Towards the top: niche expansion of *Taraxacum officinale* and *Ulex europaeus* in mountain regions of South America

RICARDO ENRIQUE HERNÁNDEZ-LAMBRAÑO,[1]* PABLO GONZÁLEZ-MORENO[2,3] AND JOSÉ ÁNGEL SÁNCHEZ-AGUDO[1]

[1]*Instituto Hispano-Luso de Investigaciones Agraria (CIALE) Universidad de Salamanca, Parque Científico, C/ Del Duero, 12; 37185 Villamayor, Salamanca, España (Email: ricardohl123@usal.es)*, [2]*Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (EBD-CSIC), Isla de la Cartuja, Sevilla, Spain, and* [3]*CABI, Bakeham Lane, Egham, UK*

Abstract   In the current context of ongoing global change, the understanding of how the niches of invasive species may change between different geographical areas or time periods is extremely important for the early detection and control of future invasions. We evaluated the effect of climate and non-climate variables and the sensitivity to various spatial resolutions (i.e. 1 and 20 km) on niche changes during the invasion of *Taraxacum officinale* and *Ulex europaeus* in South America. We estimated niche changes using a combination of principal components analyses (PCA) and reciprocal Ecological Niche Modelling (rENM). We further investigated future invasion dynamics under a severe warming scenario for 2050 to unravel the role of niche shifts in the future potential distribution of the species. We observed a clear niche expansion for both species in South America towards higher temperature, precipitation and radiation relative to their native ranges. In contrast, the set of environmental conditions only occupied in the native ranges (i.e. niche unfilling) were less relevant. The magnitude of the niche shifts did not depend on the resolution of the variables. Models calibrated with occurrences from native range predicted large suitable areas in South America (outside of the Andes range) where *T. officinale* and *U. europaeus* are currently absent. Additionally, both species could increase their potential distributions by 2050, mostly in the southern part of the continent. In addition, the niche unfilling suggests high potential to invade additional regions in the future, which is extremely relevant considering the current impact of these species in the Southern Hemisphere. These findings confirm that invasive species can occupy new niches that are not predictable from knowledge based only on climate variables or information from the native range.

Key words: biological invasion, ecological niche models, Niche shift, *Taraxacum officinale*, *Ulex europaeus*.

INTRODUCTION

Globalization (i.e. expansion of transport and global trade) has led to an increase in the geographical scope and impact of biological invasions (Mack *et al.* 2000). In fact, along with changes in atmospheric chemistry and climate, biological invasions have been added to the list of important drivers of global change with significant effects on biodiversity and ecosystem functioning (Kriticos *et al.* 2003). Despite the growing knowledge on biological invasions, we still lack a thorough understanding of the processes driving the distribution of invasive species and the changes that might occur between the native and introduced ranges (Guisan *et al.* 2014).

The environmental requirements of an invasive species (i.e. ecological niche) (Peterson & Vieglais 2001; Peterson 2003; Santana *et al.* 2008) define the boundaries of its potential distribution in both native

and introduced regions. Identifying these key factors is useful to prioritize areas for the detection and control of early invasions (Peterson & Vieglais 2001; Peterson 2003; Franklin 2010; Elith 2013). A common approach is to make predictions about the potential introduced ranges using the data about the species distribution in either the native or the introduced range (Peterson 2003; Herborg *et al.* 2007; Franklin 2010). This approach is based on the assumption that invasive species have similar niche characteristics in native and introduced ranges (i.e. niche conservatism) (Peterson & Vieglais 2001; Peterson 2003; Carlos-Júnior *et al.* 2015). However, this approach has been questioned by recent studies highlighting the existence of factors that can cause invasive species to expand beyond their native environmental envelope (Guisan & Zimmermann 2000; Broennimann *et al.* 2007; Tingley *et al.* 2014; González-Moreno *et al.* 2015; Parravicini *et al.* 2015). Niche differentiation may result from different biotic factors such as the absence of competitors and/ or pathogens, evolutionary changes through genetic

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drift or selection in the introduced range (Müller-Schärer *et al.* 2004; Hierro *et al.* 2005; Richardson *et al.* 2010).

Having a clear understanding of whether ecological niches are similar in the native and introduced range is important for two main reasons: i) anticipation is the most effective management strategy to predict species occurrences in new areas and ii) detecting significant deviations from niche conservatism may highlight invasive species that are characterized by ecological or evolutionary changes during invasions, helping us to understand when such changes are likely to occur (Broennimann & Guisan 2008; Alexander & Edwards 2010; Petitpierre *et al.* 2012). For example, observed shifts into novel climates in the introduced range that are not occupied in the native range (i.e. expansion) suggest that changes in biotic interactions or rapid evolution may have extended the species climatic tolerances (Petitpierre *et al.* 2012; Guisan *et al.* 2014). Furthermore, the presence of suitable climates in the introduced range not yet occupied by the species (i.e. unfilling) is critically important because it suggests the likelihood of invading additional geographical regions in the future (Petitpierre *et al.* 2012; Guisan *et al.* 2014).

Niche conservatism in invasive species is usually studied with regard to climate variables (Broennimann *et al.* 2007; Rödder & Lötters 2009; Gallagher *et al.* 2010; Petitpierre *et al.* 2012; Parravicini *et al.* 2015). These studies assume that climate variables at coarse spatial resolution (e.g. 10, 20 and 50 km) are the leading factors of the distribution of invasive species (Austin & Van Niel 2011b; Guisan *et al.* 2014). This assumption ignores the importance of local environmental heterogeneity in shaping species distribution (Austin & Van Niel 2011b). For example, a species might occur under conditions in specialized habitats (e.g. mountains or stream banks) that could generally be characterized at a finer spatial grain (e.g. 1 km) (Bertrand *et al.* 2012).

However, niche changes may be observed when non-climate variables are included in the analyses (Bertrand *et al.* 2012; Guisan *et al.* 2014; González-Moreno *et al.* 2015). For example, solar radiation has long been known to influence plant distribution based on known biophysical processes such as chlorophyll inhibition or resistance to ultraviolet radiation (Tranquillini 1964; Austin & Van Niel 2011b). Furthermore, topographic diversity as a proxy of available soil moisture and nutrients has been shown to determine a significant part in the distribution of the plants (Austin & Van Niel 2011a). Although previous studies pinpoint the climate at large scales as the main factor driving species distributions and niche shifts for invasive species, the role of non-climate components or microclimates is largely unknown, despite the fact that they could provide important insights into the understanding of niche shifts for invasive species.

We carried out a large biogeographical study on *Taraxacum officinale* G. H. Weber ex Wiggers. (Asteraceae) and *Ulex europaeus* L. (Fabaceae). Both species are native to Eurasia and Europe, respectively, but are largely invading temperate areas worldwide with a significant impact. Thus, these species are ideal for testing the existence of niche shifts associated with biological invasions. We used occurrence data fully covering the large environmental gradients in their native and introduced ranges, to examine a) the effect of climate and non-climate variables (solar radiation and topographic diversity) and b) sensitivity to various spatial resolutions (i.e. 1 and 20 km) in the niche changes during the invasion of these species. We further investigated future invasion dynamics under a severe warming scenario for 2050 (HadGEM2; RCP-8.5) to unravel the role of niche shifts in their future distribution. This study represents the first assessment of niche dynamics for *T. officinale* and *U. europaeus* in South America and can provide insights into climatic influences driving species range expansions and potential adaptive physiological shifts now and into the future.

