ORIGINAL PAPER

# Assessing the importance of disturbance, site conditions, and the biotic barrier for dandelion invasion in an Alpine habitat

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**Abstract** Several factors have been identified as relevant in determining the abundance of non-native invasive species. Nevertheless, the relative importance of these factors will vary depending on the invaded habitat and the characteristics of the invasive species. Due to their harsh environmental conditions and remoteness, high-alpine habitats are often considered to be at low risk of plant invasion. However, an increasing number of reports have shown the presence and spread of non-native plant species in alpine habitats; thus, it is important to study which factors control the invasion process in these harsh habitats. In this study, we assessed the role of disturbance, soil characteristics, biotic resistance and seed rain in the establishment and abundance of the non-native invasive species *Taraxacum officinale* (dandelion) in the Andes of central Chile. By focusing on human-disturbed patches, naturally disturbed patches, and undisturbed patches, we did not find that disturbance per se, or its origin, affected the establishment and abundance of *T. officinale*. The abundance of this non-native invasive species was not negatively related to the diversity of native species at local scales, indicating no biotic resistance to invasion; instead, some positive relationships were found. Our results indicate that propagule pressure (assessed by the seed rain) and the abiotic soil characteristics are the main factors related to the abundance of this non-native invasive species. Hence, in contrast to what has been found for more benign habitats, disturbance and biotic resistance have little influence on the invasibility of *T. officinale* in this high-alpine habitat.

**Keywords** Invasion · Disturbance · Biotic resistance · *Taraxacum officinale* · Alpine · Seed rain · Andes

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## Introduction

Recent reviews have identified several factors as pivotal in determining the establishment and spread of non-native invasive species (e.g. Richardson et al. 2000; Dietz and Edwards 2006; Theoharides and Dukes 2007). For instance, while the resident native

community and the abiotic features of the invaded habitat have been considered as important barriers for invasion, propagule pressure of the non-native invasive species and anthropogenic disturbances are considered as invasion promoters (Richardson et al. 2000). Nonetheless, it is still not possible to predict when or how a particular process or mechanism will be more important than others for invasion success (Lambrinos 2002; Theoharides and Dukes 2007) because that importance will depend on the characteristics of both the invaded habitat and the non-native invasive species involved (Rejmánek et al. 2005; Dietz and Edwards 2006). Much of our current knowledge of the factors that control the invasion process of exotic species has been built from studies carried out at low-elevation environments, where high levels of human disturbances and dispersal of propagules are key in explaining biological invasions at large spatial scales (Pauchard et al. 2009).

Alpine habitats are considered harsh environments characterized by strong winds, short growing seasons, high solar radiation, low temperatures, and low nutrient availability (Körner 1999). Although alpine environments have been considered less susceptible to biological invasions than other ecosystems due to their severe environmental conditions, limited propagule pressure, and low presence of human disturbances (Weaver et al. 2001; Becker et al. 2005), an increasing number of studies have started to report the presence of several non-native invasive species in alpine environments (Johnston and Pickering 2001; Becker et al. 2005; McDougall et al. 2005; 2011; see also Pauchard et al. 2009; Alexander et al. 2011). Many of the non-native invasive species reported in these studies present a low cover and are restricted to disturbed sites (Johnston and Pickering 2001; Weaver et al. 2001; McDougall et al. 2005; Parks et al. 2005; Arévalo et al. 2005). However, some non-native invasive species have started to establish in undisturbed alpine plant communities, negatively affecting native species (e.g. Daehler 2005; Muñoz and Cavieres 2008). Thus, it is important to study the role of different factors in explaining the invasion process in alpine habitats.

Disturbances are considered a major driver of plant invasions (Hobbs and Humphries 1995; Londsale 1999). In alpine habitats, disturbances can be caused both by natural geomorphological processes such as landslides and cryogenic soil movement (Johnson and Billings 1962) and by human-related activities such as road building and mining or recreational activities (Grieve 2000). As most of the non-native invasive species reported in alpine habitats have been found in disturbed sites, disturbances are expected to play a key role in the establishment of introduced species in these harsh habitats (Alexander et al. 2009). However, the different origin of the disturbances found in alpine environments (i.e. natural vs. human-caused) opens the question about their equivalence for the invasion process. In other environments, the few studies that have compared the effect of anthropogenic and natural disturbances on the establishment of non-native invasive species have shown that while anthropogenic disturbances promote invasions, natural disturbances have either a negative effect or no effect on the establishment of non-native invasive species (Kim 2005; Pyle 1995).

