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Monitoring and modeling the invasion of the fast spreading alien *Senecio inaequidens* DC. in an alpine region

G. Vacchiano, E. Barni, M. Lonati, D. Masante, A. Curtaz, S. Tutino & C. Siniscalco

Abstract

We modeled the distribution of the South African alien *Senecio inaequidens* DC. in the Aosta Valley, Western Italian Alps, using data extracted from the Regional floristic database and from an intensive field survey carried out in years 2009–2010. The aims of the work were (1) to evaluate whether the species is in the introduction, colonization, or establishment stage of invasion, (2) to detect the environmental factors that drive the invasion process, and (3) to highlight the potential range of distribution of the alien species. The modeling framework was a stepwise generalized linear model (GLM), using gridded presence/absence data and environmental predictors such as topography, climate, land use, and anthropogenic and natural disturbances. GLM were fit both with and without an additional independent variable to take into account current dispersal limitations. *S. inaequidens* displayed a very fast spread in the Aosta Valley in the years 1990–2010. The species was positively associated with roads and rivers, southern slopes, and negatively with elevation. However, it was found at an elevation of 1600 m, showing the ability to reach higher elevations than those observed for other invasive alien species, and confirming to be pre-adapted to mountain conditions. The difference between the species distribution models, with and without dispersal constraints, suggested that the availability of seed sources still limits the potential distribution of the species, rather than the environmental variables, and that the realized regional niche differs to a great extent from the equilibrium niche. When limitations to the seed source cease (i.e., in the establishment stage), the species will likely invade large areas that are currently characterized by pastures and grasslands with native species of high agricultural importance. The invasion of *S. inaequidens* should therefore be considered a serious threat, due to its potential to invade mountain regions, and in particular to colonize habitats used for grazing and forage, thus leading to a high risk for cattle and human health. We discuss the relevance of the results both concerning communication with the public and to support local eradication and control activities. The inclusion of *S. inaequidens* in the “black list” of the regional law for the conservation of alpine flora (L.R. 45/2009) will help to transfer the information and support invasion control, in particular at medium elevations.

Keywords:: Alien species, biomod2, dispersal, potential distribution, species distribution model, Aosta Valley,

Introduction

Invasive species not only colonize anthropogenic environments but may also invade semi-natural and natural areas as recently shown, e.g., in freshwaters, coastal dunes (Pretto et al. 2010 PrettoF, Celesti-GrapowL, CarliE, BlasiC. 2010. Influence of past land use and current human disturbance on non-native plant species on small Italian islands. *Plant Ecol*210: 225–239., 2012 PrettoF, Celesti-GrapowL, CarliE, BrunduG, BlasiC. 2012. Determinants of non-native plant species richness and composition across small Mediterranean islands. *Biol Invasions*14: 2559–2572.), and grasslands in mountain areas (Curtaz et al. 2011 CurtazA, TalichetM, BarniE, BassignanaM, MasanteD, PauthenetY, SiniscalcoC. 2011. Specie esotiche invasive e dannose nei prati di montagna. Aosta: Institut Agricole Régional.).

Senecio inaequidens DC. (Asteraceae), a perennial herbaceous or a partially woody shrub, is one of the fastest spreading invasive plant species in Europe, mainly in mountain systems. Like congeneric species, it contains pyrrolizidine alkaloids, which are toxic to livestock and can cause health issues on human beings via milk consumption (Dimande et al. 2007 DimandeAFP, BothaCJ, ProzeskyL, BekkerL, RösemannGM, LabuschagneL, RetiefE. 2007. The toxicity of *Senecio inaequidens* DC. *J S Afr Vet Assoc*78: 121–129.). For this reason, its spread in the Alps is extremely alarming, especially in regions where the economy is largely based on cattle grazing and high-quality dairy production, such as Aosta Valley Autonomous Region. Owing to its negative effects, *S. inaequidens* has been introduced in the “black list” of the recent regional law on the conservation of alpine flora (L.R. 45/2009), with the aim of disseminating knowledge on the risks of its occurrence, reducing its spread by preventing the cultivation for ornamental purposes and supporting control and eradication activities.

The species is native to the mountain regions of South Africa (Hilliard 1977 HilliardOM. 1977. *Compositae in Natal*. Pietermaritzburg, South Africa: University of Natal Press.) and also occurs in Mozambique, Namibia, Lesotho and Swaziland (EPPO 2006 EPPO (European Plant Protection Organization). 2006. Data sheet on invasive plants: *Senecio inaequidens*. Available: www.eppo.org/QUARANTINE/plants/Senecio_inaequidens/SENIQ_ds.pdf. Accessed May 2013 20.; Dimande et al. 2007 DimandeAFP, BothaCJ, ProzeskyL, BekkerL, RösemannGM, LabuschagneL, RetiefE. 2007. The toxicity of *Senecio inaequidens* DC. *J S Afr Vet Assoc*78: 121–129.). In its native range, it occurs at elevations from 1400 to 2850 m, over a wide range of natural and human disturbed habitats, such as river banks, rocky slopes, heavily grazed or recently burned areas, and roadsides (Lachmuth et al. 2011 LachmuthS, DurkaW, SchurrFM. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: The role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol*192: 529–541.).