METHODS

Study species

Taraxacum officinale (dandelion) is a perennial herb from Eurasia that has spread worldwide. It is believed that it originated in Greece or perhaps Asia and spread across temperate areas to Europe and Asia Minor (Holm *et al.* 1997; CABI 2001; Stewart-Wade *et al.* 2002). This species has a fossil record that goes back to glacial and interglacial times in Europe, and it is thought to have colonized the Americas post-Pleistocene via Beringia (Holm *et al.* 1997; CABI 2001; Stewart-Wade *et al.* 2002; Molina-Montenegro & Cavieres 2010). *Taraxacum officinale* has apomictic reproduction and in its introduced range can be found growing in sites with contrasting climates and disturbance regimes and shows a wide range of adaptability to light, being able to grow vigorously in full sunlight, or in diffused light in the shade of trees or buildings (Stewart-Wade *et al.* 2002; Molina-Montenegro & Cavieres 2010).

Ulex europaeus (gorse) is a fast-growing woody legume of the family Fabaceae, native to the western coastal area of Europe and the British Isles including Ireland where it is an important component of native heathland vegetation (Gaynor & MacCarter 1981; Holm *et al.* 1997; Rees & Hill 2001; Hill *et al.* 2007; ILDIS 2007). *Ulex europaeus* has been introduced worldwide as a hedge plant to contain grazing animals, as fodder, and even to assuage the nostalgia of European colonists (CABI 2001). It has become naturalized elsewhere in Europe, North Africa and the Middle East (Holm *et al.* 1997; Bojnanský & Fargašová 2007; Hill *et al.* 2007). Its status as native to Italy and other countries of central Europe, and in localized montane districts of

North Africa, remains uncertain (CABI 2001; ILDIS 2007). The species is considered as invasive in many parts of the world at different latitudes, including New Zealand, Australia, South and North America (Chile, Colombia, California, Oregon, etc.) and tropical islands (Hawaii, Reunion), in altitudes that vary from 0 to 4000 m (Lowe *et al.* 2000; Hornoy *et al.* 2011).

Occurrence datasets

Data on the native distributions of *T. officinale* (Eurasia) (*n* = 7887) and *U. europaeus* (Europe) (*n* = 5541) were compiled from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and Invasive Species Compendium from the Centre for Agriculture and Biosciences International (CABI; www.cabi.org).

To assess the effect of spatial resolution on the significance of the climate and in combination with non-climate variables in measuring the niche shift, we used two grid resolutions of 30 arc-seconds and 10 arc-minute to remove duplicate records (i.e. only one occurrence record per grid square of 1 km and 20 km, respectively) thereby reducing clustering (spatial bias). This filtering decreased the number of records for *T. officinale* to 423 grids of 1 km and 398 of 20 km and for *U. europaeus* to 333 and 301 grids, respectively. Occurrence data points for these species from the South American introduced ranges were collated from GBIF and CABI (*T. officinale* *n* = 199 and *U. europaeus* *n* = 53) and were prepared in the same way with the procedure described above (*T. officinale:* 199 grids of 1 km and 156 grids of 20 km; *U. europaeus:* 53 and 38 grids, respectively). The compiled database is the result of an extensive search of the occurrence of the species in the study area. Nevertheless, we acknowledge that this database may not represent the full range of environmental conditions in which the species can be found (e.g. other introduced areas) as in other studies elsewhere (e.g. Petitpierre *et al.* 2012).

Environmental variables

Our initial variable set was composed of 19 bioclimatic variables, solar radiation and topographic diversity. Bioclimatic variables were available from WorldClim climate database at 30 arc-seconds and 10 arc-minute spatial resolutions (about 1 and 20 km at the equator) (Hijmans *et al.* 2005). Solar radiation was calculated using the Area solar tool from program ArcGIS 10.0 (ESRI 2015), which calculates clear-sky insolation across a Digital Elevation Model (DEM) at 1-km spatial resolution (US Geological Surveys; www.usgs.gov) accounting for aspect, slope and topographic shading. Topographic diversity was calculated using the Neighborhood toolset in ArcGIS 10.0. For each DEM grid cell, it calculates the diversity of elevation values considering all surrounding cells within a 3-km radius. Both layers were resampled to 20 km. Future climate projections under a severe warming scenario for 2050 (HadGEM2-RCP-8.5 at 1 km) (Martin *et al.* 2011) were also downloaded from the WorldClim climate database.

In order to avoid the cross-correlation within the selected environmental variables, a multi-collinearity test was conducted using Pearson's correlation coefficient. Variables with cross-correlation coefficient values of $r > \pm\, 0.7$ were excluded. The final explanatory variables selected were annual mean temperature (T_AM), mean diurnal range (T_DR), maximum temperature of warmest month (T_WM), temperature annual range (T_AR), mean temperature of wettest quarter (T_WQ), annual precipitation (P_A), precipitation of wettest month (P_WM), precipitation of driest month (P_DM), precipitation seasonality (P_S), topographic diversity (topo_div) and solar radiation (sun_l) (Appendix S1). All spatial information processing was handled using the Spatial Analyst Tool from ESRI ArcGIS 10.0 (ESRI 2015).

Measuring Niche Shifts

We used the Broennimann *et al.* (2012) and Petitpierre *et al.* (2012) approach to measure the niche shift related to climate and non-climate factors (i.e. radiation and topography) for *T. officinale* and *U. europaeus* between the native and introduced ranges. In this approach, a PCA is calibrated using the set of all environmental conditions in both ranges. Then, the available environmental conditions for the species within the full studied background are compared to those conditions in areas that are effectively occupied by the species in each of its ranges (native *vs.* introduced). First, we extracted the environmental conditions for both native and introduced ranges at two spatial resolutions (i.e. 1 and 20 km). Based on these data, we performed a PCA for each spatial resolution and used its first two axes to characterize the environmental space within which we could compare the native and introduced niches. We then divided this environmental space into a grid of 100×100 cells, as in Broennimann *et al.* (2012). Next, we used a kernel density function to convert occurrences of *T. officinale* and *U. europaeus*, and the available environments in each range into densities in order to correct for sampling bias and environmental availability, respectively, and to ensure that the results were independent of the grid resolution (Broennimann *et al.* 2012). Later, for each species and spatial resolution, we assessed the niche overlap between native and introduced ranges using Schoener's *D* metric which expresses an overall fit between niches over the full environmental space and determines whether we can infer the characteristics of the introduced niche from the native niche. This metric varies from 0 (totally dissimilar) to 1 (complete overlap) (Warren *et al.* 2008; Broennimann *et al.* 2012). Following Petitpierre *et al.* (2012), we also measured the proportion of the native niche non-overlapping with the introduced niche (i.e. unfilled), and the proportion of the introduced niche non-overlapping with the native niche (i.e. expansion), considering either the common environmental space for native and introduced ranges or the whole environmental space. These metrics were calculated using the 75th percentile of environments available in each range to avoid bias due to artefacts of the density function. Finally, we calculated the median of the distribution density and the median of the available environmental space in both ranges in order to

assess the overall direction of the shifts (Broennimann *et al.* 2012; Petitpierre *et al.* 2012; González-Moreno *et al.* 2015). All analyses were run using ecospat packages in R 3.1.3 (R Core Team 2015).