Based on the important role that negative interactions have in structuring plant communities, it has been suggested that the resistance to invasions at local scales increases with the diversity of the native community (e.g. Tilman 1996; Knops et al. 1999; Levine 2000). In stressful environments, like alpine habitats, the role of the resident community in controlling the success of non-native invasive species has been seldom examined. The few studies conducted so far have shown that the native species richness does not affect, and sometimes even facilitates, biological invasions (Dethier and Hacker 2005; Von Holle 2005). For alpine habitats, it has been shown that facilitative interactions with nurse cushion species are important for the establishment and growth of some non-native invasive species (Cavieres et al. 2005, 2007, 2008). Thus, given that in alpine environments positive interactions play a key role in shaping plant communities (Callaway et al. 2002), a positive relationship between native species richness and abundance of non-native invasive species could be expected.

It has been shown that greater propagule dispersal increases the probability of invasion success (Lodge 1993; Williamson 1999; Lockwood et al. 2005), even in environments where abiotic and biotic features restrict the establishment (Richardson and Bond 1991; D'Antonio et al. 2001; Foster 2001; Rouget

and Richardson 2003; Lockwood et al. 2005; Lambrinos 2006). Propagule pressure of exotic species is expected to be lower in alpine habitats compared to lowland areas (Pauchard et al. 2009). Nevertheless, it is ignored if a high propagule pressure can account for the success of non-native invasive species in these environments, despite the harsh abiotic constraints encountered by these species.

A conspicuous component of the alien alpine flora of the central Chilean Andes is the perennial herb *T. officinale* Weber or common dandelion. *T. officinale* is an invasive weed that was introduced to Chile from Europe ca. 150 years ago (Matthei 1995). This exotic species has been found growing abundantly in several alpine zones around the world (McDougall et al. 2011), and the alpine zone of central Chile is especially abundant in human disturbance patches or within undisturbed native vegetation dominated by cushion plants (Cavieres et al. 2005, 2008). However, field observations indicate that *T. officinale* is not equally successful in all human-disturbed or naturally disturbed sites, suggesting that the abiotic conditions generated after the disturbance, the propagule pressure, and the relationship with the resident native plant species are important in determining the establishment and abundance of this non-native species. Recent studies have shown that the abundance of some native herbs (e.g. *Phacelia secunda, Oxalis compacta*) decreased with the presence of *T. officinale* (Cavieres et al. 2005). In addition, a high abundance of *T. officinale* decreased pollinator visitation rates and seed output of some native species (Muñoz and Cavieres 2008), demonstrating the negative effect of this non-native species on native vegetation. In this study, we examined the relationship between disturbance type, the diversity of the resident community, the abiotic conditions of soil, and the propagule pressure with the abundance of *T. officinale* in an alpine environment. Specifically, we asked: (1) Is the abundance of *T. officinale* increased in disturbed patches? (2) Which is (are) the abiotic soil variable(s) most related to the abundance of *T. officinale*? (3) Is the early establishment of *T. officinale* increased in disturbances of different origin? (4) Is the abundance of *T. officinale* negatively correlated with resident species richness or diversity? (5) Is propagule pressure positively correlated with the abundance of this exotic species on different patches?