The species is currently spreading throughout Europe at an exceptionally high speed, following the accidental introduction of seeds in wool transport to several locations in the late 19th and early 20th centuries, in Germany, Belgium, France, and Italy (Kuhbier 1977 KuhbierH. 1977. *Senecio inaequidens* DC. Ein Neubürger der nordwestdeutschen Flora. *Abh Naturwiss Ver Bremen*38: 383–396.; Ernst 1988 ErnstWHO. 1998. Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in The Netherlands: From wool alien to railway and road alien. *Acta Bot Neerl*47: 131–151.; Jaenmonod 2002 JeanmonodD. 2002. Nouvelles stations pour le *Senecio inaequidens* DC. ou la conquete irresistible du senecon du Cap. *Saussurea*32: 43–50.; Lachmuth et al. 2011 LachmuthS, DurkaW, SchurrFM. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: The role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol*192: 529–541. and references therein). In Italy, it has been reported to be invasive in almost all regions (16 out of 21 and is absent only in Apulia) (Celesti-

Grapow et al. 2009 Celesti-Grapow L, Alessandrini A, Arrigoni PV, Banfi E, Bovio M, Brundu G, et al. 2009. The inventory of the alien flora of Italy. *Plant Biosyst* 143(2): 386–430., 2010 Celesti-Grapow L, Alessandrini A, Arrigoni PV, Assini S, Banfi E, Barni E, et al. 2010. Non-native flora of Italy: Species distribution and threats. *Plant Biosyst* 144: 12–28.). In its native range, the species has both diploid and tetraploid cytotypes, while the invaded European range seems to comprise only tetraploids and to have originated from two overlapping source regions in the Drakensberg and Maloti Mountains (Lafuma et al. 2003 Lafuma L, Balkwill K, Imbert E, Verlaque R, Maurice S. 2003. Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Syst Evol* 243: 59–72., Monty & Mahy 2009 Monty A, Mahy G. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. *Oecol* 159: 305–315.; Lachmuth et al. 2010 Lachmuth S, Durka W, Schurr FM. 2010. The making of a rapid plant invader: Genetic diversity and differentiation in the native and invaded range of *Senecio inaequidens*. *Mol Ecol* 19: 3952–3967.). For this reason, the plants introduced into Europe are considered to be pre-adapted to mountainous climatic conditions (Lafuma et al. 2003 Lafuma L, Balkwill K, Imbert E, Verlaque R, Maurice S. 2003. Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Syst Evol* 243: 59–72.; Bossdorf et al. 2008 Bossdorf O, Lipowsky A, Prati D. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib* 14: 676–685.).

However, the species is able to adapt to a wide range of climatic conditions, i.e., annual rainfall ranging from 500 to 1000 mm and mean annual temperature from 10 to 20°C (EPPO 2006). Even these limits seem to be excessively narrow, since it has been shown that low winter temperatures do not limit the survival of the species (Monty & Mahy 2009 Monty A, Mahy G. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. *Oecol* 159: 305–315.), which can maintain a viable taproot in the soil, especially when covered by snow. Recent studies have demonstrated that the species can change its reproductive and competitive ability according to the intensity of biotic competition, switching its resource allocation priorities between vegetative and reproductive structures (Lachmuth et al. 2011 Lachmuth S, Durka W, Schurr FM. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: The role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol* 192: 529–541.). *S. inaequidens* can produce up to 10–30,000 seeds per plant per year (López-García & Maillet 2005 López-García MC, Maillet J. 2005. Biological characteristics of an invasive South African species. *Biol Invasions* 7: 181–194.; EPPO 2006 EPPO (European Plant Protection Organization). 2006. Data sheet on invasive plants: *Senecio inaequidens*. Available: www.eppo.org/QUARANTINE/plants/Senecio_inaequidens/SENIQ_ds.pdf. Accessed May 2013 20.). These seeds are dispersed by wind, animals and vehicles (Ernst 1998 Ernst WHO. 1998. Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in The Netherlands: From wool alien to railway and road alien. *Acta Bot Neerl* 47: 131–151.; Heger & Böhmer 2006 Heger T, Böhmer HJ. 2006. NOBANIS – Invasive Alien Species Fact Sheet – *Senecio inaequidens*. Online database of the North European and Baltic Network on Invasive Alien Species. Available: http://www.nobanis.org/files/factsheets/Senecio_inaequidens.pdf. Accessed May 2013 20.; Monty et al. 2008 Monty A, Stainier C, Lebeau F, Pieret N, Mahy G. 2008. Seed rain pattern of the invasive weed *Senecio inaequidens* (Asteraceae) Belg. *J Bot* 141(1): 51–63.). The latter are the preferential vectors for long-distance dispersal, and lead to the initial invasion of ruderal habitats along traffic routes, roads, and railways, soon after the introduction of the species to a new area. In the invaded range, *S. inaequidens* has also started to colonize disturbed habitats other than roadsides, such as heavily grazed grasslands in Southern Europe (Schreiber et al. 2003 Schreiber C, Crawley MJ, Porembski S. 2003. The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). *Divers Distrib* 9: 415–426.; Garcia Serrano et al. 2004 Garcia Serrano H, Escarré J, Sans FX. 2004. Factors that limit the emergence and establishment of the related aliens *Senecio inaequidens* and *Senecio pterophorus* and the native *Senecio malacitanus* in Mediterranean climate. *Can J Bot* 82: 1346–1355.), temporary ponds, rock cliffs, walls, and vineyards.

