



# Range expansion and potential distribution of the invasive grass *Bromus tectorum* in southern South America on the base of herbarium records



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## ABSTRACT

We reconstructed the invasion history and modelled the potential distribution of the invasive grass *Bromus tectorum* in southern South America. On the base of herbarium data, we described two aspects of *B. tectorum*'s range expansion over time: area of occupancy and extent of occurrence. A maximum entropy model was used to identify both climatic variables associated with *B. tectorum*'s current distribution and potentially invadable areas. The area-of-occupancy curve showed a steady increase of the occupied area since the first collection in 1937, with no obvious asymptote. However, the extent-of-occurrence curve indicated that range expansion was not homogeneous through time, but faster between 1965 and 1980. Most invadable areas were arid and semiarid with markedly Mediterranean precipitation regime. Within this susceptible region, there were large areas containing only a few known records of *B. tectorum*. Our results indicate that *B. tectorum* has successfully expanded over much of southern South America. In addition, there seems to be room for further local invasion (i.e. an increase of its area of occupancy) over large susceptible areas within the invaded region. Overall, our results confirm the suitability of southern South America's arid environments to *B. tectorum* invasion, and stress the importance of long-distance dispersal in accelerating its expansion across the region.

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## 1. Introduction

Biological invasions are widely recognized as important drivers of biological diversity loss and changes in ecosystem functioning (Davis, 2009; Lockwood et al., 2007). Characterizing the pattern of spread of invasive species, as well as predicting their potential geographic distribution constitute necessary steps in managing biological invasions (Hulme, 2006; Wittenberg and Cock, 2001). Research on past and potential distributions of organisms should be ideally based on presence–absence or abundance data collected systematically over space and time (Hastings et al., 2005; Higgins and Richardson, 1996). However, such data are usually spatially and temporally restricted, so they are seldom available for analyses at large geographical or temporal scales (Kent and Carmel, 2011).

Conversely, presence-only data arising from specimen collections are widely available and usually span a relatively large period of time (Elith et al., 2006). Indeed, herbarium data have been successfully employed to reconstruct the historical development of invasions (e.g. Crawford and Hoagland, 2009; Delisle et al., 2003; Mihulka and Pyšek, 2001; Pyšek and Prach, 1993; Salo, 2005) and to predict future species distributions (Elith et al., 2006). Here we use herbarium data to reconstruct the invasion history and to model the potential distribution of the invasive grass *Bromus tectorum* over arid and semi-arid regions of southern South America.

Historical reconstructions of invasion dynamics have often involved the analysis of the cumulative number of invaded localities over time, where the increase in this number (or its ratio to the explored area) has been interpreted as an increase in the invaded area (e.g. Crawford and Hoagland, 2009; Douglas et al., 1990; Pyšek and Prach, 1993). The number or the proportion of invaded localities actually refer to the “area of occupancy” of a species (i.e. the area detected to be actually occupied), which is one way of quantifying a species' geographic range (Gaston, 1991; Gaston and Fuller,

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2009). However, estimating the area of occupancy only provides a partial view of an invasion process because invaded localities are not considered explicitly in space. For instance, a number of invaded localities may be either clustered together or widely scattered over a given area, and methods that estimate the area of occupancy cannot account for this difference. Such spatial differences can be captured through the quantification of the distance or the area between the outermost limits of a species' occurrence. This is another way of quantifying a species' geographic range that is referred to as "extent of occurrence", and can be complementary with measures of area of occupancy (Gaston, 1991; Gaston and Fuller, 2009). That is, area-of-occupancy measures would mostly reflect environmental effects on the local increase of invading populations (see e.g. Delisle et al., 2003; Salo, 2005), whereas extent-of-occurrence measures would be most sensitive to factors affecting the spatial dispersal of invaders.

*B. tectorum* (cheatgrass, downy brome) is a cool-season annual grass native to the southwest Asia and the Mediterranean Basin (Novak and Mack, 2001; Thill et al., 1984; Upadhyaya et al., 1986). It has invaded temperate grasslands and shrublands worldwide, including Japan, Australia, New Zealand, South Africa, Hawaii, and North and South America (Novak and Mack, 2001; Upadhyaya et al., 1986). This species is particularly problematic for arid and semiarid shrub- and grass-steppe native communities of the Great Basin in North America, where its presence modifies fire and biogeochemical cycles (Knapp, 1996; Sperry et al., 2006). This species can also be highly noxious for a variety of winter crops and pastures (Thill et al., 1984; Upadhyaya et al., 1986). According to a simulation study, the geographic spread of *B. tectorum* is dictated mostly by climatic conditions (Bradford and Lauenroth, 2006). However, there is little empirical evidence on the invasion patterns of this species in climatically susceptible areas outside North America.