Fitting reciprocal Ecological Niche Modelling, future prediction and evaluation

To explore niche conservatism across ranges of *T. officinale* and *U. europaeus*, we generated reciprocal Ecological Niche Models (Broennimann *et al.* 2007; Medley 2010; González-Moreno *et al.* 2015) using the Maxent program (Phillips *et al.* 2006). The Maxent model is a maximum entropy-based machine learning programme that estimates the potential distribution for a species based on the environmental constraints (Phillips *et al.* 2006). To generate reciprocal models, first we made distribution models of potential suitable habitats with the same occurrence points and environmental variables that were used in our PCA analyses for the two species and for each of the ranges at two spatial resolutions. Then, we projected native models into introduced ranges and visually compared them with models calibrated with data occurrence in the introduced range. We then repeated this step but projected the introduced models into the native range and then compared them in the same way.

In fitting these models, we used 75% of the data for calibration and the other 25% for evaluation, a convergence threshold of 10^{-5}, the selection of feature classes (autofeature), regularization multiplier value of 1, a maximum of 5000 iterations and 10000 background points. To select the background points or pseudo-absences, we generated a Kernel Density map to draw background points at random in Maxent. This limits the background points to areas that we assume were surveyed for the species, which provides Maxent with a background file with the same bias as the present locations (Elith *et al.* 2011). We measured variable importance by comparing jackknife of training gain values when models were made with individual variables. To avoid projections into environments outside which the models were trained upon, we used the 'fade-by-clamping' option in Maxent, which removes heavily clamped pixels from the final predictions (Phillips *et al.* 2006). The outputs generated by Maxent were converted into binary maps using the 10th percentile training presence threshold to define suitable or unsuitable habitats for both species.

Predictive performance of each model was assessed using 15-fold cross-validation and the area under a receiver operating characteristic curve (AUC), which measures a model's ability to discriminate presence from background records (0.5 = random, 1 = perfect). We also calculated binary omission rates as the proportion of evaluation points that were not predicted by the models (Medley 2010).

Finally, the climate models for each species were projected into future climate scenarios to generate species distribution maps of the introduced range under a severe warming scenario for 2050 (HadGEM2; RCP-8.5). Models were calibrated with all the occurrence data points (native plus South America) to account for potential niche differences between native and introduced ranges (Broennimann & Guisan 2008; Jiménez-Valverde *et al.* 2011; González-Moreno *et al.* 2015).

RESULTS

Environmental niche shift

A niche shift of *T. officinale* and *U. europaeus* between native and introduced ranges was observed at different spatial resolutions of environmental variables and using both climate and climate-plus non-climate variables as predictors. Niche shifts metrics mostly varied with respect to the variables included in the analyses (i.e. higher shifts when considering both groups of variables). Nevertheless, shift metrics were rather constant across spatial resolutions (Table 1).

For both species, the change in the mean niche position between the native and introduced ranges was similar to the change in the background climate (continuous and dashed arrows, respectively, Figs 1 and 2, Appendices S10 and S11). For both species, the niche overlap between the native and introduced environmental spaces was lower when climate-plus non-climate variables were considered (*D*, Table 1). For *T. officinale*, the introduced niche exhibits a proportion outside of its native niche, occupying wetter and warmer environments with higher solar radiation relative to its native range (Fig. 1, Appendices S10 and S12). However, the analysis showed a small proportion of suitable environments in the introduced range not yet occupied by the species (unfilling) when climate-plus non-climate variables were considered and in opposite direction to the niche expansion (Fig. 1c and Table 1).

Similarly, the introduced niche of *U. europaeus* was expanded to areas with higher temperature, solar radiation and precipitation during the driest months relative to its native range (Fig. 2, Appendices S11 and S13). Furthermore, when climate-plus non-climate variables were considered, the species niche showed unfilling in areas of very low solar radiation and high temperature seasonality (Fig. 2c and Table 1).

However, when we considered only the common environmental space between the native and introduced ranges, expansion and unfilling were reduced for both species (Table 1). However, niche expansion was still relevant when considering climatic and non-climatic variables together (>11%).

Reciprocal ecological niche modelling

Climate-only and climate-plus non-climate models at different spatial resolutions for both species were all significantly better than random with high AUC (>0.83) and relatively low omission values (<22%), indicating that for each species, the most suitable habitats predicted were highly correlated with the

Table 1. Niche metrics from PCA analysis for each species, resolution and variable included in the analysis. D = Schoener's D statistic of niche overlap. Environmental space indicates what quantile of the environmental density used to remove marginal climates was retained to calculate niche expansion and unfilling metrics; full indicates analysis was performed on the whole environmental extent native and invaded, and ∩ indicates analysis was performed at the intersection between native and invaded range

Species	Resolution	Variables	D	Environmental space	Expansion %	Unfilling %
Taraxacum officinale	1 km	Climate	0.351	Full	21.1	0
				∩	9.10	0
		Climate-plus non-climate	0.075	Full	48.2	12.2
				∩	39.3	0.22
	20 km	Climate	0.402	Full	19.8	0
				∩	6.61	0
		Climate-plus non-climate	0.081	Full	39.8	11.5
				∩	28.9	0.10
Ulex europaeus	1 km	Climate	0.264	Full	45.3	0
				∩	5.10	0
		Climate-plus non-climate	0.061	Full	71.1	19.2
				∩	48.2	0
	20 km	Climate	0.263	Full	52.0	0
				∩	6.90	0
		Climate-plus non-climate	0.070	Full	70.4	17.5
				∩	11.0	0

actual occurrences of the species (Table 2). AUC and omission values were rather constant across spatial resolutions and both groups of variables selected.

Temperature annual range was the most important variable for both species in their native ranges (Appendices S2–S9). While in the introduced range solar radiation, annual precipitation, maximum temperature of warmest month and mean temperature of wettest quarter were the most important variables for both species (Appendices S2–S9).

The native model for *T. officinale* projected onto South America identified part of Ecuador, northern Peru, a small isolated area in northern Brazil, southern Brazil and Paraguay, Uruguay and southern Argentina and Chile, as potentially suitable areas. The native model failed to predict the known occurrences along the Andes Mountain Range in Colombia, Peru and Bolivia (Fig. 3a and b; Appendices S13, S16 and S18). The introduced model for *T. officinale* predicted a portion of the native distribution mostly in the Mediterranean region, north of India and south of China, but failed to predict nearly all actual occurrences in northern Europe (Fig. 3c and d; Appendices S13, S16 and S18).