## Materials and methods

### Study site

This study was carried out in the Molina River basin (33°20′S, 70°16′W), located in the central Chilean Andes, between 3,200 and 3,400 m a.s.l. In central Chile, the alpine zone extends from just above the treeline of *Kageneckia angustifolia* (Rosaceae) located at 2,200 m to the upper limit of plant growth at 3,800-m elevation (Cavieres et al. 2000). The predominant climate in the study area is alpine with a strong influence of the Mediterranean-type climate of lower elevations (Cavieres and Arroyo 1999). Precipitation mainly occurs in the form of snow during the south hemisphere winter months, with annual estimations of 900 mm at 3,000-m elevation. Mean air temperatures at 3,150-m elevation are 1.7 and 6.8°C during winter and summer, respectively (Cavieres and Arroyo 1999). In this area, the growing season usually starts at the end of November with the snow melting, and it ends during the first weeks of April with the first snow falls.

Given that at the elevations studied native vegetation is highly patchy (Cavieres et al. 2000), we focused our study on three frequent patch types that stand out across the study area: a) human-disturbed patches, b) naturally disturbed patches, and c) undisturbed patches where vegetation was dominated by cushion plants. Human-disturbed patches result from the removal of biomass by activities related to the construction and maintenance of ski facilities. On these disturbances, the soil surface is completely removed and the remaining plant cover is very low (ca. 1.43%; Chacón and Cavieres 2008). Naturally disturbed patches result from cryogenic soil movements during the snow-melting period. The cryogenic movement partially remove soil surface, enabling a higher plant cover (ca. 3.76%), dominated by the perennial herb *Phacelia secunda*. Undisturbed patches are defined as those where there is no evidence of any disturbance and show a high plant cover dominated by the cushion plant *Azorella madreporica (*ca. 30% Cavieres et al. 2005). Other native species present on these patches are the perennial herbs *Erigeron andicola*, *Phacelia secunda*, and *Perezia carthamoides*. Between the studied elevations, there are no native herbivores and only occasional herbivory by livestock can be observed on

the small peat-bog areas (vegas) that can be found across the study site.

## Study species

*Taraxacum officinale* agg. (Asteraceae) probably originated in east Europe, but is now found in most countries of the world, being considered a noxious weed in many of them (Holm et al. 1997). *T. officinale* is a stemless, deeply rooted perennial herb having a thick taproot and leaves in rosettes at soil level. Each plant has one or more 2–5-cm-diameter capitula or flower heads terminally positioned on 5–45-cm-long, hollow, cylindrical peduncles. Each capitulum has 50–250 small bright yellow ligulate or ray florets (Holm et al. 1997). The life history traits of this species include asexual reproduction, wind dispersal, non-dormant seeds, and the ability to form transient seed banks (Holm et al. 1997).

## Sampling of native plant diversity and abundance of *Taraxacum officinale*

We sampled the resident vegetation present in ten undisturbed patches, ten naturally disturbed patches, and nine human-disturbed patches. Between the altitudinal limits established for this study, along a dirty road used for the maintenance of ski facilities, we selected all the patches of >1,000 m$^2$ size located on east-facing slopes and with clear evidence of vegetation removal by human-related activities. We found nine of these patches, distanced between 200 and 3,000 m. In addition, across this area, we selected ten naturally disturbed patches and ten patches with no evidence of disturbance of any type. All these patches were randomly distributed also along east-facing slopes found between the altitudinal limits established for this study. The size of patches varied between 1,000 and 2,500 m$^2$, and the minimum distance from patches (of any type) was 100 m. On each patch, two transects of 25 m long were delineated in a random direction. Along each transect, a quadrat of 1 m × 1 m was placed every 5 m, where we identified and recorded all the individuals present. Thus, for each quadrat, we obtained the abundance of *T. officinale*, native species richness, and the number of individuals/m$^2$. In addition, we calculated Shannon diversity index (*H'*) according to Magurran (2004).

## Abiotic characterization of soil

On each patch selected for vegetation sampling, we randomly selected one point in the bare ground, where a soil sample of 20 cm depth and 150 g weight was taken and stored in a sealed plastic bag. Soil samples were then sent to the Laboratory for Soil Analyses (Agronomy Faculty, U. de Concepción) where pH, organic matter (OM), nitrogen (N), phosphorous (P), and potassium (K) content were determined for each sample. In addition, soil texture (i.e. percentage of sand, lime, and clay) was also determined.