A relatively large proportion of the southern cone of South America is climatically and physiognomically similar to the shrub- and grass-steppes of the Great Basin in North America (Páruelo et al., 1995). For this reason, arid and semiarid communities of southern South America have been predicted to be highly susceptible to invasion by *B. tectorum* (Bradford and Lauenroth, 2006). Within this region the main plant functional groups are perennial grasses and forbs; *B. tectorum* would represent a novel (or rare) functional type that could modify ecosystem functioning (Bradford and Lauenroth, 2006). We specifically asked: (1) Has the distribution of *B. tectorum* expanded over the southern portion of South America? (2) Was this process homogeneous over time? (3) Which climatic variables are most associated with its current distribution? And (4) what areas are particularly susceptible to be invaded? On the base of herbarium data, we reconstructed the invasion history of *B. tectorum* using estimates of both area of occupancy and extent of occurrence. We also used herbarium data to predict the geographic distribution of *B. tectorum* as a function of climatic variables using maximum entropy modelling (Phillips and Dudík, 2008; Phillips et al., 2006).

## 2. Methods

### 2.1. Study area

The study area covered the southern end of continental South America, including Patagonia and adjacent northern areas from 31° to 52° S (Fig. 1). Three geographic features influence major climatic patterns in the area (Veblen et al., 2007). First, the large latitudinal extension determines a temperature gradient from north to south, from 23 °C and 8 °C mean temperatures in summer and winter respectively in the north to 9 °C and –2 °C in the southern end. Second, the presence of the Andean range determines a gradient of

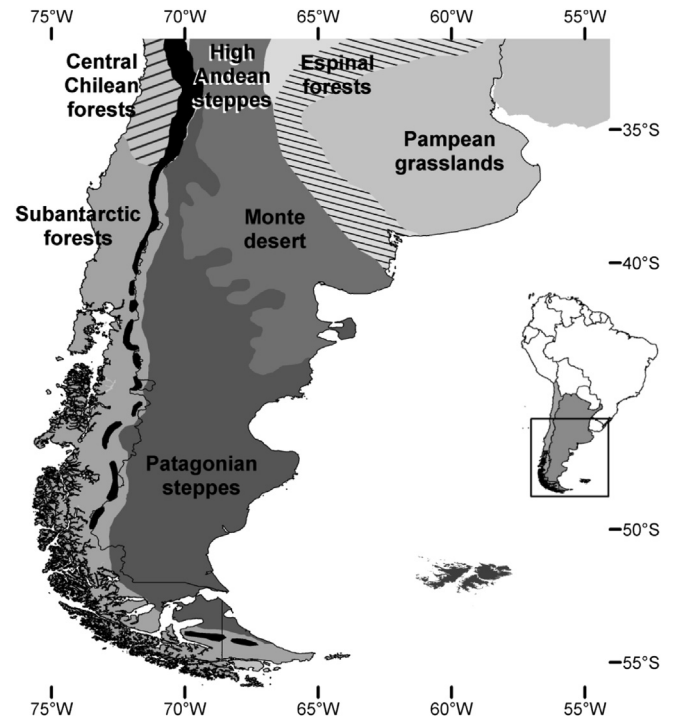


Fig. 1. Study area with biogeographic divisions (modified from Cabrera and Willink, 1973).

decreasing temperature with altitude, and a contrasting west-east mountain-side precipitation pattern: total annual precipitation ranges from >6000 mm on the west side of the Andes to <200 mm in the tablelands on the east side (see Veblen et al., 2007). Third, from this arid region, total annual precipitation increases north-eastward, reaching 1000 mm in the north-eastern corner of our study area. Coincidentally with climatic patterns, the vegetation in the area varies roughly from wet forests in the west, to deserts, steppes and grasslands in the east (Fig. 1; Cabrera and Willink, 1973). Most of the study area corresponds to the Patagonian steppes and the Monte desert (Fig. 1), which are arid and semi-arid, relatively flat areas where grasses and shrubs alternate dominance.

### 2.2. Data compilation and preparation

We obtained location and date of collection data from herbarium records of *B. tectorum* and of native Poaceae species. Here, native Poaceae were used as background species to separate true invasion dynamics of *B. tectorum* from the increase in collection effort within the study area (see below). *B. tectorum*'s data were obtained from three sources. First, data were collected from 17 herbaria in Argentina and Chile [117 specimens; BA, BAA, BAB, BAF, BBB, BCRU, CONC, CORD, CTES, HRP, JBPE-CENPAT, LIL, LP, MERL, SGO, SI and SRFA; abbreviations following Thiers (2010), except for JBPE-CENPAT, Jardín Botánico de la Patagonia Extraandina – Centro Nacional Patagónico, Puerto Madryn, Argentina]. Second, we searched the literature for specimen data in published floristic and taxonomic reports (18 specimens). Third, we carried out two gap-aimed field trips in 2008 and 2009 that covered the southern and eastern edges of *B. tectorum*'s distribution (46 specimens). Data on native Poaceae (i.e. the background species; Frey, 2009) were gathered from the four main herbaria in the study area (BAA, CONC, LIL and SI) using the DFA<sup>®</sup> database of the Instituto de Botánica Darwinion ([www.darwin.edu.ar](http://www.darwin.edu.ar)). Duplicates and specimens with imprecise information on location or date were discarded. Overall,

information of 181 *B. tectorum* specimens and of 15,832 native Poaceae specimens was compiled.