The native model for *U. europaeus* predicted a broad distribution across central South America; however, its current distribution also covers the southern Andes (Fig. 4a and b; Appendices S15, S17 and S19). Finally, when we projected the introduced model for *U. europaeus* into the native range, it predicted a very small portion of the native distribution to the north-west of France, Alps and south-west of England with areas in the eastern Europe beyond the native distribution of the species (Fig. 4c and d; Appendices S15, S17 and S19).

Predicting future potential distribution

The best models calibrated with pooled data from all ranges (native plus South America) at 1-km resolution performed slightly better than those calibrated only with reciprocal models for both *T. officinale* (AUC: 0.95 ± 0.05, % omission 13.2 ± 0.01) and *U. europaeus* (AUC: 0.96 ± 0.03, % omission 11.2 ± 0.12). When we projected these models into the introduced range for 2050, the habitats along the northern Andes remained stable for both species (Fig. 5a and b). For *T. Officinale*, the model predicted an increase in a wide range of areas in the southern part of the continent (Fig. 5a). In contrast, for *U. Europaeus*, models predicted an increase of the range along the central Andes, south-eastern Brazil and southern Argentina (Fig. 5b).

DISCUSSION

Assessing whether the environmental niche of a species may change between different geographical areas or time periods is extremely important for predicting the spread of invasive species in the context of ongoing global change (Alexander & Edwards 2010; Guisan *et al.* 2014; González-Moreno *et al.* 2015). Adding new relevant variables to characterize the niche-space of invasive species offers an important
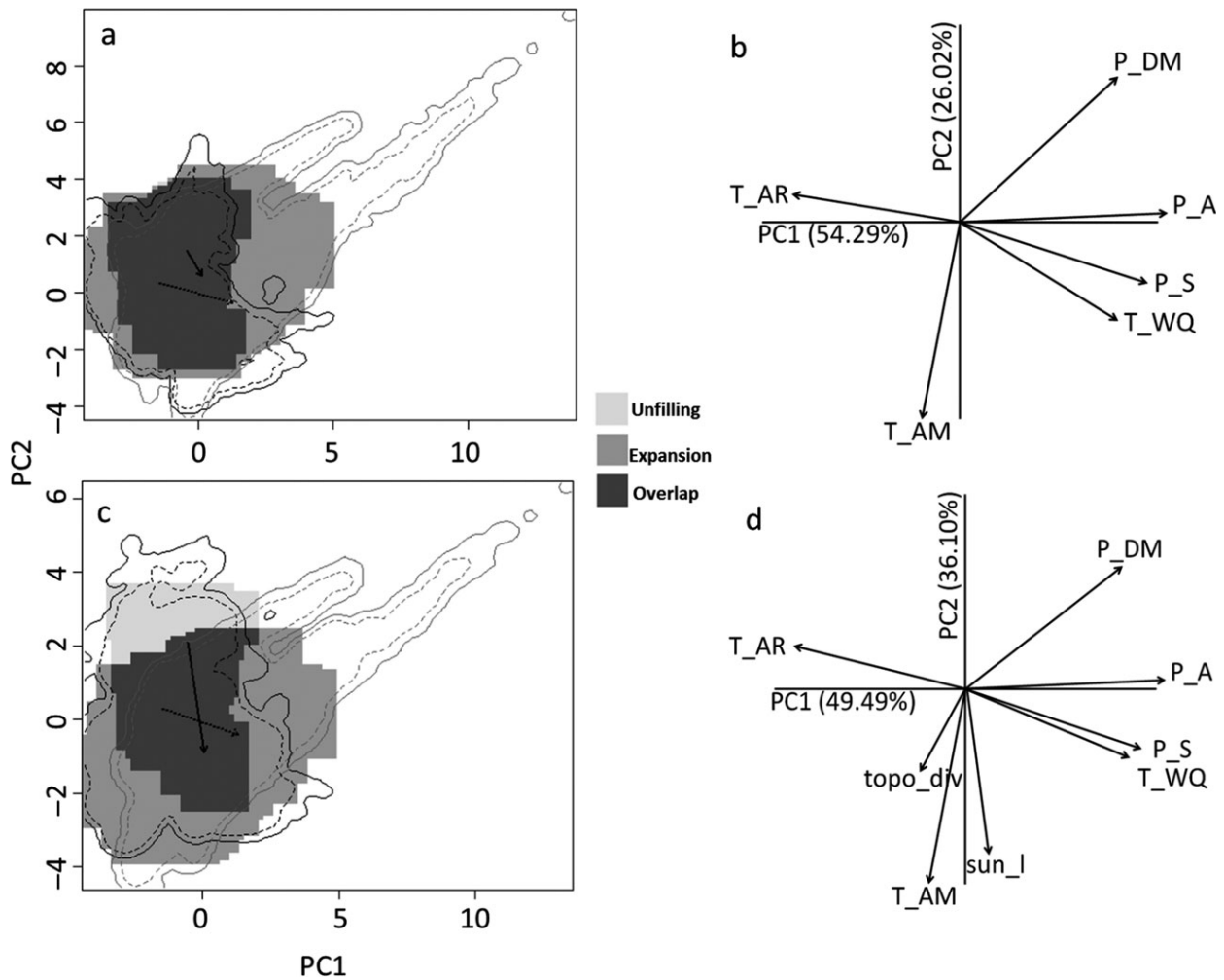
Fig. 1. Niche overlap between the native and introduced ranges of *Taraxacum officinale* using a grid resolution of 1 km. (a) Composed niche overlap of both ranges only using climate variables. (b) The contribution of the climate variables on the two axes of the PCA. (c) Composed niche overlap of both ranges considering climate-plus non-climate variables. (d) The contribution of the climate-plus non-climate variables on the two axes of the PCA. For each PCA axis in (b) and (d), the percentage of inertia explained is shown. The solid and the dashed contour lines in (a) and (c) correspond to 100% and 75%, respectively, of the available (background) environment for each range of *T. officinale* considered in the analyses. Shaded areas represent the portion of these conditions actually occupied by *T. officinale*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey for the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between the median of the available environmental space in each range. See *Materials and Methods* for variable descriptions.

opportunity to study the complexity of niche dynamics and to explore how the niches change after an introduction to novel environments (Guisan *et al.* 2014; González-Moreno *et al.* 2015). Here, although some of the invading populations still grow under similar climatic conditions as the native populations, we demonstrated that adding solar radiation and topographic diversity to climatic variables resulted in a substantial change in the measure of niche shift metrics of *T. officinale* and *U. europaeus*. These observations highlight the importance of defining species niches more broadly than simply by climate because

other factors may have important effects on niche shifts (Bertrand *et al.* 2012; González-Moreno *et al.* 2015). Thus, both for *T. officinale* and *U. europaeus*, considering only climatic factors might underestimate their potential to invade new regions.