## Establishment of *Taraxacum officinale*

To evaluate the effect of the different patch types on the establishment of *T. officinale*, on December 2006 (beginning of the growing season), we selected three patches per patch type. On each of these patches, 25 2-week-old seedlings were transplanted. The seedlings were planted in groups of five individuals each into each of five previously randomly selected points. Seedlings were watered during 2 days. The seedlings that died during this period were replaced by others, assuming that this loss was due to the transplant manipulation. Seedlings were planted distanced 5 cm from each other, and their survival was recorded at the end of the growing season in March 2007.

## Propagule pressure

Seed rain was used as an estimation of the propagule pressure arriving to each patch. For this, three replicates per patch type were selected. On each replicate, during the seed dispersal period (February to March), twenty 59-cm$^2$ paper discs were randomly placed on the ground. The discs were impregnated with waterproof glue (The Tanglefoot Company, USA), maintained in the patch for 1 month, and then replaced for new paper discs impregnated with waterproof glue for another month. Paper discs were carried to the laboratory where the achenes of *T. officinale* trapped were counted under a binocular microscope. For each patch, we calculated the total number of seed trapped on each sampling point by summing the seed trapped during February and March.

## Data analyses

Differences in the abundance of *T. officinale* between patch types were assessed with a one-way ANOVA, where the mean abundance of this species on each patch was used as the response variable. Patch types were compared by means of their abiotic soil variables with a multivariable analysis of variance (MANOVA). The relationship between patch types and their soil abiotic variables and the abundance of *T. officinale* was assessed by a stepwise multiple regression with categorical predictor variables where the mean abundance of *T. officinale* on each patch was the response variable. Since the abundance of adults follows a Poisson distribution (counts), we log-transformed the data in order to achieve normality. The categorical predictor variable included in the regression model was patch type, while the continuous predictor variables included were soil texture (lime and clay percentages), pH, and soil nutrient content of nitrogen (N), phosphorous (P), potassium (K), and organic matter (OM). We used both backward and forward stepwise procedures in order to obtain the variables that consistently contributed to the best significant model for explaining the abundance of *T. officinale* ($P < 0.05$). The variables selected as significant in both procedures where included in the final model.

The number of seedling survived at the end of the growing season was compared among the different patch types by means of a Kruskal–Wallis nonparametric test.

The relationship between native species richness and abundance of *T. officinale* was assessed with the Pearson correlation coefficient, after log-transforming the abundance to achieve normality. To evaluate the relationship between other metrics of the diversity of the invaded community and the abundance of the invasive species, we also assessed the correlation of the abundance of *T. officinale* with Shannon diversity index and the total density of individuals at each patch. These analyses were performed by pooling all the patches evaluated, and for each patch type. In this last case, it is expected that certain factors, such as disturbance levels, remained constant.

For each patch where we sampled the seed rain of *T. officinale*, we estimated the mean seed rain density as the average of the total captured seeds dm$^{-2}$ per sampling point during the dispersal period. Then, both the mean seed rain density and the abundance of *T. officinale* on each patch (number of individuals m$^{-2}$) were log-transformed to achieve normality, and a Pearson correlation analysis was used to assess the relationship between propagule pressure and the abundance of the non-native invasive species.

## Results

There were no differences in the mean abundance of *T. officinale* among the patch type studied (Fig. 1; $F_{2.25} = 0.25$; N.S.). In addition, patch types did not differ among them regarding the abiotic soil variables sampled (Table 1; MANOVA $F_{14.38} = 1.80$; $P = 0.076$).

When we assessed the relationship of the abundance of *T. officinale* with patch type and their abiotic soil characteristics, the best model for the abundance of *T. officinale* did not include patch type as a significant factor, indicating that patch type was not related to the abundance of *T. officinale* (Table 2). The best regression model included pH, P, and K as significant factors ($F = 3.33$; $P < 0.05$; Table 2), where the variable with the highest partial correlation with the abundance of *T. officinale* was potassium content (K), followed by pH and phosphorous content (P), respectively (Table 2).