### 2.3. Data analysis

Point-location data of specimens were transformed into grid-based data (e.g. Aagesen et al., 2009; Delisle et al., 2003). Following Aagesen et al. (2009), we explored a range of grid sizes (0.1°, 0.2°, 0.25°, 0.5°, and 1°) and found that results of the procedures explained below were qualitatively similar among trials (data not shown). We decided to use 0.5° grids, which were considered adequate given the amount of specimen collections and the scale of spatial climatic heterogeneity within our study area. Maps showing the accumulated collections of *B. tectorum*'s specimens (referred to here as invasion maps) were created for five moments over the invasion history (1940, 1960, 1980, 2000, and 2010). In these maps and in the analyses below, we declared invaded cells as those where a collection of *B. tectorum* was preceded by at least one collection of a background species, i.e. native Poaceae. Manipulation and plotting of spatial data were done with DIVA-GIS ([www.diva-gis.org](http://www.diva-gis.org)).

Area-of-occupancy dynamics of *B. tectorum* were described using a proportion curve (sensu Delisle et al., 2003; Pyšek and Prach, 1993). For each year on record, we calculated the ratio of the cumulative number of invaded cells and the cumulative number of background cells. This ratio plotted against time gives our proportion curve. This approach aims to separate true invasion dynamics from the increase in collection effort on the base of two assumptions: collectors of background species were also likely to collect specimens of the target species, and populations of background species did not expand over the studied period (Crawford and Hoagland, 2009; Delisle et al., 2003). Thus, the proportion of invaded cells is a relative measure of area of occupancy. Data of *B. tectorum* collected in the gap-aimed field trips were excluded from this analysis.

Extent-of-occurrence dynamics of *B. tectorum* were described following a similar approach. For each year on record, extent of occurrence of invaded localities was estimated following the minimum convex polygon method (Moat, 2007). For this analysis, which requires point-location data (Moat, 2007), collections of *B. tectorum* outside background grid cells were filtered out, so that invaded point-localities are equivalent to invaded grid cells. The method calculates the area within the smallest convex polygon (i.e. with no internal angle exceeding 180°) containing all the invaded localities. An extent-of-occurrence curve was constructed by plotting the area within successive minimum convex polygons against time. Data of *B. tectorum* collected in the gap-aimed field trips were excluded from this analysis. The area within minimum convex polygons is only a coarse approximation to the actual extent of occurrence of a species (cfr. Gaston and Fuller, 2009). Nevertheless, the method gives a complementary view to the invasion dynamics of *B. tectorum* that would otherwise be ignored if solely based on absolute or relative measures of area of occupancy.

We modelled the relationship between the observed distribution of *B. tectorum* in 2010 and different climatic variables using a maximum entropy model (Maxent; Phillips et al., 2006; Phillips and Dudík, 2008). Maxent is a machine learning algorithm that estimates the most uniform distribution of a species (maximum entropy) across the study area, with the constraint that the expected value of each explanatory variable should match its observed average (Phillips et al., 2006). We used this model to identify climatic variables that were most associated with the current distribution of *B. tectorum*, and to predict areas potentially susceptible to the invasion of this species. Model predictions were in the form of probability of occurrence of *B. tectorum* in each map grid cell [referred to as “logistic output” in Phillips et al. (2006) and

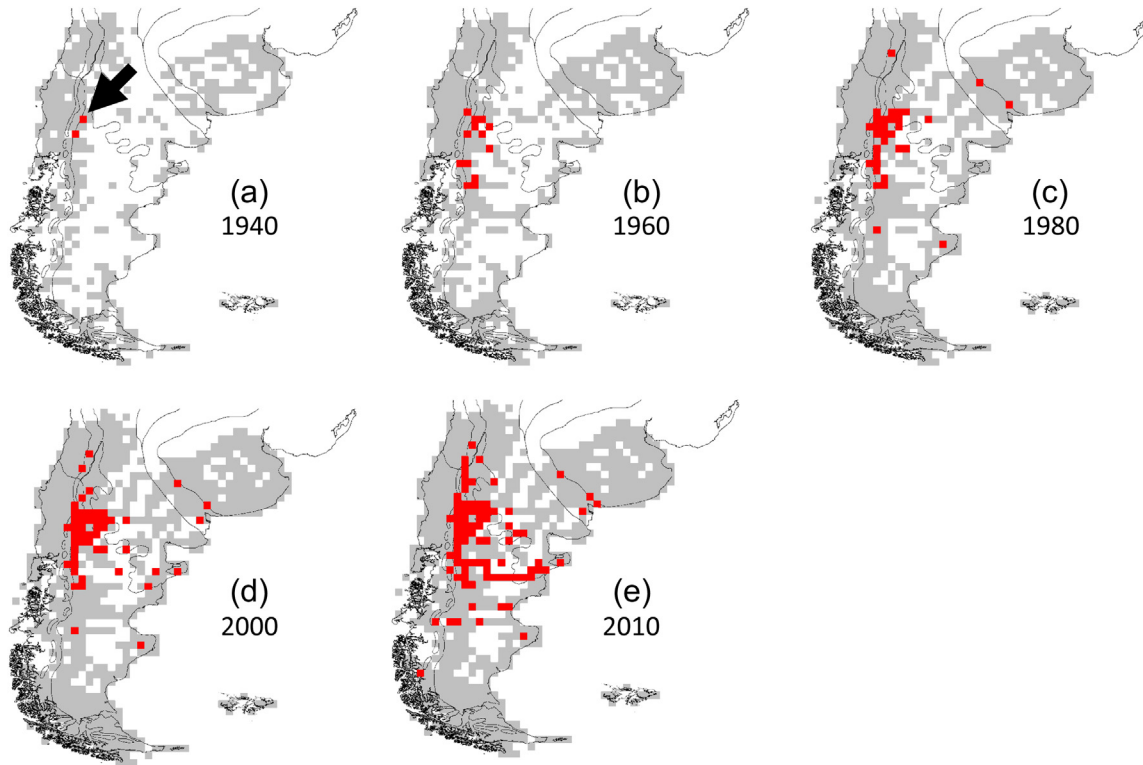
Phillips and Dudík (2008)]. For this analysis, we used the complete dataset, including the 46 specimens collected in our gap-aimed field trips.