Species distribution models (SDMs) have been used to project the potential distribution and to support effective mitigation or eradication activities of invasive species in the adventive range at a global or, more often, regional scale (Guisan & Thuiller 2005 GuisanA, ThuillerW. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecol Lett*8: 993–1009.[CrossRef], [Web of Science ®]; Wilson et al. 2007 WilsonJRU, RichardsonDM, RougetM, ProcheS, AmisMA, HendersonL, ThuillerW. 2007. Residence time and potential range: Crucial considerations in modelling plant invasions. *Divers Distrib*13: 11–22.[CrossRef]; Gallien et al. 2010 GallienL, MünkemüllerT, AlbertCH, BoulangeatI, ThuillerW. 2010. Predicting potential distributions of invasive species: Where to go from here?*Divers Distrib*16: 331–342.). By fitting a relationship between the occurrence of the observed species and environmental factors, SDMs can be used to assess the role of natural or anthropogenic disturbance, vegetation types, and climatic variables as invasion drivers. Finally, SDMs can provide “early warnings” in areas of major concern for the potential spread of invasive species, and help evaluate whether the species is in the introduction, colonization, or establishment stage of invasion (Theoharides & Dukes 2007 TheoharidesKA, DukesJS. 2007. Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytol*176(2): 256–273.). Dispersal constraints must be included in SDMs for species in the first two stages of invasion, in order to optimize their fit by taking into account the geographical limitations in the seed source (Vaclavik & Meentemeyer 2009 VaclavikT, MeentemeyerRK. 2009. Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions?*Ecol Model*220: 3248–3258.).

In the present study, the occurrence of *S. inaequidens* has been monitored in the Autonomous Aosta Valley Region, and its distribution has been modeled with the following aims: (i) to evaluate whether the species is in the introduction, colonization, or establishment stage of invasion; (ii) to detect the environmental factors that drive the invasion process; and (iii) to highlight the potential range of distribution, in order to support control activities by either private citizens or public administrations.

Materials and methods

Study area

The study area is the Aosta Valley Autonomous Region (Italy), a 3263 km² area on the south-western side of the European Alps. The region occupies the drainage basin of the higher course of the Dora Baltea river and is characterized by a main valley that runs eastwards and by north–south tributary valleys on both orographic sides. This mainly mountainous region has a wide elevation range (312–4810 m a.s.l.), and only 20% of the territory lies below 1500 m. Climate shows the typical continental conditions of inner alpine valleys (Schwabe & Kratochwil 2004 SchwabeA, KratochwilA. 2004. Festucetalia valesiaca communities and xerothermic vegetation complex in the central Alps related to environmental factor. *Phytocoenologia*34: 329–446.), with minor variations due to local topographic and geographic conditions (e.g., aspect). Mean annual temperature varies from 10.3°C at the valley bottom (600 m) to 7.5°C at 1200 m a.s.l., 3 and – 2°C at 2000 and 2500 m, respectively, and is nearly always below 0°C above 3100 m. Mean annual rainfall is 950 mm and ranges from less than 600 mm/year in the innermost lowlands to over 1800 mm/year in upland areas. The rainfall regime is subcoastal-alpine and usually presents two peaks in spring and fall and two minima in winter and summer (Mercalli et al. 2003 MercalliL, Cat BerroD, MontuschiS, CastellanoC, RattiM, Di NapoliG, et al. 2003. *Atlante climatico della Valle d'Aosta*. Torino: Soc Met Subalpina.).

Forests and natural or semi-natural open areas cover more than 90% of the territory, while artificial surfaces and agricultural lands, which are located at lower elevations, occupy less than 10%. The population density is only 38 inhabitants/km², and the inhabitants live mostly in the main valley,

where urbanization is concentrated in few settlements. Important transport infrastructures run across the main valley, since the Aosta Valley has always been an important crossroad in the western Alps. In the last 50 years, trade and touristic traffic increased remarkably due to the construction of a highway and of the Mont Blanc and the Grand Saint Bernard Tunnels that connect the region to France and Switzerland, respectively. Agriculture is extensive and is predominantly based on dairy farming for the production of high quality cheese. The agricultural lands in the region are mostly covered by permanent lowland grasslands and native mountain pastures (above 1800 m a.s.l.). Besides agro-pastoral activities, both summer and winter tourism are highly developed, determining high human impacts in areas at higher elevations.

Species distribution data

S. inaequidens was found for the first time in 1990 in the lower part of the Aosta Valley (i.e., near its mouth) on roadsides and river gravel. It was detected in the central part of the valley in 1994, and at its western end in 2004, near the Mont Blanc Tunnel to France (Poggio et al. 2010 PoggioL, Vanacore FalcoI, BovioM. 2010. New Red Checklist and Black Checklist of the vascular flora of Valle D'Aosta (Italy, North-western Alps). Rev Valdôtaine Hist Nat64: 41–54.).

A complete picture of the current distribution of *S. inaequidens* in the region has been obtained by gathering two data-sets. The first data-set, containing 2369 georeferenced occurrences, was obtained from an intensive field survey carried out in 2009 and 2010, which was specifically aimed at monitoring *S. inaequidens* distribution. More than 1200 km of roads and rivers running through urban and agricultural areas as well as woodlands were covered. Each occurrence of the species was recorded using a GPS logger. The second data-set, containing 75 georeferenced occurrences, was extracted from the Aosta Valley floristic database (source: Servizio Aree Protette), which contains records from herbaria, literature, and recent field surveys (years 1985–2012) that were carried out throughout the region with the aim of assembling a complete inventory of the regional vascular flora.