The establishment of *T. officinale* assessed as the survival of planted seedling varied between 5 and
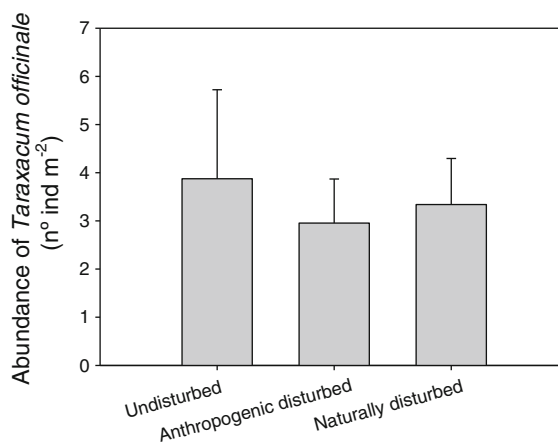


**Fig. 1** Abundance of *T. officinale* in different patch types (undisturbed, anthropogenic disturbed, and naturally disturbed) between 3,200 and 3,400 m a.s.l. in the high Andes of central Chile. *Error bars* indicate two standard errors

**Table 1** Mean values of abiotic variables (pH, content of organic matter, available nitrogen (N), phosphorous (P) and potassium (K), texture assessed by the percentage of lime and clay) of soil samples taken in different patch types between 3,200 and 3,400 m a.s.l. in the high Andes of central Chile

| Patch type | pH | Organic matter (ppm) | N (ppm) | P (ppm) | K (ppm) | Lime (%) | Clay (%) |
|---|---|---|---|---|---|---|---|
| Undisturbed | 6.79 (0.09) | 1.20 (0.44) | 4.02 (0.72) | 12.23 (1.39) | 396.37 (71.96) | 29.73 (1.31) | 14.76 (1.51) |
| Anthropogenic disturbed | 7.00 (0.29) | 0.27 (0.16) | 2.82 (0.46) | 6.56 (1.42) | 157.49 (25.54) | 29.03 (3.21) | 10.90 (2.20) |
| Naturally disturbed | 6.36 (0.29) | 0.72 (0.20) | 3.64 (0.85) | 15.04 (3.64) | 195.70 (33.11) | 31.10 (2.28) | 13.41 (1.53) |

Standard errors are shown in parenthesis

**Table 2** Results of the multiple regression analysis performed to assess the relationship between patch types, their abiotic soil variables, and the abundance of the non-native invasive species *T. officinale* in the high-alpine zone of the Andes of central Chile

| Factor | Parameter estimate | $t$ | $P$ |
|---|---|---|---|
| Intercept | −0.908 | −1.99 | 0.058 |
| pH | 0.171 | 2.63 | 0.015* |
| Phosphorous content (P) | 0.017 | 2.54 | 0.018* |
| Potassium content (K) | −0.001 | −2.96 | 0.007* |

* indicates significant variables included in the model

20% among the different patches and did not differ among them (Fig. 2; $H = 1.17$; $P = 0.56$).

Considering all the patches together, the assessment of the relationship between the abundance of
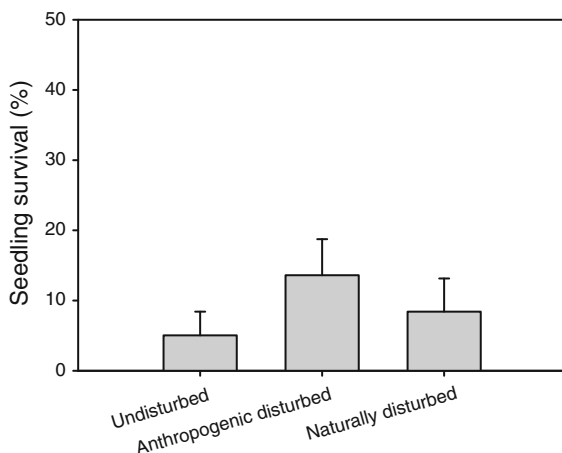


**Fig. 2** Survival of seedlings of *T. officinale* planted in different patch types (undisturbed, anthropogenic disturbed, and naturally disturbed) between 3,200 and 3,400 m a.s.l. in the high Andes of central Chile. *Error bars* indicate two standard errors

*T. officinale* and different metrics of the diversity of the resident community showed that the abundance of *T. officinale* was positively correlated with the number of native species (Fig. 3). Shannon diversity index and density of individuals were not significantly correlated with the abundance of *T. officinale*. The assessment of the relationship between the metrics of diversity of the resident community and the abundance of *T. officinale* for each patch type mostly showed no significant correlations. Only in naturally disturbed patches, we found significant positive correlations of the abundance of *T. officinale* with species richness and Shannon diversity index (Fig. 3).

