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

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We modeled the distribution of the South African alien Senecio inaequidens DC. in the Aosta Valley, Western Italian Alps,

G. VACCHIANO¹, E. BARNI², M. LONATI¹, D. MASANTE², A. CURTAZ⁴, S. TUTINO³ &

Abstract

C. SINISCALCO²

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- 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 80 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 85 1600 m, having 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 distribution models, with and without dispersal constraints, has 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 predominantly characterized by pastures and grasslands with native species of high agricultural importance. The invasion of 90 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. 95

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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., freshwaters (Brundu et al. 2013), coastal dunes (Pretto et al. 2010, 2012), and grasslands in mountain areas (Curtaz et al. 2011).

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 pyrrholizidine alkaloids, which

are toxic to livestock and can cause negative effects 100 on human beings via milk consumption (Dimande et al. 2007). For this reason, its spread in the Alps and in particular in areas such as the Autonomous Aosta Valley Region is extremely alarming as the economy is largely based on cattle grazing and high-105 quality dairy production. 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 110 occurrence, and of reducing its spread by preventing

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115 the cultivation for ornamental purposes and supporting control and eradication activities.

The species is native to the mountain regions of South Africa (Hilliard 1977) and also occurs in Mozambique, Namibia, Lesotho and Swaziland (EPPO 2006; Dimande et al. 2007). 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).

The species is currently spreading throughout-in Europe at an exceptionally high-invasion speed, following the accidental introduction of seeds in wool transport to several locations in the late nineteenth and early twentieth centuries, in Germany, Belgium, France, and Italy, (Kuhbier 1977; Ernst 1988; Jaenmonod 2002; Lachmuth et al. 2011 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, 2010). 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, Monty & Mahy 2009; Lachmuth et al. 2010). For this reason, the plants introduced into Europe are considered to be preadapted to mountainous climatic conditions (Lafuma et al. 2003; Bossdorf et al. 2008).

According to the literature (EPPO 2006), 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. 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), 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 accordingly to the biotic competition-intensity, switching its resource allocation priorities between vegetative and reproductive structures (Lachmuth et al. 2011). S. inaequidens can produce up to 10-30,000 seeds per plant per year (López-García & Maillet 2005; EPPO 2006). These seeds are dispersed by wind, animals and vehicles (Ernst 1998; Heger & Böhmer 2006; Monty et al. 2008). The latter are the preferential vectors for longdistance 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 (Schreber et al. 2003; Garcia Serrano et al. 2004), temporary ponds, rock cliffs, walls, and vineyards.

Species distribution models (SDMs) have been 175 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, at a regional scale (Guisan & Thuiller 2005; Wilson et al. 2007; Gallien et al. 2010). By 180 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 185 can provide "early warnings" of 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). Dispersal 190 constraints must be included in SDMs for species in the first two stages of invasion, in order to optimize its fit (Vaclavik & Meentemever 2009).

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 Autonomous Aosta Valley Region (Italy), a 3263 km² area on the south-western 210 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 215 region has a wide elevation range (312–4810 m a.s. 1.), and only 20% of the territory lies below 1500 m. The climate shows the typical continental conditions of inner alpine valleys (Schwabe & Kratochwil 2004), with minor variations due to local topographic and 220 geographic conditions (e.g., aspect). The mean annual temperature varies from 10.3°C at the valley bottom (600 m) to 7.5° C at 1200 m_b and 3 and -2° C at 2000 and 2500 m, respectively, and stays nearly always below 0°C above 3100 m. Mean annual 225 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-

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alpine and usually presents two peaks in spring and fall and two minima in winter and summer (Mercalli et al. 2003).

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 235 population density is only 38 inhabitants/km², and the inhabitants live mostly in the main valley, where urbanization is concentrated in just few settlements. Important transport infrastructures run across the main valley, since the Aosta Valley has always been an 240 important crossroad in the western Alps. During the last half century, for trade and tourism, 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 245 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 250 pastures (above 1800 m). Besides the agro-pastoral activities, both summer and winter tourism is highly developed, thus determining an increase in human impacts in areas at higher elevations.

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Species distribution data

S. inaequidens was found for the first time in 1990 in the lower part of the Aosta Valley (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).

A reliable complete picture of the current distribution of S. inaequidens in the region has been obtained by gathering two data-sets. The first dataset, containing 2369 georeferenced occurrences, was obtained from an intensive field survey carried out in 2009 and 2010, which was specifically aimed at monitoring the 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.