Presence/absence data from the two data-sets were joined and resampled on a 500 m × 500 m regular grid, a slightly finer grain than that of the coarsest explanatory variable (Table I), but coarser than the likely spatial autocorrelation extent of both the response and the explanatory variables. Cells in which *S. inaequidens* occurred at least once were classified as presence points, while the remaining ones were classified as absences. Due to the habitat preference of the species (Heger & Böhmer 2006 Heger T, Böhmer HJ. 2006. NOBANIS – Invasive Alien Species Fact Sheet – *Senecio inaequidens*. Online database of the North European and Baltic Network on Invasive Alien Species. Available: http://www.nobanis.org/files/factsheets/Senecio_inaequidens.pdf. Accessed May 2013 20.), all cells above 2500 m a.s.l. were filtered out and 8967 landscape cells were selected for further analyses.

Table I Summary of the explanatory variables calculated for each landscape cell (500 m × 500 m) and used in the analyses.

Code	Description	Units	Min	Max	Mean	Std. error	Minimum Mapping Unit	Source
<i>Topographical variables</i>								
ALTTT	Altitude	m a.s.l.	310	2500	1750	5.8	900 m ²	ASTER GDEM (2011)
SLOPE	Slope	°	0	77	21	0.1		
SOUTH	Southness	°	0	179	90	0.5		
<i>Climatic variables</i>								
BIO01	Annual mean temperature	°C	-9.2	11.1	3.6	0.03	1 km ²	Hijmans et al. (2005)
BIO05	Max temperature of warmest month	°C	-0.1	26.7	16.7	0.04		
BIO06	Min temperature of coldest month	°C	-17.8	-2.9	-7.8	0.02		
BIO10	Mean temperature of warmest quarter	°C	-3.0	20.0	11.3	0.03		
BIO11	Mean temperature of coldest quarter	°C	-14.8	2.0	-3.9	0.02		
BIO12	Annual precipitation	mm	800	2580	1395	3.0		
BIO18	Precipitation of warmest quarter	mm	226	587	359	0.6		
<i>Human-related variables</i>								
BUILD	Buildings (agricultural, residential, commercial, industrial, military, transit stations, transmission towers, etc.)	m ² cell ⁻¹	0	113500	1291	52.9	5 m	Regione Autonoma Valle Aosta (1998)
WALLS	Walls, retaining walls	m cell ⁻¹	0	8313	280	7.5		
ROADS	Roads (highways, paved, and unpaved roads (except tunnels))	m cell ⁻¹	0	11603	1274	19.9		
RAILS	Railways (except tunnels)	m cell ⁻¹	0	4922	11	1.1		
CANAL	Canals (artificial waterways and irrigation, except underground tracts)	m cell ⁻¹	0	1826	17	1.2		
SKITR	Ski tracks and lifts	m cell ⁻¹	0	3528	27	2.1		
<i>Natural disturbance variables</i>								
EROSI	Landslides and eroded areas	m ² cell ⁻¹	0	45700	522	20.0	5 m	Regione Autonoma Valle Aosta (1998)
RIVER	Rivers and streams	m cell ⁻¹	0	6199	169	4.2		
<i>Land-use variables</i>								
URBAN	Urban areas	m ² cell ⁻¹	0	250000	4972	276.9	0.25 km ²	Corine Land Cover 2006 – seamless vector data, level 3 (BEA 2012)
VINEY	Vineyards	m ² cell ⁻¹	0	211900	376	69.8		
MEADO	Meadows and orchards	m ² cell ⁻¹	0	250000	15296	479.5		
GRASS	Grasslands	m ² cell ⁻¹	0	250000	60063	820.4		
ALPSH	Subalpine and alpine shrublands	m ² cell ⁻¹	0	250000	11765	420.1		
WOOD	Forests and woodlands (evergreen, broadleaves, and mixed)	m ² cell ⁻¹	0	250000	81855	995.6		

Explanatory variables

The environmental variables that could be responsible for the *S. inaequidens* distribution included topography, climate, human and natural disturbances, and land cover at a spatial resolution of 500 m × 500 m (Table I). All calculations were carried out using the Spatial Analyst extension of ArcGIS 10.1 (ESRI 2011 ESRI. 2011. ESRI ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.).

Topographical variables were obtained from the NASA ASTER Digital Elevation Model (DEM) at a 30 m grain (ASTER GDEM Validation Team 2011 ASTER GDEM Validation Team. 2011. ASTER global DEM validation summary report. Available: <https://lpdaac.usgs.gov/lpdaac/products/aster-products-table/routine/global-digital-elevation-model/v1/astgtm>). A southness index was calculated as a linear transformation of aspect (southness = 180 - |aspect - 180|) (Chang et al. 2004 ChangC, LeeP, BaiM, LinT. 2004. Predicting the geographical distribution of plant communities in complex terrain: A case study in Fushian Experiment Forest, northeast Taiwan. Ecology27: 577–588.). Elevation, slope, and southness were resampled at the base grid resolution (500 m) using a weighted mean algorithm.