Although most studies of niche shifts consider environmental variables at coarse spatial resolution, data at a finer grain (e.g. 1 km) might provide complementary answers to questions on climatic niche changes and improve our ability to predict and anticipate invasions (Guisan *et al.* 2014). However, we found similar niche changes and model
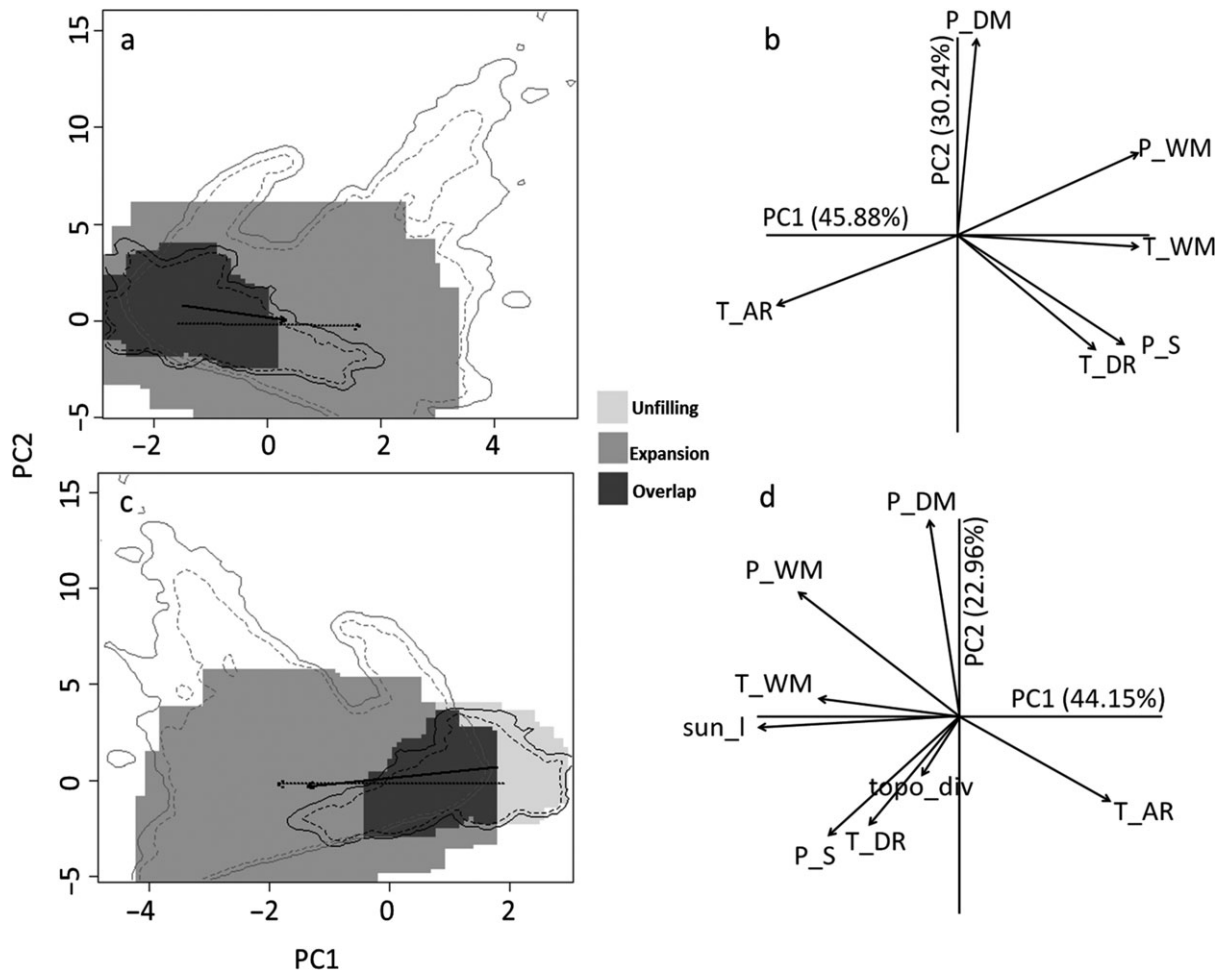
Fig. 2. Niche overlap between the native and introduced ranges of *Ulex europaeus* using a grid resolution of 1 km. (a) Composed niche overlap of both ranges only using climate variables. (b) The contribution of the climate variables on the two axes of the PCA and the percentage of inertia explained by the two axes. (c) Composed niche overlap of both ranges considering climate-plus non-climate variables. (d) The contribution of the climate-plus non-climate variables on the two axes of the PCA and the percentage of inertia explained by the two axes. The solid and the dashed contour lines in (a) and (c) correspond to 100% and 75%, respectively, of the available (background) environment for each range of *U. europaeus* considered in the analyses. Shaded areas represent the portion of these conditions actually occupied by *U. europaeus*: medium grey for niche expansion (presence only in the introduced range), light grey for niche unfilling (presence only in the native range) and dark grey for the conditions that are occupied in both ranges. The continuous black arrow shows the environmental distance between the median of the distribution density for each range. The dashed black arrow shows the environmental distance between median of the available environmental space in each range. See *Materials and Methods* for variable descriptions.

fitness across the two resolutions tested (i.e. 1 and 20 km). These findings suggest that at a continental scale, broad resolutions (>20 km) can fairly represent the climatic niche of invasive plants with broad geographical range. In fact, as invasion success in plants and birds is related to broad climate tolerances (Vazquez 2006; Hayes & Barry 2008), we expect similar patterns for a wide range of invasive species.

Both species showed niche expansion in South America (>11%) towards higher temperature, precipitation and solar radiation in relation to their native range. Previous studies from a variety of invasive species have also

reported niche shifts during different stages of biological invasions (Broennimann *et al.* 2007; González-Moreno *et al.* 2015; Parravicini *et al.* 2015). Although a recent review of studies from various taxonomic groups suggested that only about 50% of 180 species showed niche shifts (Guisan *et al.* 2014), comparative analyses of niche conservatism are difficult because of the varied ways (e.g. variables types, species characteristics and methods used) in which niche changes have been quantified (Guisan *et al.* 2014).

