of resources. Whereas it was predicted that in the most disturbed extreme of a disturbance gradient, the susceptibility to invasion will be greater, we observed that in our case, the higher invasion was seen in an intermediate disturbance situation. Under high disturbance intensity, ruderals would be favored, whereas in the other extreme, in sites with low disturbance intensity, competitive species had advantage. In the middle of the intensity gradient, stress tolerant species proliferates.

Acknowledgements: We thank to Mr. E. O’Byrne from Cullen Ranch for his hospitality and to J. Bonilla for his help for the field work. We also are very grateful to Dr. D. Steinaker for a friendly review and critical reading of the English version, and to the two anonymous reviewers, whose suggestions greatly improved 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.

References

- Anchorena, J., A. Cingolani, E. Livraghi, M.B. Collantes and S. Stoffella. 2001. *Manejo del pastoreo de ovejas en Tierra del Fuego*. EDIPUBLI S.A., Buenos Aires. ISBN 987-99049-2-3.
- Augustine, D.J. and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildl. Manag.* 62: 1165-1183.
- Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3: 187-200.

- Bishop, G.F. and A.J. Davy. 1994. *Hieracium pilosella* L. (*Pilosella officinarum* F. Schultz & Schultz-Bip.). *J. Ecol.* 82: 195-210.
- Catford, J.A., C.C. Daehler, H.T. Murphy, A.W. Sheppard, B.D. Hardesty, D.A. Westcott, M. Rejmánek, P.J. Bellingham, J. Pergl, C.C. Horvitz and P.E. Hulme. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspect. Plant. Ecol. Evol. Syst.* 14: 231-241.
- Chapman, H.M., D. Parh and N. Oraguzie. 2000. Genetic structure and colonizing success of a clonal, weedy species, *Pilosella officinarum* (Asteraceae). *Heredity* 84: 401-409.
- Cipriotti, P.A., R.B. Rauber, M.B. Collantes, K. Braun and C. Escartín. 2010. *Hieracium pilosella* invasion in the Tierra del Fuego steppe, Southern Patagonia. *Biol. Inv.* 12: 2523-2535.
- Collantes, M.B., J. Anchorena and A.M. Cingolani. 1999. The steppes of Tierra del Fuego: floristic and growthform patterns controlled by soil fertility and moisture. *Plant. Ecol.* 140: 61-75.
- Collantes, M.B., J. Anchorena, S. Stoffella, C. Escartín and R. Rauber. 2009. Wetlands in the fuegian steppe (Tierra del Fuego, Argentina). *Folia Geobot.* 44: 227-245.
- Covacevich, N. 2009. Magallanes: veinte años de pilosella. *Revista Tierra Adentro* N° 83. <http://www.inia.cl/biblioteca-digital/>. Accessed 19 November 2012
- De Rosario-Martinez H. 2013. phia: Post-Hoc Interaction Analysis. R package version 0.1-2. <http://CRAN.R-project.org/package=phia>
- Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M., Robledo C.W. 2008. *InfoStat, versión 2008*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Duggin, J.A. and C.B. Gentle. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. *Forest Ecol. Manag.* 109: 279-292.
- Dunn, P. 2013. tweedie: Tweedie exponential family models. R package version 2.1.7.
- El-Shaarawi A.H., Zhu R. and H. Joe. 2011. Modelling species abundance using the Poisson-Tweedie family. *Environmetrics* 22: 152-164
- Fan, J. and W. Harris. 1996. Effects of soil fertility and cutting frequency on interference among *Hieracium pilosella*, *H. praealtum*, *Rumex acetosella*, and *Festuca novae-zelandiae*. *N. Z. J. Agric. Res.* 39: 1-32.
- Ferraro, D.O. and M. Oesterheld. 2002. Effect of defoliation on grass growth. A quantitative review. *Oikos* 98:125-133.
- Fleischner, T.L. 1994. Ecological costs of livestock grazing in Western North America. *Conserv. Biol.* 8: 629-644.