Climate variables, with a spatial resolution of 1 km, were obtained from the bioclimatic WorldClim geodataset (Hijmans et al. 2005 HijmansRJ, CameronSE, ParraJP, JonesPG, JarvisA. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Clim25: 1965–1978.) and resampled at a 500 m resolution by linear interpolation. Climate variables included mean annual temperature and precipitation, maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the warmest quarter, mean temperature of the coldest quarter, and precipitation of the warmest quarter (Table I).

Disturbed and riparian areas are known to be sensitive to invasion by *S. inaequidens*, especially when affected by human activities (EPPO 2006 EPPO (European Plant Protection Organization). 2006. Data sheet on invasive plants: *Senecio inaequidens*. Available: www.eppo.org/QUARANTINE/plants/Senecio_inaequidens/SENIQ_ds.pdf. Accessed May 2013 20.). Six human-related variables (area of buildings, total length of walls, roads, railways, canals, and ski runs per cell) and two natural disturbance variables (area subject to erosion and total river length) were included in the explanatory data-set (see Table I for details). The respective areas (m²) and lengths (m) were obtained for each 500 m × 500 m cell from the 1:10,000 Numeric Regional Cartography (Regione Autonoma Valle d'Aosta 1998 Regione Autonoma Valle d'Aosta. 1998. Carta Topografica Regionale Numerica. Assessorato dei lavori pubblici, infrastrutture e assetto del territorio. Direzione assetto del territorio e infrastrutture di rete. Servizio cartografia e assetto idrogeologico.).

In order to determine whether certain land use facilitate the spread of *S. inaequidens*, we computed the total area covered by the following CORINE 2006 Level 3 categories (European Environment Agency 2012 European Environment Agency. 2012. Corine Land Cover 2006 – Seamless vector data, Level 3. The European Topic Centre on Spatial Information and Analysis. Available: <http://www.eea.europa.eu/legal/copyright>. Date of delivery: April 2012.): urban, open habitats (vineyards, meadows, and grasslands), and wooded habitats (shrublands and woodlands) (Table I).

Since colonization of *S. inaequidens* in the region began in 1990 (Poggio et al. 2010 PoggioL, Vanacore FalcoI, BovioM. 2010. New Red Checklist and Black Checklist of the vascular flora of Valle D'Aosta (Italy, North-western Alps). Rev Valdôtaine Hist Nat64: 41–54.), it was hypothesized that the species has still not reached the establishment stage yet. If this hypothesis is realistic, the probability of finding the species in each cell in the landscape should exhibit a significant inverse correlation with distance to current occurrences. For this reason, we tested how the current species distribution model behaved when an additional independent variable was included to account for dispersal limitation. The probability of dispersal to each cell was computed as the sum of $1/d_i^2$, where d is the distance between the center of the focus cell and each presence point i . The higher the dispersal term, the more likely it is for a propagule to reach the focus cell (Vaclavik & Meentemeyer 2009 VaclavikT, MeentemeyerRK. 2009. Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions?Ecol Model220: 3248–3258.).

Species distribution model

The current distribution of *S. inaequidens* in the region was modeled by fitting a generalized linear model (GLM) to presence/absence data.

Only uncorrelated predictors ($R < |0.7|$) were retained in the model. All the climatic variables were highly collinear to elevation ($R > 0.95$) and therefore were excluded. All the predictors also had to satisfy a threshold of variance inflation factor (VIF) < 4 .

The GLM was fit to a binomial distribution with a logit link, using the following parameters: positive convergence tolerance = 10^{-8} , no interactions between the predictors, and maximum iterations = 999. Overdispersion was checked by fitting a GLM to a quasibinomial distribution and ensuring that the fitted dispersion parameter was < 1 .

A stepwise fit was carried out eliminating one predictor at a time, until all the effects were significant ($p \leq 0.05$). Predictors were standardized in order to obtain comparable effect sizes.

Randomized quantile residuals from the binomial model (Dunn & Smyth 1996 DunnPK, SmythGK. 1996. Randomised quantile residuals. *J Comput Graph Statist*5: 236–244.) were checked for normality and plotted against predicted values and against each of the independent variables. In order to eliminate trends in the residual plots, outliers from highly skewed predictors, such as dispersal, roads, and railways, were iteratively eliminated. Data with the most extreme modified z score (Iglewicz & Hoaglin 1993) (i.e., the difference between each value and the median, divided by the median absolute deviation) were labeled as outliers.

We evaluated the model goodness of fit by examining Akaike's information criterion (AIC) and percent deviance explained (DEV). Two concurrent GLMs, with and without the dispersal terms, were fitted to assess whether the species was already in equilibrium with the environment. The highest DEV and lowest AIC were indicative of the best model. After calibrating a “full” model (100% of the data), we carried out a k -fold cross-validation by subdividing the data into a validation and calibration dataset, according to a 1:3 proportion ($k = 4$). The threshold to convert continuous predictions into binary ones was iteratively chosen to maximize the validation metrics, i.e., true skill statistics (TSS) (Allouche et al. 2006 AlloucheO, TsoarA, KadmonR. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol*43: 1223–1232.), and area under the curve (AUC). Model specificity and sensitivity were computed for the selected thresholds. Finally, we spatialized over the study region the predictions of the models, with and without the dispersal term, in order to obtain a map of the species distribution, for the current conditions and at equilibrium (i.e., at maximum potential dispersal, assuming niche and environment conservation), respectively. All analyses were carried out using the Biomod2 package (Thuiller et al. 2013 Thuiller W, Georges D, Engler R. 2013. Biomod2: Ensemble platform for species distribution modeling. Available: <http://cran.univ-lyon1.fr/web/packages/biomod2/biomod2.pdf>. Accessed June 2013 24.) for R (R Core Development Team 2013 R Core Development Team. 2013. R: A language and environment for statistical computing Vienna, Austria: R Foundation for Statistical Computing. Available: <http://www.R-project.org>).