For *T. officinale* and *U. europaeus*, the fact that the realized niche differs between native and introduced ranges suggests that both species have the ability to

Table 2. Model accuracy results on evaluation dataset (25% independent data) using area under the curve (AUC) and binary tests of omission for each species, resolution and variables included in the analyses. A significant binomial test indicates that the predicted omission rate was less than a random prediction. *P*-values for all omission tests were <0.001

Species	Resolution	Variables	Calibration	Projection	AUC	Omission %
Taraxacum officinale	1 km	Climate	Native	Introduced	0.89 ± 1.01	16.4 ± 0.10
			Introduced	Native	0.93 ± 0.12	15.4 ± 0.29
		Climate-plus non-climate	Native	Introduced	0.84 ± 0.41	14.5 ± 0.10
			Introduced	Native	0.94 ± 0.72	15.1 ± 0.39
	20 km	Climate	Native	Introduced	0.87 ± 0.08	16.2 ± 0.05
			Introduced	Native	0.91 ± 0.82	14.1 ± 0.17
		Climate-plus non-climate	Native	Introduced	0.88 ± 0.21	15.6 ± 1.04
			Introduced	Native	0.93 ± 0.43	20.1 ± 0.18
Ulex europaeus	1 km	Climate	Native	Introduced	0.83 ± 0.01	12.0 ± 0.03
			Introduced	Native	0.95 ± 0.02	16.7 ± 0.10
		Climate-plus non-climate	Native	Introduced	0.84 ± 0.02	12.5 ± 0.06
			Introduced	Native	0.95 ± 0.03	13.3 ± 0.11
	20 km	Climate	Native	Introduced	0.85 ± 0.02	12.5 ± 0.03
			Introduced	Native	0.94 ± 0.04	16.7 ± 0.12
		Climate-plus non-climate	Native	Introduced	0.85 ± 0.01	13.5 ± 0.04
			Introduced	Native	0.95 ± 0.04	22.0 ± 0.16

Data of AUC and omission rate are expressed as mean $\pm$ SD.
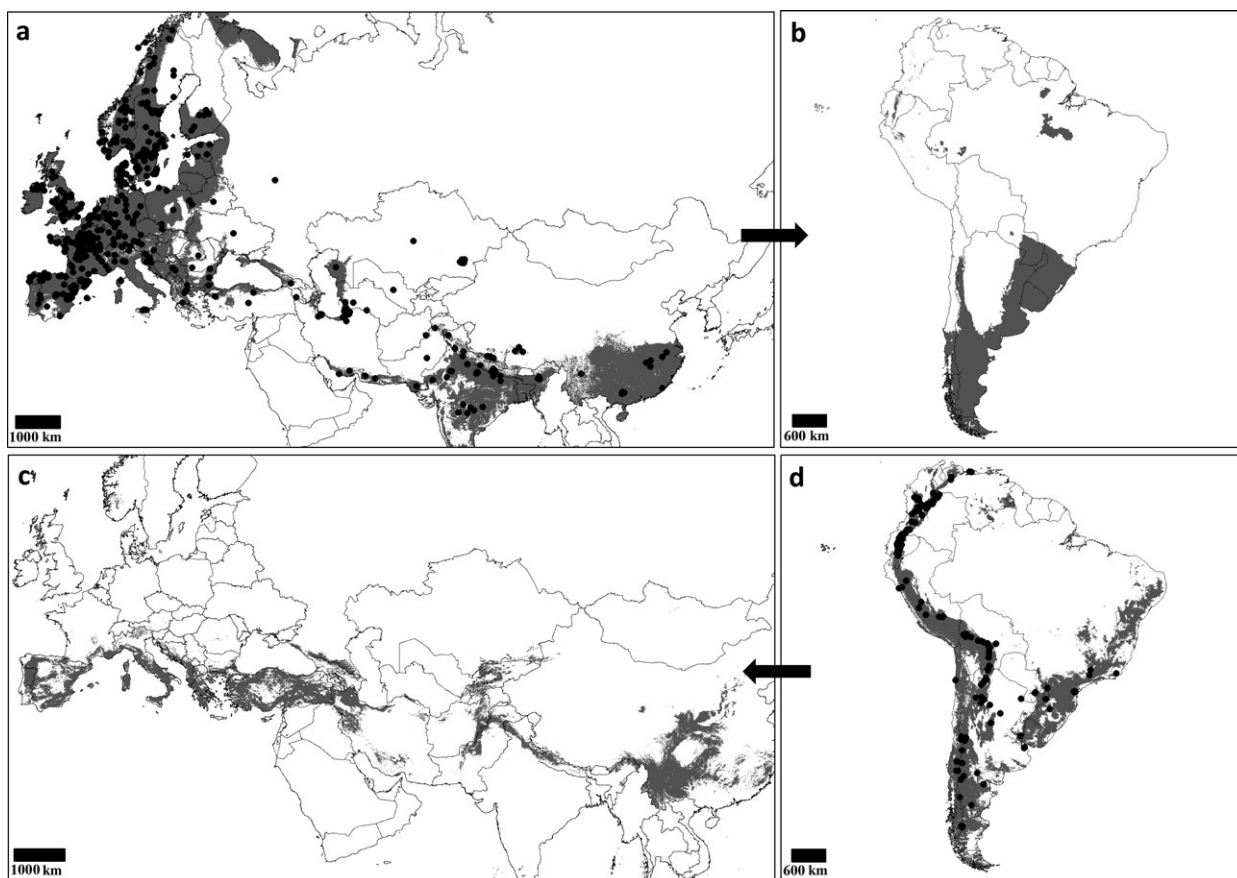

