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Non-native species distribution along the elevation gradient in the western Italian Alps

C. Siniscalco, E. Barni & G. Bacaro

Abstract

In this work the occurrence of non-native species was recorded along the elevation gradient in the Alps, in order to establish their distribution pattern, their current altitudinal limits and to elucidate which species are presumably adapted to higher elevations. Plots were located along the course of rivers in five valleys from 100 to 2100 m a.s.l. Sixty-eight non-natives were recorded in the study area. The proportion of invasives was found to be much higher in the study area than in the whole administrative region. The number of non-natives per plot decreased strongly with increasing elevation. The great majority (94%) of the non-native species grows at the lowest elevations, while only 6% survive up to 1500 m and none was found above this limit. Results were interpreted considering the factors driving the invasion process (disturbance, the native communities' resistance to invasion, propagule pressure, climatic conditions) and plant traits with particular respect to pre-adaptation to the harsh climate, which increases progressively with elevation. Results confirm that the Alps are not immune from invasion, at least up to medium elevation.

Introduction

Mountain regions, widely recognized as important biodiversity hot spots with rich, distinct floras (Körner 2002), are increasingly threatened by invasive non-native plants as a consequence of human impact (Johnston & Pickering 2001; Bear et al. 2006). Because of recent invasion, mountain systems provide the opportunity to study the process from the beginning, and offer good opportunities to analyze mechanisms and causes of invasion over short spatial distances along the elevation gradient (Becker et al. 2005; Körner 2007; Kueffer et al. 2008), even if recent studies pinpointed the difficulties in discriminating the effects of the elevational gradient from human impact (Nogués-Bravo et al. 2008).

As for the pattern of non-native plant distribution in mountain systems, areas at highest elevation show in general consistently low levels of invasion (Pauchard et al. 2009) although a recent comparison among different world mountain systems illustrates that altitudinal richness of non-native species varies across regions having a unimodal distribution in sub-tropical oceanic mountains (Tassin & Riviere 2003; Arévalo et al. 2005) and a continuous decrease on temperate mountains (Pauchard & Alaback 2004; Becker et al. 2005; Mallen-Cooper & Pickering 2008) with areas above the timberline not affected by non-natives (Becker et al. 2005; McDougall et al. 2005).

As for the mechanisms of plant invasion, four main factors have been suggested to explain the general rule of decreasing numbers of non-native species along the elevation gradient (Pauchard et al. 2009): the first is the general lack of pre-adaptation to harsh

environmental conditions in non-native plants, the second is the decreasing levels of anthropogenic disturbance, the third is the resistance of native plant communities, and the fourth is the low amount of introduced plant propagules.

Almost all the introduced non-native species grow at low elevation in their native range (Arévalo et al. 2005; Daehler 2005) and are thus thought to be unable to survive the effects of frost and snow and the short growing season (Rejmánek 1989; Rejmánek & Randall 1994). Disturbance is a well-documented factor playing an important role in increasing the opportunities for alien invasion by reducing the resistance of native plant communities and increasing the availability of sites and resources (Pauchard & Alaback 2004; Parks et al. 2005). For this reason, increased tourist activity at higher elevation is of concern (Pickering & Hill 2007), particularly in the mountains of Europe.

Mountains near regions below them with dense populations, intense agriculture and urbanisation are probably more subject to invasion due to high level of traffic (Gelbard & Belnap 2003; McDougall et al. 2005) than isolated mountains into which propagules are less likely to be introduced (Stohlgren et al. 1999; Pauchard & Alaback 2004). River systems characterized by the combined action of anthropogenic and natural disturbance favour upward spread of non-native species in the valleys (Planty-Tabacchi et al. 1996; Stohlgren et al. 1998; Hood & Naiman 2000; Magee et al. 2008).

Results collected in Italy by the national project 'Survey of the Italian non-native flora', funded by the Italian Ministry for the Environment and reporting on current knowledge of the non-native flora (Celesti-Grappo et al. 2009, 2010), showed that the largest number of non-native species occurs in northern regions, such as Lombardy, Piedmont, Veneto and Friuli in which the Po Plain occupies a wide area. Here a high concentration of people in large cities, the construction and use of a dense network of communication routes and the development of intensive agriculture resulted in widespread transformation of the landscape. This lowland is connected to the mountains by rivers and by roads which can carry heavy traffic if linked to international passes. Both these types of linear vector are corridors and habitat for non-native species.