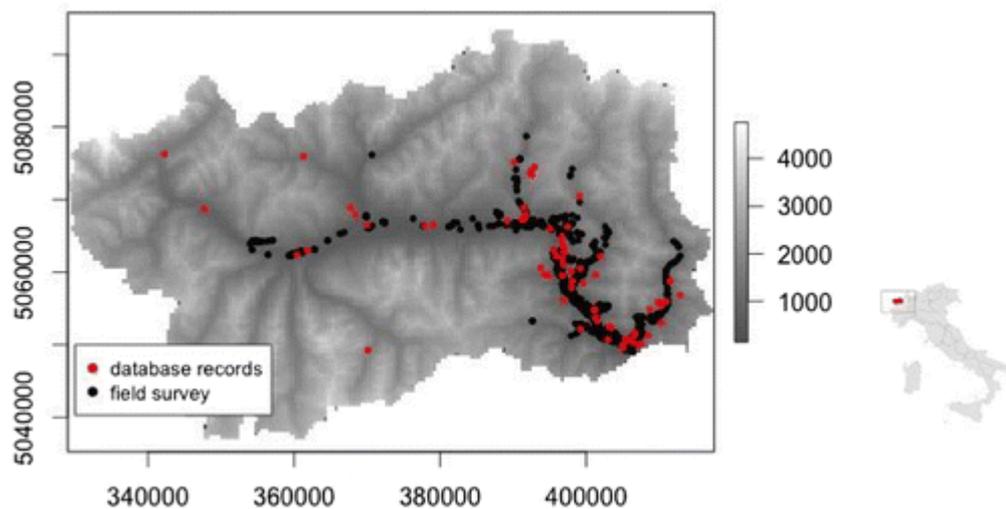
Results

Introduction and spread

The first occurrence of *S. inaequidens* was recorded in the Aosta Valley in 1990 along a road in the lower valley; the colonization continued inwards along traffic routes, roads, and railways. At first, the invasion only affected the main valley bottom and proceeded rapidly to the north and then to the west, reaching the central part of the region at the city of Aosta (580 m a.s.l.). The species was then found near the road leading to the tunnel to Switzerland, and was found near the tunnel to France at Mont Blanc. The database records have shown that the species has recently reached some of the tributary valleys, up to an elevation of 1600 m.

During the intensive field survey that was carried out in 2009 and 2010, the species was detected almost continuously along the main valley, with a higher density in the lower (eastern) part, while in the central and upper (western) parts the occurrence was scattered. The presence in the tributary valleys reflected the same trend: the lower, eastern ones were more colonized than the upper, western ones (Figure 1).

Figure 1 Digital elevation (m) model of the study area (coordinate system: UTM WGS 1984, zone 32N) and presence points for *S. inaequidens* from the regional flora database (red, 1985–2012) and from the intensive field survey (black, 2009–2010).



Species distribution model

The presence of *S. inaequidens* was found to be a rare event, and to occur in 216 of the 8839 landscape cells retained for the analysis, i.e., a 2.4% relative frequency. However, the response variable was not affected by overdispersion, since the dispersion parameter of a quasibinomial model fit was 0.374 (i.e., lower than 1). The final GLM had nine environmental predictors, all of which were significant by design. Residuals were normally distributed and did not show any trend when plotted against the fitted values and individual predictors. When dispersal was included among the predictors, the GLM displayed a nontrivial increase in DEV (37% to 54%) and a decrease in AIC (Table II).

Table II GLM statistics with and without the dispersal predictor.

Model fit	Full model (with dispersal)	Reduced model (no dispersal)	df
Residual deviance	930.6	1279.5	8828
Null deviance	2030.1	2030.1	8838
DEV	0.54	0.37	
AIC	952.2	1299.5	