Average seed rain density per patch was positively correlated with the abundance of *T. officinale* (Fig. 4; $r = 0.91$; $P < 0.05$), suggesting a positive relationship between propagule pressure and abundance of this non-native invasive species.

## Discussion

The abundance of the non-native invasive species *T. officinale* in the high-alpine zone of the Andes of central Chile was not related to patch type. That is, disturbed patches either naturally or anthropogenically created contained similar number of individuals of this non-native invasive species as undisturbed patches. Diversity of the resident community was not negatively related to the abundance of this invasive species. Interestingly, thus, the spread of *T. officinale* does not appear to be promoted by disturbance or restrained by the resident community. We found support for the importance of abiotic factors and propagule pressure at local scales for the success of this non-native invasive species.
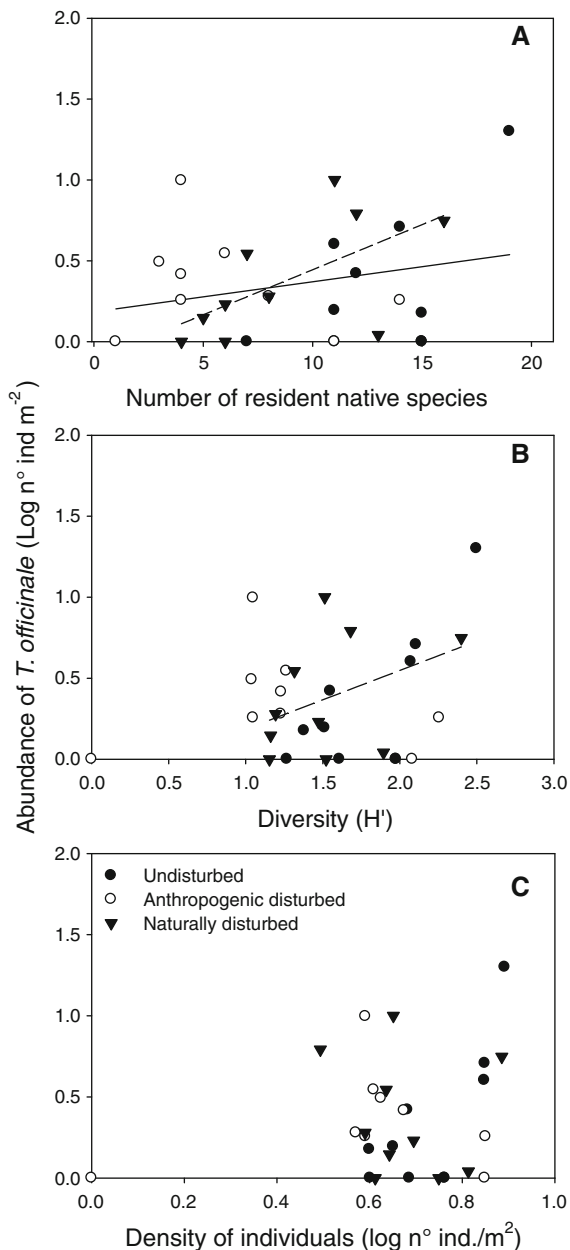
Fig. 3 Correlations between abundance of *T. officinale* and community attributes in the study area, **a** species richness, **b** diversity estimated with Shannon's *H'* index, and **c** density of individuals. Each point represents the mean of ten 1-m² quadrants per patch. The significant correlation found considering all patches together is shown with *solid line* ($r = 0.44$; $P < 0.05$). The significant correlations found for naturally disturbed patches are shown with *dashed line* ($r = 0.67$ and $r = 0.64$; $P < 0.05$ for species richness and diversity, respectively). No other significant correlations were found (see text)
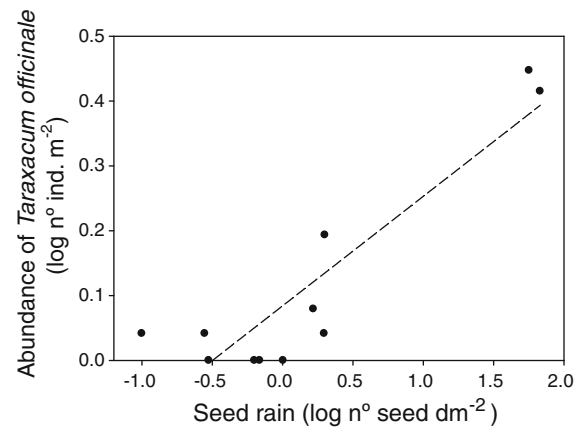