After joining the two data-sets, they were resampled on a 500 m \times 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), all cells above 2500 m a.s.l. were filtered out and 8967 landscape cells were selected for further analyses.

Explanatory variables

The environmental variables that could be responsible for the S. inaequidens distribution, including topography, climate, human and natural disturbances, and land cover were sampled for each 500 m \times 500 m cell (Table I). All calculations were carried out using the Spatial Analyst extension of ArcGIS 10.1 (ESRI 2011).

The topographical variables were obtained using the NASA ASTER Digital Elevation Model (DEM) 305 at a 30 m grain (ASTER GDEM Validation Team 2011). Aspect was linearized as southness (southness = [Q3] 180 - |aspect - 180|) (Chang et al. 2004). Elevation, slope, and southness were resampled at the base grid resolution (500 m) using a weighted mean algorithm. 310

The climate variables, with a spatial resolution of 1 km, were obtained from the bioclimatic WorldClim geodataset (Hijmans et al. 2005) and resampled at a 500-m resolution through linear interpolation. The variables included the mean annual temperature and 315 precipitation, the maximum temperature of the warmest month, the minimum temperature of the coldest month, the mean temperature of the warmest quarter, the mean temperature of the coldest quarter, and the precipitation of the warmest quarter 320 (Table I).

Disturbed and riparian areas are known to be sensitive to invasion by S. inaequidens, especially when affected by human activities (EPPO 2006). Six human-related variables (area of buildings, total 325 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 therefore included (see Table I for details). The areas (m²) and lengths (m) were obtained for each 330 $500 \,\mathrm{m} \times 500 \,\mathrm{m}$ cell from the <u>Vector</u> Regional Cartography at a 1:10,000 scale (Regione Autonoma Valle d'Aosta 1998).

In order to determine whether land use facilitates the spread of S. inaequidens, the total covered area 335 was calculated for each cell using vectorial CORINE 2006 Level 3 categories (European Environment Agency 2012), and urban, open habitats (vineyards, meadows, and grasslands), and wooded habitats (shrublands and woodlands) were included (Table I). 340

Since colonization of S. inaequidens in the region began in 1990 (Poggio et al. 2010), it was 300

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hypothesized that the species has still not reached the establishment stage. If this hypothesis is realistic, the probability of finding the species in each cell in the landscape should exhibit a significant inverse 460 correlation with distance to current occurrences. For this reason, it was tested how the current species distribution model behaved when an additional independent variable was included for dispersal limitation. The probability of dispersal of each cell 465 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 of a propagule reaching the target cell (Vaclavik & Meentemeyer 2009). 470

Species distribution model

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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. This means that, among others, all the climatic variables that were highly collinear to elevation (R > 0.95) were excluded. After the model fitting, all the predictors also had to satisfy a threshold of variance inflation factor < 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 ($p \le 0.05$). Predictors were standardized in order to assess the effect size by obtaining comparable model parameters.

Randomized quantile residuals from the binomial model (Dunn & Smyth 1996) were checked for normality and plotted against fitted values and 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 MAD scores (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 better model was associated to the higher DEV and lower AIC. After calibrating a "full" model (100% of the data), we carried out k-fold cross-validation by subdividing the data into a 3:1 proportion (k = 4). The threshold to convert continuous predictions into binary ones 515 was iteratively chosen to maximize the validation metrics, i.e., true skill statistics (TSS) (Allouche et al. 2006), and area under the curve (AUC). Model specificity and sensitivity were computed for the selected thresholds. Finally, we spatialized over the 520 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 (potential dispersal assuming niche and environment conservation), respectively. 525 All analyses were carried out using the Biomod2 package (Thuiller et al. 2013) for R (R Core Development Team 2013).

Results

Introduction and spread

The Regional floristic database has shown that S. inaequidens was found for the first time in the Aosta 535 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 540 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. In the last few years, the database records have shown 545 that the species has 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 550 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 555 (Figure 1).

Modeling the spread of the species

The presence of S. *inaequidens* was found to be a rare 560 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 0.374 565 (i.e., lower than 1). The final GLM had nine environmental predictors, all of which were significant by design. The GLM residuals were normally distributed and did not show any trend when plotted against the fitted values and individual predictors. 570

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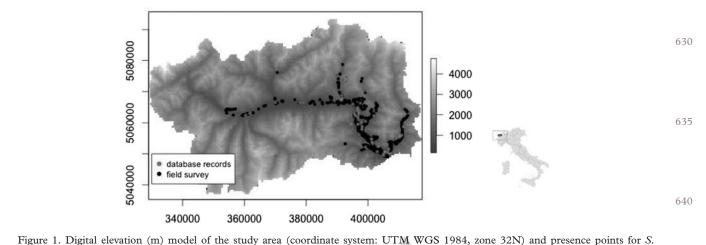
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590 When dispersal was included among the predictors, the GLM displayed a nontrivial increase in DEV and a decrease in AIC (Table II).