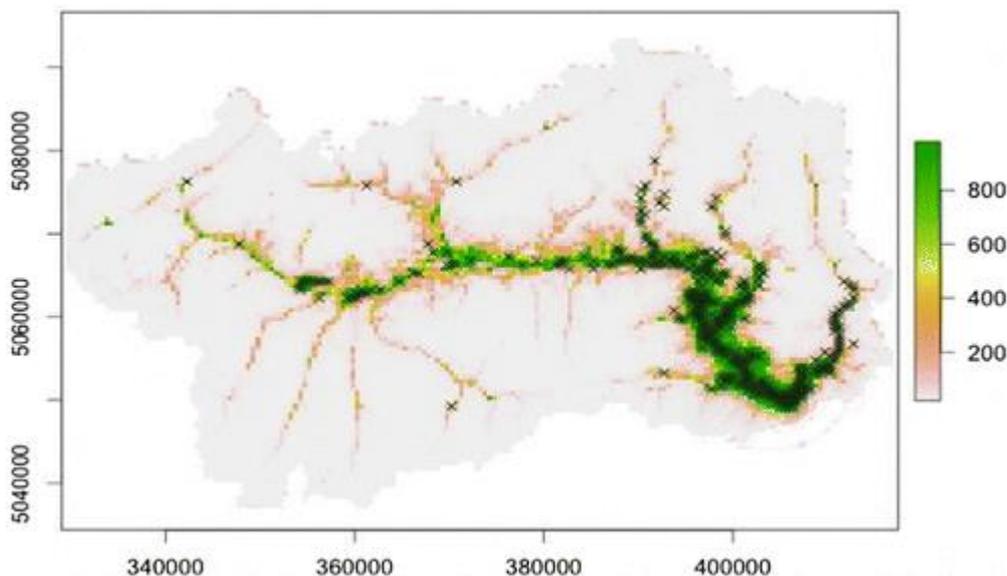
Among the predictors, dispersal had the strongest effect, and indicated a positive influence of proximity to existing plants on the probability of finding the species. In decreasing order of importance, the species was found to be positively associated to roads, grasslands, woodlands, rivers, meadows and orchards, and railroads, and negatively to irrigation canals. Regarding topography, *S. inaequidens* showed a preference for low-elevation, southerly sites (Table III).

Table III GLM parameters for the dispersal model.

GLM model parameters	Beta	Std. error	<i>p</i>
Intercept	-5.54	0.27	<0.001
<i>Topographical variables</i>			
ALTTT	-0.56	0.15	<0.001
SOUTH	0.28	0.10	0.005
<i>Human-related variables</i>			
ROADS	0.72	0.09	<0.001
RAILS	0.10	0.03	0.003
CANAL	-0.12	0.06	0.040
<i>Natural disturbance variables</i>			
RIVER	0.37	0.07	<0.001
<i>Land-use variables</i>			
MEADO	0.36	0.10	<0.001
GRASS	0.73	0.15	<0.001
WOODS	0.68	0.20	0.001
<i>Species colonization status</i>			
DISPERSAL	0.83	0.05	<0.001

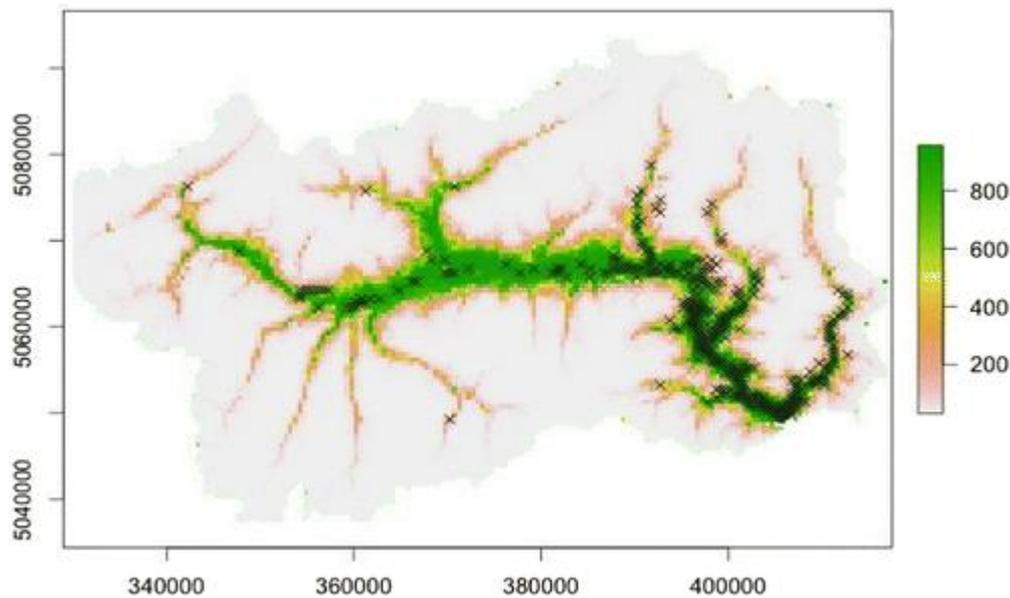
Model evaluation yielded encouraging results: in the four model runs, TSS ranged from 0.83 to 0.90, and AUC from 0.97 to 0.98. The probability of occurrence of *S. inaequidens* was higher in the less elevated, easternmost part of the region (Figure 2), where most of the current presence points were recorded.

Figure 2 Presence probability ($\times 1000$) of *S. inaequidens* in the study area according to a distribution model that includes dispersal constraints. The crosses indicate actual presence points.



On the other hand, the model that did not include dispersal was dominated by the negative influence of elevation, which determined a progressive reduction of presence probability along the altitudinal gradient. However, probability remained high (50–60%) for the bottom and the south facing slopes of the main valley and of the largest, lowest-lying tributary valleys, up to 1500–1600 m a.s.l. (Figure 3).

Figure 3 Presence probability ($\times 1000$) of *S. inaequidens* in the study area according to a distribution model that does not include dispersal constraints. The crosses indicate actual presence points.



Discussion

S. inaequidens underwent a very fast spread in the Aosta Valley in the years 1990–2010, and reached an elevation of 1600 m. The difference between the distribution models with and without dispersal constraints suggests that the availability of seed sources still limits the potential distribution of the species, more so than the environmental variables (Gallien et al. 2012), and that the realized regional niche differs to a great extent from the equilibrium niche. When limitations to the seed source cease (i.e., in the establishment stage), the species will likely invade large areas along the main and tributary valley bottoms and on the slopes up to 1600 m a.s.l. The tributary valleys on the left orographic side and their south-facing slopes will be more at risk.