Since the non-native invasion has not yet been analysed in the Western Italian Alps, we decided to focus on this area. As a first approach, the present study aims to test the following hypotheses: (i) non-native species reduce their density depending on the altitudinal gradient along the rivers of five Italian alpine valleys, (ii) altitude is a strong limitation of distribution for exotic species, and (iii) some species are not restricted in their distribution due to elevation.

Material and methods

Study area

The Italian Alps rise from the Po Plain, from 100–200 m to 3500–4000 m a.s.l. with steep gradients across a distance of only few kilometres. The study area is located in the western Italian Alps (Piedmont: 45°16'N, 8°43'E).

The abrupt elevation increase causes rapid changes in troposphere air mass dynamics, generating rapid variations in weather even in contiguous areas. Moving a few kilometres from the plain into the valleys, the scenery rapidly changes, bringing with it big differences in climate: mean annual temperatures range in areas 50–100 km apart from 11 to 12°C near the plain to 1°C at 2400 m and frost days vary from 40 each year in the plain to more than 200 at over 2000 m.

Mean annual precipitation varies widely but less regularly from 700 to 800 mm in the plain and in some valleys to more than 2000 mm where humid air masses encounter the mountains. In the part of the Alps considered, valleys run parallel, formed by quaternary glaciers and then by the subsequent rivers. The ridges between are high, 2500–2800 m or more and so the valleys are isolated from one each other. Human settlements are found below 1800 m, while roads and structures for tourist activities go higher. Thus access to a valley is usually possible mainly or only through the road which enters at the mouth, and goes along the valley parallel and near to the main water course.

The whole river course is affected by natural disturbance, due to flooding which periodically destroys vegetation leaving bare surfaces. Flood damage is repaired with extensive use of heavy machinery and soil displacement even at high elevations.

Five valleys were chosen as sampling sites, Tanaro, Po, Susa, Sesia and Ossola, spaced along the western Alps from South to North (Figure 1). The vegetation in these valleys is strongly determined by the elevation gradient: lower down, the mixed broadleaf deciduous forests are almost completely replaced by meadows and crops; at medium elevations *Fagus sylvatica* woods are dominant, while *Larix decidua* and *Picea abies* woods are widespread above these up to the timberline which occurs at 2000–2100 m. Alpine pastures, dwarf shrubs and debris occupy the highest areas. Rivers are bordered by typical mixed riparian vegetation with *Alnus*, *Salix* and *Populus* woods, shrub communities dominated by *Salix* spp. and scattered herbaceous communities on the gravel riverbeds.