> 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).

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 the presence of *S. inaequidens* as indicated by the dispersal model was higher in the lower, easternmost part of the region (Figure 2), where most of the current presence points were recorded.

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).

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 than the environmental variables [Q5]
 (Gallien et al. 2012), and that the realized regional

niche differs to a great extent from the regional 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 southern slopes will be more at risk.

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	

Table III. GLM parameters for the dispersal model.

GLM model parameters	Beta	Std. error	P	
Intercept	-5.54	0.27	< 0.001	670
Topographical variables				010
ALTIT	-0.56	0.15	< 0.001	
SOUTH	0.28	0.10	0.005	
Human-related variables				
ROADS	0.72	0.09	< 0.001	
RAILS	0.10	0.03	0.003	675
CANAL	-0.12	0.06	0.040	015
Natural disturbance variables				
RIVER	0.37	0.07	< 0.001	
Land-use variables				
MEADO	0.36	0.10	< 0.001	
GRASS	0.73	0.15	< 0.001	680
WOODS	0.68	0.20	0.001	080
Species colonization status				
DISPERSAL	0.83	0.05	< 0.001	

Note: See Table I for description of the variables.

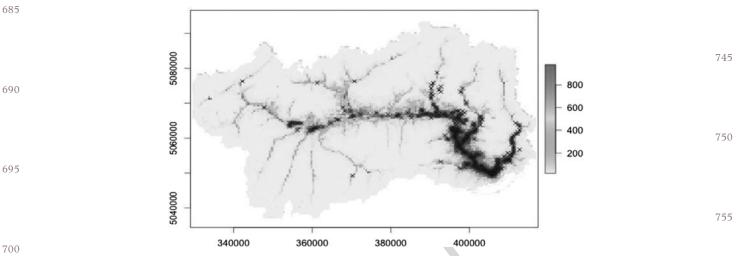


Figure 2. Presence probability (tenths of percent) of S. inaequidens in the study area according to a distribution model that includes dispersal constraints. The crosses indicate actual presence points.

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; Bossdorf et al. 2008; Lachmuth et al. 2011).

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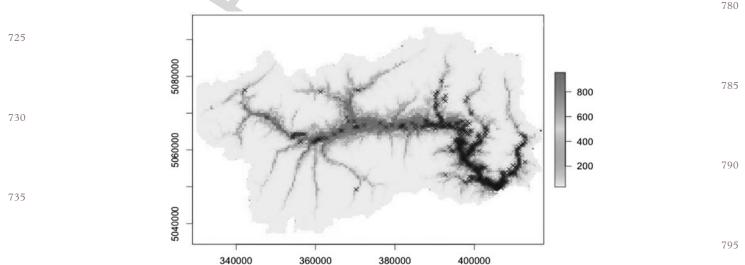
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This potential distribution of S. inaequidens is limited by altitude, as a proxy of temperature, as has already been shown for other alien species (Siniscalco et al. 2011; Barni et al. 2012 and references therein). However, the European populations of S. inaequidens originated from the mountain regions of South Africa (Lafuma et al. 2003) 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) which is correlated to drought and frost resistance. Moreover, prioritizing resource allocation to the root system translates into 765 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).

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 in dry inner alpine valleys such as the Aosta Valley, moisture limitations usually determine a sparse plant cover (Kelly & Connolly



740 Figure 3. Presence probability (tenths of percent) of S. inaequidens in the study area according to a distribution model that does not include dispersal constraints. The crosses indicate actual presence points.

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2000). 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).

Local eradication and control of the species are needed but are problematic, since the production of a 810 very high number of small seeds with pappus (Monty et al. 2008), 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 815 ecological corridors for invasion, in accordance to what has been observed for this and many other alien species (Hood & Naiman 2000; Alexander et al. 2009). However, the spread already observed within semi-natural and natural habitats such as grasslands, 820 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 825 studied species, awareness campaigns have already been carried out (Curtaz et al. 2011), and it is highly recommended that these campaigns are continued for farmers, professionals, and garden center owners in order to disseminate knowledge of this species and 830 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 835 medium and high elevations.

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