These areas are currently characterized by pastures and grasslands with native species of high agricultural importance: invasion by *S. inaequidens* should therefore be considered a serious threat, due to its potential to invade mountainous regions, and in particular to colonize habitats used for grazing and forage, thus causing high risks for cattle and human health (Lafuma et al. 2003 LafumaL, BalkwillK, ImbertE, VerlaqueR, MauriceS. 2003. Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Syst Evol*243: 59–72.; Bossdorf et al. 2008 BossdorfO, LipowskyA, PratiD. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib*14: 676–685.; Lachmuth et al. 2011 LachmuthS, DurkaW, SchurrFM. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: The role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol*192: 529–541.).

This potential distribution of *S. inaequidens* is limited by altitude, as a proxy of temperature, as has already been shown for other alien species (Siniscalco et al. 2011 SiniscalcoC, BarniE, BacaroG. 2011. Alien species distribution along the elevation gradient in the western Italian Alps. *Plant Biosyst*145: 150–158.; Barni et al. 2012 BarniE, BacaroG, FalzoiS, SpannaF, SiniscalcoC. 2012. Establishing climatic constraints shaping the distribution of alien plant species along the elevation gradient in the Alps. *Plant Ecol*213: 757–767. and references therein). However, the European

populations of *S. inaequidens* originated from the mountain regions of South Africa (Lafuma et al. 2003 LafumaL, BalkwillK, ImbertE, VerlaqueR, MauriceS. 2003. Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Syst Evol*243: 59–72.) and have genetic traits that confer them with a high adaptation potential to mountainous conditions and the ability to reach higher elevations than those reached by other alien invasive species. Such traits include a high root/shoot ratio (Bossdorf et al. 2008 BossdorfO, LipowskyA, PratiD. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib*14: 676–685.) which is correlated to drought and frost resistance. Moreover, prioritizing resource allocation to the root system translates into a higher phenotypic plasticity of the introduced populations with respect to the native lowland ones, and facilitates plants that have to endure a long cover by snow and relatively short growing seasons (Bossdorf et al. 2008 BossdorfO, LipowskyA, PratiD. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers Distrib*14: 676–685.).

S. inaequidens does not produce a very large amount of biomass, and is therefore limited to the colonization of vegetation characterized by a low plant cover due to disturbance (e.g., roadsides, riverbeds, and urban areas) or soil dryness. In grasslands and forests of dry inner alpine valleys such as the Aosta Valley, moisture limitations usually determine a sparse plant cover (Kelly & Connolly 2000 KellyDL, ConnollyA. 2000. A review of the plant communities associated with Scots Pine (*Pinus sylvestris*) in Europe, and an evaluation of putative indicator/specialist species. *Investig Agr Sist Recursos For Fuera de Serie*1: 15–39.). Similarly to what happens following disturbances, bare ground areas, in which the alien species can germinate and develop without the competition of native species, are common. For this reason, the vegetation of dry areas can be more invasible than other vegetation types. Moreover, forest fires can produce bare patches that can facilitate the spread of the species, as observed in a recent work on the regeneration of *Pinus sylvestris* forests in the Aosta Valley (Vacchiano et al. 2013 VacchianoG, LonatiM, BerrettiR, MottaR. 2013. Drivers of *Pinus sylvestris* L. regeneration following small, high-severity fire in a dry, inner-alpine valley. *Plant Biosyst*, 10.1080/11263504.2013.819821.).

Local eradication and control of the species are needed but are problematic, since the production of a very high number of small seeds with *pappus* (Monty et al. 2008 MontyA, StainierC, LebeauF, PieretN, MahyG. 2008. Seed rain pattern of the invasive weed *Senecio inaequidens* (Asteraceae) *Belg. J Bot*141(1): 51–63.), which can be dispersed by wind, is a very powerful tool for the invasion. So far, the invasion pattern has been linear: the species has preferentially dispersed along roads and rivers, which act like ecological corridors for invasion, in accordance to what has been observed for this and many other alien species (Hood & Naiman 2000 HoodWG, NaimanRJ. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecol*148: 105–114.; Alexander et al. 2009 AlexanderJM, NaylorB, PollM, EdwardsPJ, DietzH. 2009. Plant invasions along mountain roads: The altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography*32: 334–344.). However, the spread already observed within semi-natural and natural habitats such as grasslands, meadows and open woodlands, will progressively increase and provide propagules for a wider isotropic invasion.

Since the grasslands on the south facing slopes in the mapped area can be particularly invasible by the studied species, awareness campaigns have already been carried out (Curtaz et al. 2011 CurtazA, TalichetM, BarniE, BassignanaM, MasanteD, PauthenetY, SiniscalcoC. 2011. Specie esotiche invasive e dannose nei prati di montagna. Aosta: Institut Agricole Régional.). We highly recommend that these campaigns are continued for farmers, professionals, and garden center owners in order to disseminate knowledge of this species and its risks in the Aosta Valley. The inclusion of *S. inaequidens* in the “black list” of the regional law for the conservation of alpine flora (L.R. 45/2009)

will help to transfer the information on this species and support eradication activities, particularly at medium and high elevations.

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