Fig. 4 Correlation between the abundance of *T. officinale* and its seed rain during the seed dispersal period (February–March) in the study area

## The role of disturbances and abiotic constraints for the success of *Taraxacum officinale*

Since disturbances are supposed to provide resource opportunities for the arrival of new species (Davis et al. 2000; Shea and Chesson 2002), it is expected that non-native invasive species will be able to take advantage to any kind of disturbance (Shea and Chesson 2002; Rose and Hermanutz 2004). However, we did not find evidence for the importance of the presence of soil disturbance, nor its origin, in determining the abundance of *T. officinale*. For alpine environments, it has been predicted that non-native invasive species are unlikely to extend their range of distribution unless some process relaxes the environmental constraints (e.g. global warming, disturbances) (Dullinger et al. 2003; Pauchard et al. 2009). It is widely assumed that disturbance enhances resource availability (e.g. Burke and Grime 1996; Davis et al. 2000), and some studies that have examined the effect of disturbances in alpine environments have shown increased nutrient availability after disturbance (Chambers et al. 1990; Stanton et al. 1994; Grieve 2000). However, other studies report that disturbance does not increase nutrient availability, and in some cases, disturbed areas were poorer in soil nutrients than adjacent undisturbed areas (e.g. Burt and Rice 2009; Guleryus et al. 2010). In our study, disturbances, either

natural or human related, did not have any relationship with the abiotic soil variables evaluated, which might explain the absence of relationship with the abundance of *T. officinale*. The absence of a strong effect of disturbance per se on invasion success in high-elevation habitats has also been recently highlighted in Radford et al. (2010), who studied the factors behind the spread of the invasive *Hieracium lepidulum* in New Zealand.

We found that the abundance of *T. officinale* in the study area was highly related to the pH, phosphorous (P), and potassium (K) contents in soils, suggesting that the variation of the suitability for the establishment of *T. officinale* among patch types is due to differences in abiotic characteristics that occur at levels that are not necessarily determined by patch type. This is in accordance with the study of Radford et al. (2010) whose data also implied that the availability of nutrient is the main factor behind the spread of the invasive *Hieracium lepidulum* in high-elevation zones of New Zealand.

The abiotic variable that showed the highest relationship with the abundance of *T. officinale* was potassium (K) soil content, presenting a negative relationship with the abundance of this exotic species. This is in line with a previous study (Quiroz et al. 2009) where we showed that *T. officinale* is damaged by high levels of K as it can be found in several zones around the study area. Likewise, Cavieres et al. (2008) showed that the highly species-specific nurse effect provided by cushion plants on this invasive species is highly related to the amount of K found in the soil beneath nurses, where *T. officinale* was less abundant and performed worse on cushions with higher amount of K in the soil underneath them. Despite the fact that potassium is an essential nutrient for plant growth (Taiz and Zeiger 1998), high concentrations of this cation in the soil have been reported to have negative effects in plants. With high amounts of potassium, Ca and Mg are competitively influenced, generating deficiency symptoms for Mg (Taiz and Zeiger 1998).