Fig. 3. Predictions of the potential distributions of *Taraxacum officinale* with maximum entropy model (Maxent) using a grid resolution of 1 km and considering climate-plus non-climate variables. The grey shaded area represents areas suitable for *T. officinale*, (a) model calibrated with occurrences points from native range, (b) native model projected onto introduced range, (c) introduced model projected onto Eurasia, (d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections. Black points represent the observed distribution of *T. officinale* in the study area.
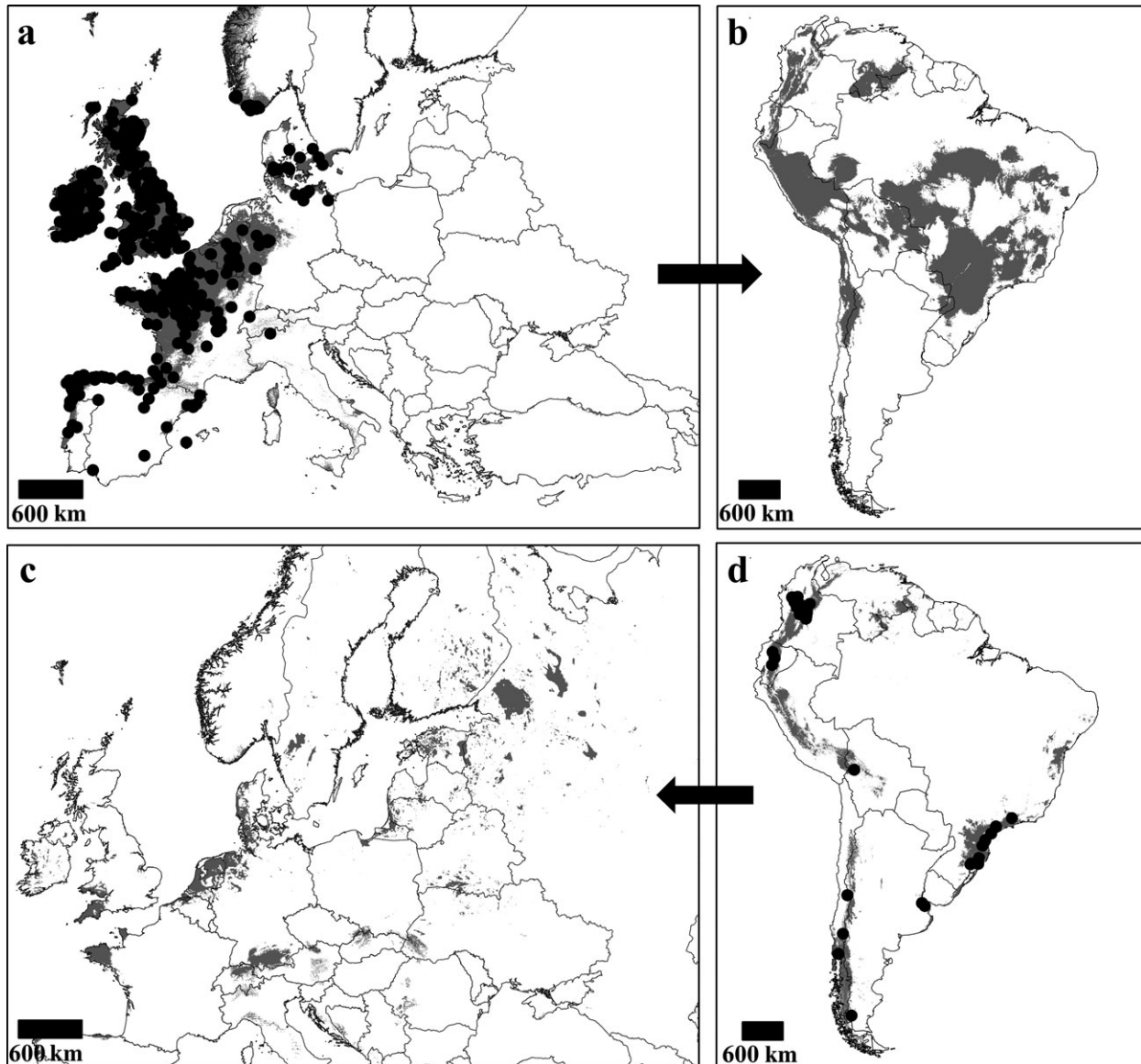
Fig. 4. Predictions of the potential distributions of *Ulex europaeus*. with maximum entropy model (Maxent). The grey shaded area represents areas suitable for *U. europaeus* using a grid resolution of 1 km and considering climate-plus non-climate variables. The grey shaded area represents areas suitable for *U. europaeus*, (a) model calibrated with occurrences points from native range, (b) native model projected onto introduced range, (c) introduced model projected onto Europa, (d) model calibrated with occurrences points from South America. Arrows indicate the direction of model projections. Black points represent the observed distribution of *U. europaeus* in the study area.

establish and spread in broad environmental conditions. The presence of these characteristics in several invasive plant species is called the 'Jack-of-all-trades scenario' and 'Master-of-some scenario' (Richards *et al.* 2006) and could be the result of several non-exclusive factors such as phenotypic plasticity, genetic adaptation or biological interactions. For instance, Molina-Montenegro and Cavieres (2010) described for *T. officinale* a higher amount of pigments involved in the xanthophyll cycle in two populations growing in an altitudinal gradient in the Andes of central Chile (2600 and 3600 m). This characteristic is probably its

main asset to avoid photoinhibition and to expand its niche into the areas of high solar radiation of the introduced range (i.e. higher altitude). We cannot discount that the species was already pre-adapted to these conditions in the native range, reflecting just the expression of phenotypic plasticity. However, two common garden experiments carried out with both seedlings and adults of *T. officinale* from its native and introduced ranges suggested that the functional response of the introduced individuals to stressful habitats is the result of local adaptation and less likely due to plasticity (Molina-Montenegro *et al.* 2011).
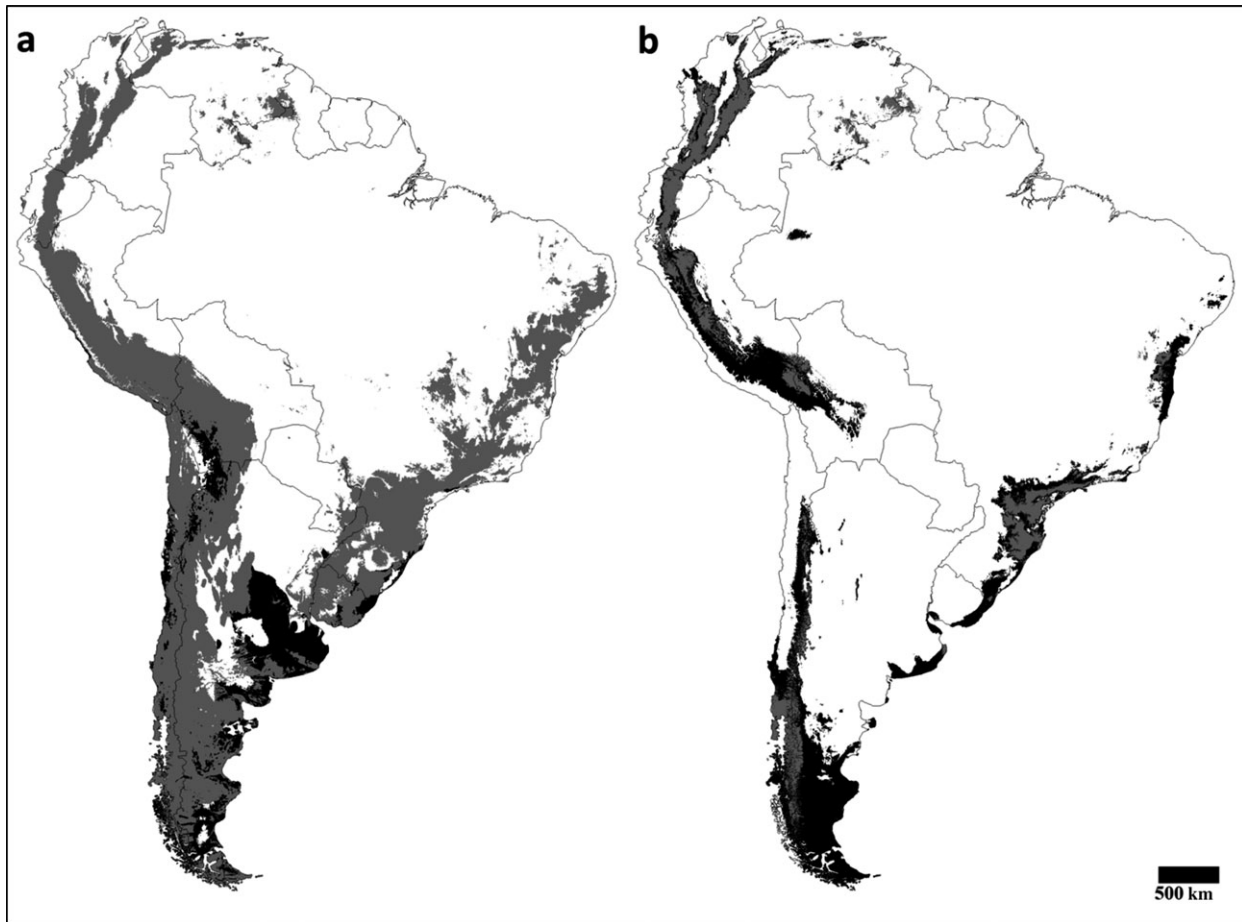
Fig. 5.   Predicted future potential distribution for (a) *Taraxacum officinale* and (b) *Ulex europaeus*. In grey, area suitable/stable and in black area gained. Future predictions are based on HadGEM2 global circulation models for 2050 (RCP-8.5A emission scenario).