- Foran, B.D., J. Bates, P. Murray, G. Heward and D. Pickens. 1992. A paddock based survey of management factors relating to mouse-ear hawkweed (*Hieracium pilosella*) dominance in Central Otago. In: G.G. Hunter, C.R. Mason, D.M. Robertson, (eds.), *Vegetation Change in Tussock Grasslands, with Emphasis on Hawkweeds*. Occasional Publication No. 2. New Zealand Ecological Society, Christchurch. pp. 64-67.
- Grime J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 169-1194.
- GRIME 1979???**
- Gros, R., L.J. Monrozier, F. Bartoli, J.L. Chotte and P. Faivre. 2004. Relationships between soil physico-chemical properties and microbial activity along a restoration chronosequence of alpine grasslands following ski run construction. *Appl. Soil Ecol.* 27: 7-22.
- Grove, P.B., A.F. Mark and K.J.M. Dickinson. 2002. Vegetation monitoring of recently protected tussock grasslands in the southern South Island, New Zealand. *J. Royal Soc. N. Z.* 32: 379-414.
- Guo, Y.-J., L. Han, G.-D. Li, J.-G. Han, G.-L. Wang, Z.-Y. Li and B. Wilson. 2012. The effects of defoliation on plant community, root biomass and nutrient allocation and soil chemical properties on semi-arid steppes in northern China. *J. Arid. Env.* 78: 128-134.
- Hierro, J.L., D. Villarreal, Ö. Eren, J.M. Graham and R.M. Callaway. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. *Am. Nat.* 168: 144-156.
- Higgins, S.I. and D.M. Richardson. 1996. A review of models of alien plant spread. *Ecol. Modell.* 87: 249-265.
- Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. In: J.A. Drake, F. diCastrì, R. Groves, F. Kruger, H. Mooney, M. Rejmanek and M. Williamson (eds.), *Biological Invasions: A Global Perspective*. Wiley and Sons, Chichester, UK, pp. 389-405.
- Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6: 324-337.
- Højsgaard, S., U. Halekoh and J. Yan. 2006. The R package geepack for generalized estimating equations. *J. Stat. Softw.* 15: 1-11.
- Hothorn, T., F. Bretz and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biom. J.* 50: 346-363.
- Jenkins, T.A. 1992. A review of characteristics of mouse-ear hawkweed (*Hieracium pilosella*). In: G.G. Hunter, C.R. Mason, D.M. Robertson, (eds.), *Vegetation Change in Tussock Grasslands, With Emphasis on Hawkweeds*. Occasional Publication No. 2, New Zealand Ecological Society, Christchurch. pp. 15-23.
- Jentsch, A. 2001. *The significance of disturbance for vegetation dynamics. A case study in dry acidic grasslands*. PhD Thesis, Bielefeld University.
- Jesson, L., D. Kelly and A. Sparrow. 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. *N. Z. J. Bot.* 38: 451-468.
- Johnstone, I.M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Biol. Rev.* 61: 369-394.
- Köhler, B., A. Gigon, P. Edwards, B. Krüsi, R. Langenauer, A. Lüscher and P. Ryser. 2005. **Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements.** *Perspect. Plant Ecol. Evol. Syst.* 7: 51-67.
- Koltunow A.M., S.D. Johnson and R.A. Bicknell. 1998. Sexual and apomictic development in *Hieracium*. *Sex Plant Reproduction* 11:213-230
- Kowarik, I. 2008. On the role of alien species in urban flora and vegetation. In: J.M. Marzluff, E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, C. ZumBrunnen and U. Simon (eds.), *Urban Ecology: An International Perspective on the Interaction Between Humans and Nature*. Springer, New York. pp. 321-338.
- Łaska, G. 2001. The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecol.* 157: 77-99.
- Linderman, M.A., L. An, S. Bearer, G. He, Z. Ouyang and J. Liu. 2006. Interactive effects of natural and human disturbances on vegetation dynamics across landscapes. *Ecol. Appl.* 16: 452-463.
- López-Fando, C. and M.T. Pardo. 2009. Changes in soil chemical characteristics with different tillage practices in a semi-arid environment. *Soil Tillage Res.* 104: 278-284.