We used data in the WorldClim database (Hijmans et al., 2005) to create our set of explanatory variables. All variables were used with a resolution of 2.5 arcmin (approx 5 km) grid cells. For each grid cell, we calculated total precipitation, minimum temperature, and maximum temperature for each of four calendar seasons (yielding 12 variables). We also calculated the average proportion of annual precipitation during summer (December, January, and February). Other explanatory variables included the 7 bioclimatic variables in the WorldClim database that do not summarize monthly or quarterly information (i.e. BIO1 to 4, BIO7, BIO12, and BIO15; Hijmans et al., 2005). Thus, the whole dataset contained 20 candidate explanatory variables. The explanatory value for each climatic variable was evaluated using the area under the curve (AUC) when included as a single variable in a Maxent model (standard Maxent output). Then, for all pairs of variables with Pearson's correlation coefficient >0.8, the variable with smaller AUC was discarded. As a result, 7 variables were included in the final model (see Appendix 1). Maxent was run using the default settings: duplicate records removed; 10,000 background points; regularization multiplier = 1; convergence threshold = 0.00001; maximum iterations = 500. It should be noted here that model predictions (based on presence data from the invaded range) depend on the current relationship between *B. tectorum*'s distribution and the climatic variables, which is likely to be not in equilibrium (see discussions in Broennimann and Guisan, 2008; Mau-Crimmins et al., 2006). Such a relationship could change in the future due to invasion of new habitats by currently established populations, evolution within these populations, or immigration of new genotypes from other regions. This means that our model could underestimate the area potentially invaded by *B. tectorum* (see Broennimann and Guisan, 2008; Wilson et al., 2007). However, this does not invalidate the results of our model, which should be regarded as a conservative estimation of the susceptible area to *B. tectorum*'s invasion.

## 3. Results

### 3.1. Collection history and invasion dynamics

The first native grass specimen in our database was collected in 1831, allowing us to document more than 170 years of continuous and geographically broad history of botanical exploration that supports our background species dataset. *B. tectorum* was first collected in 1937 in northern Patagonian steppes (Argentina), near the Andean range (Fig. 2a). By 1960, several new specimens of *B. tectorum* were collected relatively close to the first collection, and further south along the ecotone between Subantarctic forests on the Andean range and northern Patagonia steppes (Fig. 2b). By 1980, new invaded grid cells were added near older localities, as well as some isolated records near the boundaries of our study area: in Espinal forests, in southern Patagonian steppes, and in High Andean steppes on the western side of the Andean range (Fig. 2c). By 2010, most new invaded cells were contiguous to previous ones, although a new isolated collection was recorded in southern Subantarctic forests in Chile (Fig. 2d and e). The proportion of grid cells invaded increased steadily since the first collection until present, with no clear periods of faster, nor slower occupancy (Fig. 3a). In contrast, our estimate of *B. tectorum*'s extent of occurrence increased since its first collection, but particularly faster between 1965 and 1980 (Fig. 3b). After this rapid expansion, there was virtually no increase of the extent of occurrence of *B. tectorum*'s for more than 25 years, until a new expansion step occurred in the late 2000's (Fig. 3b).



**Fig. 2.** Spatial distribution *Bromus tectorum* (red cells) and of native Poaceae species pooled together (light grey cells) in five moments. The black arrow in panel (a) points to the location of the first collection of *Bromus tectorum* in the region. Contours of biogeographic divisions (see Fig. 1) are superimposed for reference.