The observed niche shift could also be a consequence of a different biotic environment in the introduced range (e.g. positive or negative interactions) (Richardson *et al.* 2000; Callaway *et al.* 2002; Lenz & Facelli 2003; Rodriguez 2006; Tecco *et al.* 2006). Indeed, it has been proposed that mutualisms between invasive plants and native organisms (plants and animals) favour the establishment of the former species, ultimately leading to successful spread (Richardson *et al.* 2000; Rodriguez 2006). For example, recent studies have demonstrated a positive association between native cushion plant *Azorella monantha* Clos and *T. officinale* in stressful habitats such as alpine environments in South America (Cavieres *et al.* 2005, 2008; Badano *et al.* 2007). Native cushion plants provide microhabitats with milder temperatures, higher water availability, optimum nutrient availability and less sun radiation (Cavieres *et al.* 2008), facilitating the establishment of exotic species adapted to more mesic conditions.

Furthermore, several hypotheses that attempt to explain invasive processes are based on missing biotic

interactions, such as the introduction without natural enemies (e.g. pathogens, parasites or herbivores) (Hornoy *et al.* 2011). Among the most influential, the Evolution of Increased Competitive Ability hypothesis (EICA) states that, in the absence of enemies, exotic plants evolve a shift in resource assignation from defence to reproduction or growth (Blossey & Notzold 1995). This increase in vegetative growth and/or reproductive effort would result in a better competitive ability of the invasive species in the introduced ranges (Hornoy *et al.* 2011). However, genetic constraints on life-history traits (i.e. genetic correlations resulting from previous correlational selection) strongly influence the invasion dynamics and the range limits of introduced species (Sinervo & Svensson 2002; Alexander & Edwards 2010; Colautti *et al.* 2010). From this perspective, Hornoy *et al.* (2011) investigated changes in both trait means and trait correlations of *U. europaeus* from native and introduced regions in a common garden experiment, in order to explore the joint evolution of life-history traits (i.e. flowering onset, pod density and plant

height) and susceptibility to seed predation. Their observations demonstrated lower correlations between life-history traits and infestation rate in the introduced range relative to the native range. These findings suggest an independent evolution of these key traits, potentially facilitating local adaptation of *U. europaeus* to a wide variety of environmental conditions in the introduced range (Hornoy *et al.* 2011).

In addition to niche expansion, we detected for both species suitable environments in South America not yet occupied by either species (unfilling). This pattern is likely due to dispersal limitation or because it represents areas where both species have never yet been introduced. The existence of unfilling could reflect an ongoing colonization, indicating that both species might invade additional geographical regions in the future (Petitpierre *et al.* 2012), primarily in the central part of the South American continent. On top of this incipient spread, climate change could alter the future spatial distribution of the species. A severe warming scenario could increase the invasion potential of both species for 2050 towards the southern part of South America. This increase could be limited by the dispersal capacity of the species and its ability to colonize natural habitats. In contrast, the new invasion scenario could also be exacerbated by modifications in their ecophysiological traits, and thus, enhance their ecological niche breadth and ability to persist under a global change scenario (Schweitzer & Larson 1999; Richards *et al.* 2006).

In the current context of ongoing global changes, the niche expansion observed during the biological invasion of *T. officinale* and *U. europaeus* in South America exemplifies how invasive species can occupy new niches that are not predictable from knowledge based only on climates factors or information from the native range. Our results indicate that neither species is fully occupying suitable environments that mirror its native range and that the observed niche expansion is towards areas with higher solar radiation and with warmer and wetter climates. Despite most of this expansion being outside the climate available in the native region, recent studies support local adaptation and enemy release as the main factors driving the shift (Hornoy *et al.* 2011; Molina-Montenegro *et al.* 2011). These evolutionary processes will certainly affect the future distribution of the species and their potential impact in the Southern Hemisphere.

Finally, while biological invasions provide a fascinating insight into species distribution limits and a unique opportunity to investigate mechanisms underlying ecological and evolutionary processes (Guisan *et al.* 2014; Tingley *et al.* 2014), understanding these basic processes also has important implications for effective management decisions under future climate change.

AUTHOR CONTRIBUTIONS

All authors contributed to the formulation of ideas and the writing of the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Pearson's correlation coefficients of the association among the variables used in the analyses for each species.

Appendix S2. Maxent models using a grid resolution of 1 km: Climate-only Model for *T. officinale*.

Appendix S3. Maxent models using a grid resolution of 1 km: Climate-plus non-climate Model for *T. officinale*.

Appendix S4. Maxent models using a grid resolution of 1 km: Climate-only Model for *U. europaeus*.

Appendix S5. Maxent models using a grid resolution of 1 km: Climate-plus non-climate Model for *U. europaeus*.

Appendix S6. Maxent models using a grid resolution of 20 × 20 km: Climate-only Model for *T. officinale*.

Appendix S7. Maxent models using a grid resolution of 20 × 20 km: Climate-plus non-climate Model for *T. officinale*.

Appendix S8. Maxent models using a grid resolution of 20 × 20 km: Climate-only Model for *U. europaeus*.

Appendix S9. Maxent models using a grid resolution of 20 × 20 km: Climate-plus non-climate Model for *U. europaeus*.

Appendix S10. Niche overlap between the native and introduced ranges of *Taraxacum officinale*.

Appendix S11. Niche overlap between the native and introduced ranges of *Ulex europaeus*.

Appendix S12. Projections of the native and introduced ranges of *T. officinale*.

Appendix S13. Projections of the native and introduced ranges of *U. europaeus*.

Appendix S14. Predictions of the potential distributions of *Taraxacum officinale* with Maxent model, with 1 km grid resolution.

Appendix S15. Predictions of the potential distributions of *Ulex europaeus* with Maxent model, with 1 km grid resolution.

Appendix S16. Predictions of the potential distributions of *Taraxacum officinale* with Maxent model, with 20 km grid resolution.

Appendix S17. Predictions of the potential distributions of *Ulex europaeus* with Maxent model, with 20 km grid resolution.

Appendix S18. Predictions of the potential distributions of *Taraxacum officinale* with Maxent model, with 20 km grid resolution, including climate plus non-climate variables.

Appendix S19. Predictions of the potential distributions of *Ulex europaeus* with Maxent model, with 20 km grid resolution, including climate plus non-climate variables.