- Makepeace, W., A.T. Dobson and D. Scott. 1985. Interference phenomena due to mouse-ear and king devil hawkweed. *N. Z. J. Bot.* 23: 79-90.
- McCann, K. 2007. Protecting biostructure. Biodiversity researchers have focused on diversity at the cost of ignoring the networks of interactions between organisms that characterize ecosystems. *Nature* 446: 29.
- McIntyre, S. and S. Lavorel. 1994. How environmental and disturbance factors shape composition in temperate Australian grassland communities. *J. Veg. Sci.* 5: 373-384.
- Meurk, C.D., S. Walker, R.S. Gibson and P. Espie. 2002. Changes in vegetation in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990-2000. *N. Z. J. Ecol.* 26: 95-106.
- Milchunas, D.G. and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* 63: 327-366.
- O'Connor, K.F., A.H. Nordmeyer and K. Svavarsdóttir. 1999. Changes in biomass and soil nutrient pools of tall tussock grasslands in New Zealand. In: O. Arnalds and S. Archer (eds.), *Case Studies of Rangeland Desertification*. Proceedings from an international workshop in Iceland. Rala Report No. 200. Agricultural Research Institute, Reykjavik. pp. 125-145.
- Pausas, J.G., F. Lloret and M. Vilà. 2006. Simulating the effects of different disturbance regimes on *Cortaderia selloana* invasion. *Biol. Conserv.* 128: 128-135.
- Pinheiro, J., D. Bates, S. DebRoy and D. Sarkar. 2009. *The nlme package: linear and nonlinear mixed effects models*. URL: <http://cran.r-project.org/src/contrib/Descriptions/nlme.html>.
- Rauber, R.B. 2011. *Invasión de Hieracium pilosella L. en pastizales de Tierra del Fuego*. Ph.D. Thesis. Universidad de Buenos Aires.
- Rauber, R.B., M.B. Collantes, P.A. Cipriotti and J. Anchorena. 2012. Biotic and abiotic constraints to a plant invasion in vegetation communities of Tierra del Fuego. *Austral Ecol.* DOI: 10.1111/j.1442-9993.2012.02427.x
- Renne, I.J., B.F. Tracy and I.A. Colonna. 2006. Shifts in grassland invasibility: effects of soil resources, disturbance, composition, and invader size. *Ecology* 87: 2264-2277.
- Rogstad, A., T.M. Bean, A. Olsson and G.M. Casady. 2009. Fire and invasive species management in hot deserts: resources, strategies, tactics, and response. *Rangelands* 31: 6-13.
- Rose, A.B., L.R. Basher, S.K. Wiser, K.H. Platt and I.H. Lynn. 1998. Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. *N. Z. J. Ecol.* 22: 121-140.
- Rose, A.B., K.H. Platt and C.M. Frampton. 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.
- Rotundo, J.L. and M.R. Aguiar. 2005. Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. *J. Ecol.* 93: 829-838.
- Scheepens, J.F. 2004. *Sexual Versus Vegetative Reproduction In Hieracium pilosella In Different Habitat Types*. Lund University Applied Work - Project Report
- Schurr, F.M., W.J. Bond, G.F. Midgley and S.I. Higgins. 2005. A mechanistic model for secondary seed dispersal by wind and its experimental validation. *J. Ecol.* 93: 1017-1028.
- Serra, J. 1990. *Relevamiento pasturas implantadas en Tierra del Fuego*. Informe técnico, Consejo Federal de Inversiones, Buenos Aires.
- Shea, K., Roxburgh, S.H. and Raushert, E.S.J. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol. Lett.* 7: 491-508.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det Kong. Danske Vidensk. Selsk. Biol. Skr.* (Copenhagen) 5: 1-34.
- Spence, L.A., J.V. Ross, S.K. Wiser, R.B. Allen and D.A. Coomes. 2011. Disturbance affects short-term facilitation, but not long-term saturation, of exotic plant invasion in New Zealand forest. *Proc. R. Soc. B* 278: 1457-1466.
- Stockfisch, N., T. Forstreuter and W. Ehlers. 1999. Ploughing effects on soil organic matter after twenty years of conservation tillage in Lower Saxony, Germany. *Soil Tillage Res.* 52: 91-101.
- Stöcklin J. and E. Winkler. 2004. Optimum reproduction and dispersal strategies of a clonal plant in a metapopulation: a simulation study with *Hieracium pilosella*. *Evol. Ecol.* 18: 563-584.
- Treskonova, M. 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. *N. Z. J. Ecol.* 15: 65-78.
- Vander Kloet, S.P. 1978. Biogeography of *Hieracium pilosella* L. in North America with special reference to Nova Scotia. *Proc. N. S. Inst. Sci.* 28: 127-134.
- Vavra, M., C.G. Parks and M.J. Wisdom. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Ecol. Manag.* 246: 66-72.
- Walker, S., J.B. Wilson and W.G. Lee. 2005. Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. *Biol. Inv.* 7: 195-211.
- Walter, H. and E.O. Box. 1983. Climate of Patagonia. In: West, N.E. (ed.) *Ecosystems of the World*, Vol. 5. Temperate deserts and semi-deserts. Elsevier, Oxford. pp. 432-435.
- West, N.E. 1993. Biodiversity of rangelands. *J. Range Manag.* 46: 2-13.
- White, P.S. and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. In: Esser, K., U. Lüttge, J.W. Kadereit and W. Beyschlag (eds.), *Prog. Bot.* 62. Springer, Berlin, Heidelberg. pp. 399-450.
- White P.S. and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. In: S.T.A. Pickett and P.S. White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida. pp. 3-13.
- Wilson, H. 1992. Regeneration after fire on the Leibig Range, Mount Cook National Park; the role of hawkweeds (*Hieracium* spp.) during the first 20 years. In: G.G. Hunter, C.R. Mason, D.M. Robertson, (eds.), *Vegetation Change in Tussock Grasslands, With Emphasis on Hawkweeds*. Occasional Publication No.2, New Zealand Ecological Society, Christchurch. p 44.
- Winkler, E. and J. Stöcklin. 2002. Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Ann. Bot.* 89: 525-536.
- Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev and G.M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer. New York, USA.

Received April 9, 2013
 Revised September 18, 2013
 Accepted September 23, 2013