3.2. Climatic correlates of current distribution, and potential distribution

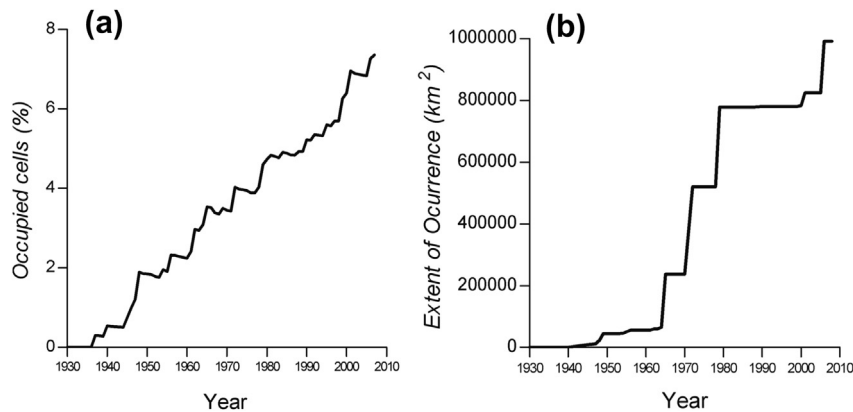
The most important variables associated with the current distribution of *B. tectorum* were: proportion of precipitation during summer, minimum winter temperature, and maximum summer temperature (Fig. 4; see Appendix 1 for a complete list of the relative importance of each climatic variable). In particular, proportion of precipitation during summer was the most important variable and areas with high invasion probability were those with approximately less than 20% of annual precipitation during summer (Fig. 4). Areas with high invasion probability had also relatively low winter minimum temperatures (mostly below 0 °C) and intermediate maximum summer temperature between 19 and 30 °C

(Fig. 4). The resulting map shows that habitat suitability for *B. tectorum* stretches south-easterly from the ecotone between Central Chile forests and High Andean steppes to where southern Monte desert and Patagonia steppes meet the Atlantic coast (Fig. 5). Small disjunct suitable areas appear further north in Pampean grasslands and Espinal open forests (Fig. 5).

4. Discussion

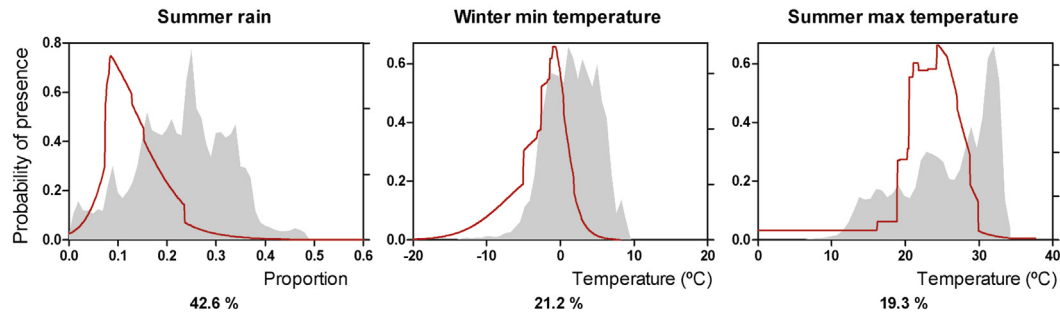
4.1. Collection history and invasion dynamics

Our analyses are based on data collected over more than 170 years of a continuous, and geographically broad history of botanic exploration (cfr. Pyšek and Prach, 1993). Grid cells in the



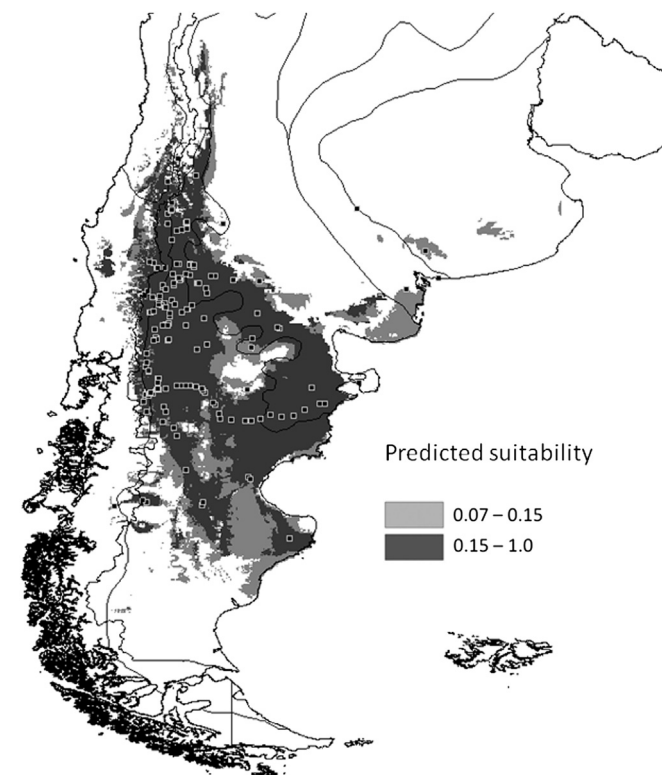
**Fig. 3.** Temporal dynamics of (relative) area of occupancy (a), and of extent of occurrence (b), of *Bromus tectorum* in southern South America. The proportion of cells occupied is the ratio of the cumulative number of grid cells invaded by *B. tectorum* and the cumulative number of grid cells with known collections of native Poaceae (i.e. background species). The extent of occurrence is the area within the smallest polygon containing all the localities, in which all internal angles do not exceed 180° (i.e. the minimum convex polygon).