We can conclude that there are important abiotic constraints operating at a local scale dictated by nutrient levels of the soil that control the establishment of the non-native invasive species *T. officinale* in the study area.

## Resistance of the resident community

We found that diversity attributes of the resident community, evaluated as species richness, H' diversity index, and density of individuals, did not restrict the invasion success of *T. officinale* in the study area. This occurred when we considered all the patches together and when we focused on each patch type, reducing the range of environmental heterogeneity. Similar results have been reported in other studies performed in stressful environments where no negative relationships between native and exotic species were found (Huston 1999; Brown and Peet 2003; Dethier and Hacker 2005; Von Holle 2005; Perelman et al. 2007; see review in Fridley et al. 2007). In contrast, we found significant positive correlations between the abundance of *T. officinale* and species richness (Fig. 3), suggesting that restrictions imposed by the abiotic environment that restrain native species richness should be more important than negative interactions with the native resident community in determining the establishment and spread of non-native invasive species in stressful environments (Alexander et al. 2009, 2011; Pauchard et al. 2009). In addition, the positive relationship found in this study suggests the presence of positive interactions between this invasive species and the resident biota, a phenomenon that has been previously described in this system (e.g. Cavieres et al. 2005, 2008; Badano et al. 2007).

## Role of propagule pressure

The availability of viable seed, termed propagule pressure, has emerged as a unique and consistent predictor of the success for some exotic species, explaining why some introductions are successful, while others fail (Lockwood et al. 2005). So far, this positive relationship between propagule pressure and abundance of exotic species has not been explored in alpine habitats, where it is expected that strong environmental barriers prevent the establishment of exotic species. The ideal test for assessing the importance of propagule pressure in invasion is to experimentally increase the amount of seeds on areas where the non-native invasive species is absent. However, such an approach was not used by

permission restrictions and for ethical reasons. *T. officinale* is an apomictic species, producing large amount of viable seeds during the entire growing season (Muñoz and Cavieres 2008). Seeds are dispersed both primarily and secondarily by wind on every direction (Tackenberg et al. 2003; Muñoz and Cavieres 2006) and did not form persistent seed banks, germinating as soon as snow melts (Arroyo et al. 1999). Hence, density of seed rain seems to be a good surrogate of propagule pressure in this non-native invasive species. In this study, higher levels of propagule pressure were related to higher abudances of *T. officinale*. This could be due to the fact that patches with higher abundances of this non-native invasive species produce more propagules than patches with lower abundances. However, propagules of *T. officinale* can be dispersed by vertical turbulences of wind, which are typical of high-alpine sites (Barry 2008), over large distances (>100 m, Tackenberg et al. 2003), decreasing the effect of standing individuals on propagule availability in the patch. Therefore, our evidence suggests that seed rain promotes the successful establishment of this non-native invasive species in this alpine area, supporting current hypothesis about the importance of propagule pressure in determining the success of biological invasions (e.g. Lockwood et al. 2005; Theoharides and Dukes 2007).

Final conclusions

Based on this study focused on the spread of *Taraxacum officinale* in the high-alpine zone of the Andes of central Chile, while we found support for some important factors included in many current invasion hypotheses (i.e. importance of propagule pressure), we also found major challenges to the importance of other factors that regulate the success of biological invasions in other environments. First, according to our results, the establishment and abundance of the non-native invasive species *T. officinale* does not depend on the presence of disturbance per se, regardless of its origin. The invasion success will depend on how the non-native invasive species will respond to resource opportunities, and to the physical environment of the introduced range (Shea and Chesson 2002). Second, biotic resistance did not play a restraining role for the establishment of the non-native species in alpine

environments. Other studies performed in the study area show that *T. officinale*, and other exotic species, can take advantage of positive interactions with native species that provide more benign environmental conditions for their establishment (Cavieres et al. 2005, 2008). These precedents and the lack of evidence for biotic resistance found in this study suggest that positive relationships between resident native and non-native invasive species might act as promoters of biological invasions in alpine habitats (Pauchard et al. 2009).

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