**Fig. 4.** Response of *Bromus tectorum* distribution to the three most important climatic variables. Each panel shows the results of a single model containing only the corresponding variable as explanatory, with variable importance shown below each panel. Grey areas represent polygons of relative frequency for each variable in the study area (right axes, scale not shown).

surroundings of the first collection of *B. tectorum* (in 1937) had been visited by botanists for at least 30 years before this date, suggesting that *B. tectorum* was indeed a new exotic species in that area (see also Parodi, 1947). Our results show that the proportion of invaded grid cells has increased steadily ever since this first collection, with no obvious approach to an asymptote or plateau. This suggests a persistent increase of the area occupied by *B. tectorum*, and that there are many localities (i.e. grid cells) where further invasion may be expected.



**Fig. 5.** Spatial distribution of the predicted suitability for *Bromus tectorum* presence in the southern cone of South America by a MAXENT model. Darker grey indicates better predicted conditions. Values delimiting classes of predicted suitability correspond to “fixed cumulative values” of 5 and 10 respectively (which generate omission rates of 2.6% and 6.4% respectively). The cumulative value assigned to a cell is the sum of the probabilities of that cell and all other cells within the study area with equal or lower probability, multiplied by 100 (Phillips et al., 2006). The black squares represent collections of *Bromus tectorum* as of 2010. Contours of biogeographic divisions (see Fig. 1) are superimposed for reference.

A persistent increase in the area-of-occupancy curve implies that there were no particular periods of either detrimental or beneficial conditions for the establishment and local population growth of *B. tectorum*. In North American rangelands, grazing-related disturbances stimulated the establishment of *B. tectorum* (Stohlgren et al., 1999). In Patagonian steppes, sheep stocks peaked around 1952, after which followed a sustained decrease associated with overgrazing and heavy rangeland impoverishment (Soriano and Movia, 1986). Despite this apparent amelioration of sheep grazing pressure, rangeland quality appeared not to have recovered during the following decades (Aagesen, 2000; Soriano and Movia, 1986). Likewise, heavy deterioration by overgrazing could have created favourable conditions for *B. tectorum*'s proliferation in Patagonian steppes that were not reverted by the decrease in sheep stocks. Furthermore, periods of rapid spread of a close relative of cheatgrass (red brome, *Bromus rubens* subsp. *madridentensis*) over southwestern USA and northern Mexico (measured in terms of area of occupancy) have been associated with climatic fluctuations (Salo, 2005). In this case, warm Pacific Decadal Oscillation regimes are linked to increased winter precipitation, and this might have benefited local population growth of red brome (see Salo, 2005). Our results, however, do not show any obvious association with climatic fluctuations [such as the Pacific Decadal Oscillation or the Southern Annular Mode/Antarctic Oscillation (sensu Garreaud et al., 2009; Aravena and Luckman, 2009; Castañeda and González, 2008; Holz and Veblen, 2011)]. Overall, our area-of-occupancy results suggest that conditions that regulate local growth of *B. tectorum* might have been relatively stable, or might have cancelled each other out, throughout the invasion period.

On the contrary, *B. tectorum*'s extent-of-occurrence curve did show a period of particularly rapid spread, between 1965 and 1980. This was due to the establishment of newly invaded grid cells far away from the apparent origin (>500 km, see Fig. 2b and c). This observation suggests either successful long-distance dispersal events from previously established populations or new independent introductions. Human activities such as tourism and sheep ranching are likely vectors of *B. tectorum* long-distance dispersal to isolated new localities (Wilson et al., 2009). Using enzyme electrophoresis analysis (Novak and Mack, 2001) found three different origins for five local populations occurring in less than 10% of our study area (i.e. one Argentinean province, Chubut). In this context, the hypothesis of a different origin for disjunct populations of *B. tectorum* appears plausible, although specific research is needed to test this. More importantly, as a result of either single or multiple introductions, our results show that *B. tectorum* currently spreads across virtually all arid and semi-arid

regions of South America above 34° S, including central and northern Patagonian steppes, southern Monte desert, and southern Espinal semi-arid forests.

#### 4.2. Climatic correlates of current distribution, and potential distribution

Although *B. tectorum* was described as not very demanding in its habitat requirements (Morrow and Stahlman, 1984), some environmental variables emerged as important controls of its distribution. Our habitat distribution model identified the area that is most likely to be invaded by *B. tectorum* as that with markedly Mediterranean precipitation regime (with less than 20% of rainfall during summer), and relatively cold winters (i.e. with minimum winter temperature mostly below 0 °C). This area corresponds mostly to Patagonian steppes. Bradley (2009) found a similar response of *B. tectorum* potential risk of invasion under climatic change within the Great Basin. She found that decreasing precipitation during summer causes an expansion of suitable areas. Our results also agree with those of a simulation study, which suggested that enhanced water availability during winter may benefit the establishment of this cool season species during spring (Bradford and Lauenroth, 2006). Further, dry summers of Patagonia may enhance the germination of *B. tectorum* through adequate after-ripening conditions (see Beckstead et al., 1996). In the eastern side of the Andes, decreasing winter temperature and increasing prevalence of winter precipitation are both correlated with increasing latitude, i.e. from summer rainfall regime in central Monte desert to winter snowfall regime in southern Monte desert and Patagonia steppes (Veblen et al., 2007). *B. tectorum* was most likely to occur in areas with intermediate maximum temperature during summer (between 19 and 30 °C). On the one hand, high maximum summer temperatures limiting the northern distribution of *B. tectorum* in our study area (i.e. above 30 °C) occur mostly in central Monte desert, where cool-season rainfall is extremely low (see e.g. Pucheta et al., 2011). On the other hand, the lower bound of maximum summer temperatures (i.e. 19 °C) may reflect the southern climatic limit for *B. tectorum*, below which the establishment of viable populations may not be possible (cfr. Bradford and Lauenroth, 2006).

In Patagonia, the most important plant functional groups are perennial grasses and forbs, with few annual and perennial herbs (mainly dicots and some monocots). Most of these species are active early in the growing season, except for some grasses that remain active during the dry summer and autumn seasons (Golluscio et al., 2005). The ability of *B. tectorum* to germinate and grow in autumn, and to remain alive during winter (Hulbert, 1955; Rice and Mack, 1991) introduces a new functional group to the Patagonian steppes. This may allow *B. tectorum* to avoid (and perhaps outcompete) native spring species by consuming soil resources very early in the growing season. At sites where *B. tectorum* became dominant, this resource-use behaviour could affect 80% of Patagonian species (Blank, 2008).

The map produced by our habitat model shows large areas of potential habitat containing just a few known records of *B. tectorum*. These areas correspond to the eastern portion of *B. tectorum* potential distribution, towards the Atlantic coast. This result suggests that *B. tectorum* has not reached its equilibrium abundance across the entire region, and supports our claim that there are still large areas where further local invasion (i.e. occupancy) may be expected. These results were based on presence-only data from the invaded range and depend on the current relationship between the distribution of *B. tectorum* and the climatic variables (see Broennimann and Guisan, 2008; Mau-Crimmins et al., 2006; Wilson et al., 2007). The populations of

*B. tectorum* are expanding and not in equilibrium with its current environment, and therefore the area potentially invaded by *B. tectorum* in southern South America may be even larger than predicted here.

## 5. Conclusions

The combination of complementary methodologies (i.e. proportion and extent-of-occurrence curves, invasion maps, and predicted distribution maps) revealed different aspects of the invasion process. On the one hand, the proportion curve suggested that *B. tectorum*'s population has been growing steadily since its introduction in the 1930's. On the other hand, the extent-of-occurrence curve and the invasion maps showed a period (1960–1980) of either successful long dispersal events or independent new introductions that expanded noticeably the regional coverage of *B. tectorum*. Overall, these results indicate that *B. tectorum* has successfully expanded over much of southern South America, and that there may be still room for additional local invasion (occupancy). Further, our habitat distribution model predicted that *B. tectorum* may readily expand towards eastern Patagonian steppes, where only a few invaded locations have been found. Both actual and potentially invaded areas are climatically and physiologically similar to those heavily invaded in the Great Basin in the USA. Thus, we believe that *B. tectorum* should be regarded as a hazardous species for arid and semiarid regions of southern South America, and that specific management practices need to be promptly developed.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2013.07.006>.

## References

- Aagesen, D., 2000. Crisis and conservation at the end of the world: sheep ranching in Argentine Patagonia. *Environmental Conservation* 27, 208–215.
- Aagesen, L., Szumik, C.A., Zuloaga, F.O., Morrone, O., 2009. Quantitative biogeography in the South America highlands – recognizing the Altoandina, Puna and Prepuna through the study of Poaceae. *Cladistics* 25, 295–310.
- Aravena, J.-C., Luckman, B.H., 2009. Spatio-temporal rainfall patterns in Southern South America. *International Journal of Climatology* 29, 2106–2120.
- Beckstead, J., Meyer, S.E., Allen, P.S., 1996. *Bromus tectorum* seed germination: between-population and between-year variation. *Canadian Journal of Botany* 74, 875–882.
- Blank, R.R., 2008. Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*). *Invasive Plant Science and Management* 1, 226–238.
- Bradford, J.B., Lauenroth, W.K., 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. *Journal of Vegetation Science* 17, 693–704.
- Bradley, B.A., 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology* 15, 196–208.
- Broennimann, O., Guisan, A., 2008. Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters* 4, 585–589.
- Cabrera, A.L., Willink, A., 1973. *Biogeografía de América Latina*. Secretaría General de la Organización de los Estados Americanos, Washington, USA.

- Castañeda, M., González, M., 2008. Statistical analysis of the precipitation trends in the Patagonia region in southern South America. *Atmósfera* 21, 303–317.
- Crawford, P.H.C., Hoagland, B.W., 2009. Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? *Journal of Biogeography* 36, 651–661.
- Davis, M.A., 2009. *Invasion Biology*. Oxford University Press, Oxford, USA.
- Delisle, F., Lavoie, C., Jean, M., Lachance, D., 2003. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *Journal of Biogeography* 30, 1033–1042.
- Douglas, B.J., Thomas, A.G., Derksen, D.A., 1990. Downy brome (*Bromus tectorum*) invasion into southwestern Saskatchewan. *Canadian Journal of Plant Science* 70, 1143–1151.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Frey, J.K., 2009. Distinguishing range expansions from previously undocumented populations using background data from museum records. *Diversity and Distributions* 15, 183–187.
- Garreaud, R.D., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day south American climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281, 180–195.
- Gaston, K.J., 1991. How large is a species' geographic range? *Oikos* 61, 434–438.
- Gaston, K.J., Fuller, R.A., 2009. The sizes of species' geographic ranges. *Journal of Applied Ecology* 46, 1–9.
- Golluscio, R.A., Oesterheld, M., Aguiar, M.R., 2005. Relationship between phenology and life form: a test with 25 Patagonian species. *Ecography* 28, 273–282.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C., Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8, 91–101.
- Higgins, S.L., Richardson, D.M., 1996. A review of models of alien plant spread. *Ecological Modelling* 87, 249–265.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965–1978.
- Holz, A., Veblen, T.T., 2011. Variability in the southern annular mode determines wildfire activity in Patagonia. *Geophysical Research Letters* 38, L14710.
- Hulbert, L.C., 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. *Ecological Monographs* 25, 181–213.
- Hulme, P.E., 2006. Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43, 835–847.
- Kent, R., Carmel, Y., 2011. Presence-only versus presence-absence data in species composition determinant analyses. *Diversity and Distributions* 17, 474–479.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert – history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* 6, 37–52.
- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2007. *Invasion Ecology*. Wiley-Blackwell, Malden, USA.
- Mau-Crimmins, T.M., Schussman, H.R., Geiger, E.L., 2006. Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States. *Ecological Modelling* 193, 736–746.
- Mihulka, S., Pyšek, P., 2001. Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *Journal of Biogeography* 28, 597–609.
- Moat, J., 2007. Conservation Assessment Tools Extension for ArcView 3. X, Version 1.2. GIS Unit, Royal Botanic Gardens, Kew.
- Morrow, L.A., Stahlman, P.W., 1984. The history and distribution of downy brome (*Bromus tectorum*) in North America. *Weed Science* 32 (Suppl. 1), 2–6.
- Novak, S.J., Mack, R.N., 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (Cheatgrass). *Bioscience* 51, 114–122.
- Parodi, L.R., 1947. Las gramíneas del género *Bromus* adventicias en la Argentina. *Revista Argentina de Agronomía* 14, 1–19.
- Paruelo, J.M., Lauenroth, W.K., Epstein, H.E., Burke, I.C., Aguiar, M.R., Sala, O.E., 1995. Regional climatic similarities in the temperate zones of North and South America. *Journal of Biogeography* 22, 915–925.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190, 231–259.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Pucheta, E., García-Muro, V.J., Rolhauser, A.G., Quevedo-Robledo, L., 2011. Invasive potential of the winter grass *Schismus barbatus* during the winter season of a predominantly summer-rainfall desert in Central-Northern Monte. *Journal of Arid Environments* 75, 390–394.
- Pyšek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *Journal of Biogeography* 20, 413–420.
- Rice, K.J., Mack, R.N., 1991. Ecological genetics of *Bromus tectorum*. I. A hierarchical analysis of phenotypic variation. *Oecologia*, 77–83.
- Salo, L.F., 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. *Biological Invasions* 7, 165–180.
- Soriano, A., Movia, C.P., 1986. Erosión y desertización en la Patagonia. *Interciencia* 11, 77–83.
- Sperry, L.J., Belnap, J., Evans, R.D., 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. *Ecology* 87, 603–615.
- Stohlgren, T.J., Schell, L.D., Vanden Heuvel, B., 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* 9, 45–64.
- Thiers, B., 2010. Index Herbariorum: a Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih> (accessed 10.05.13.).
- Thill, D.C., Beck, K.G., Callihan, R.H., 1984. The biology of downy brome (*Bromus tectorum*). *Weed Science* 32 (Suppl. 1), 7–12.
- Upadhyaya, M.K., Turkington, R., McIlvride, D., 1986. The biology of Canadian weeds. LXXV: *Bromus tectorum* L. *Canadian Journal of Plant Science* 66, 689–709.
- Veblen, T.T., Young, K.R., Orme, A.R., 2007. *The Physical Geography of South America*. Oxford University Press, New York, USA.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J., Richardson, D.M., 2009. Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24, 136–144.
- Wilson, J.R.U., Richardson, D.M., Rouget, M., Proches, S., Amis, M.A., Henderson, L., Thuiller, W., 2007. Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions* 13, 11–22.
- Wittenberg, R., Cock, M.J.W., 2001. *Invasive Alien Species: a Toolkit of Best Prevention and Management Practices*. CABI.