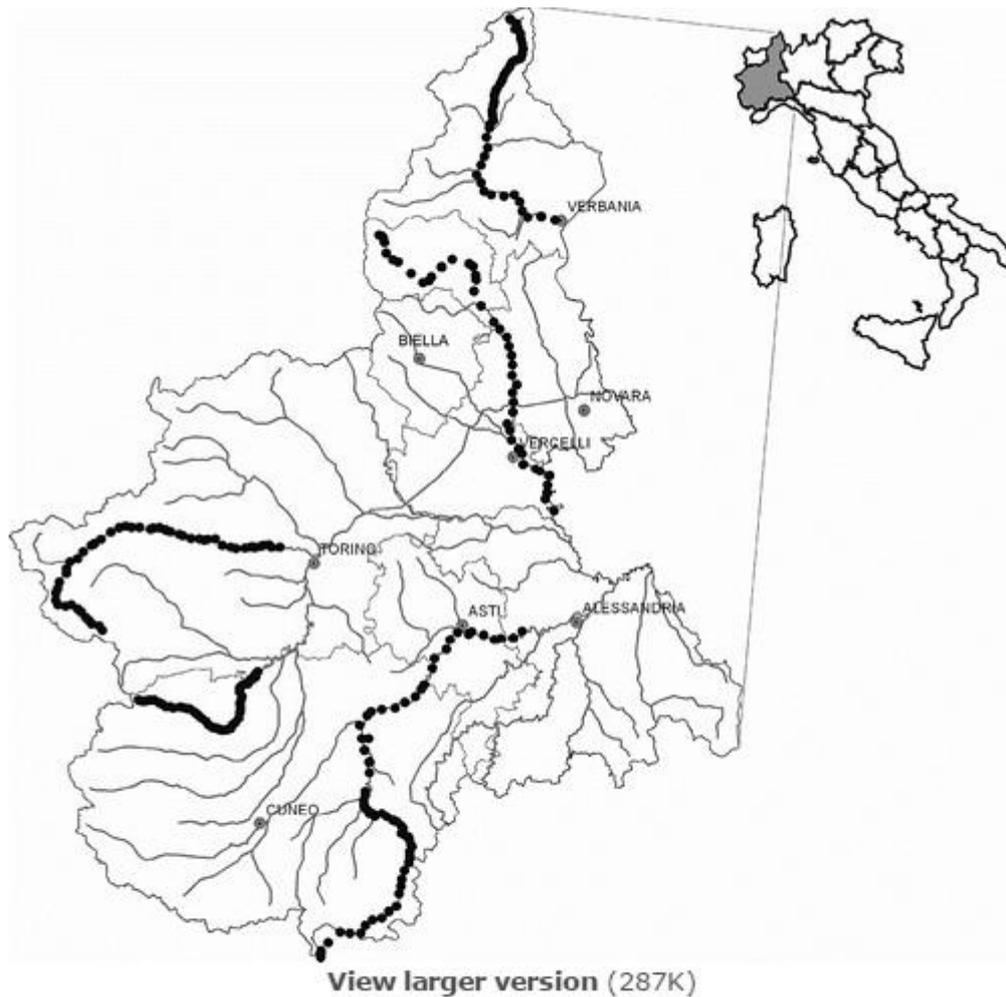


Figure 1. Distribution map of the plots along the five valleys in the western Alps.

At lower and medium elevations, agriculture and forestry are still practiced, and urban centres occur, linked by roads which often run parallel to and sometimes cross the main river course; at higher elevations traditional uses, mainly pasture, are mostly abandoned.

Sampling methods

The presence of non-native species was recorded along the river courses using a systematic sampling design, with plots regularly spaced at 2 km from 100 to 2100 m a.s.l. to ensure equal sampling intensity in each valley. Numbers of plots in each of the five valleys was proportional to their length (64 plots in Tanaro, 44 in Po, 52 in Susa, 72 in Sesia and 47 in Ossola) and were located in the riparian zone at similar distances from the stream in order to have constant site conditions and particularly similar disturbance intensities.

Occurrence of non-native species was recorded in a total of 279 rectangular plots, with an area of 21 m² each, and linear dimensions of 3 m × 7 m, with the longer axis parallel to the main river course. The plot size was chosen to detect the floristic composition as completely as possible, under uniform environmental conditions, and is based on our own research experience in the same habitats.

Species nomenclature follows Celesti-Grapow et al. (2009). For each species, data on life form, residence time, area of origin and invasion status were collected according to the criteria presented in the project "Survey of the Italian non-native flora" (Celesti-Grapow et al. 2009).

Data analysis

A preliminary explorative analysis was carried out on the distribution data of non-native species along the elevation gradient; very high similarity both for distribution and for species richness was observed among the valleys (Barni et al. submitted). Number of non-native species in relation to elevation was explored by using a generalized linear model (GLM): a Poisson distribution of error was included in the model and a log link function selected to relate the response variable with the predictor (in order to avoid negative fitted values for the number of non-native species). Once the model was checked for overdispersion, regressive coefficient was estimated and the D^2 statistic was calculated (expressing the amount of explained variance by the model, see Guisan & Zimmermann 2000; Bacaro et al. 2008). Significance test for elevation was performed using a classical χ^2 test; 95% confidence intervals on predicted values were finally calculated.

Secondly, the single-species altitudinal range in the whole study area was considered, and the frequency of each species was calculated as occurrence percentage on the total number of plots in each elevation class of approximately 300 m. The species were classified by cluster analysis to obtain groups with similar distribution and frequency along the gradient (option for clustering: Euclidean distance; resemblance coefficient: centroid). Consistency of obtained clusters was finally assessed performing a permutation tests (9999 runs) to inspect the robustness of groups. This analysis is very similar to a multivariate permutational analysis of variance (PERMANOVA, see Anderson 2001) where the classificatory factor was represented by the belonging of each species to a single cluster. The statistical analyses were performed using the *R* software 2.10 (R Development Core Team 2009) and the SPSS 17.0 software.

Results

Descriptive floristic data

In the 279 plots (Figure 1), 68 non-native species were found (Table I). Among these, 62 were neophytes, only 3 were archeophytes (*Setaria italica*, *Sorghum halepense* and *Panicum miliaceum*) and 3 were uncertain for origin and period of introduction. The most frequent species were *Bidens frondosa*, *Buddleja davidii*, *Erigeron canadensis*, *Reynoutria japonica* and *Solidago gigantea*, all found in more than 25% of the plots. Six other species occurred in more than 10% of the plots but all the others were found in less than 10% of the plots.

Table I. List of the non-native species ordered by frequency in the elevation classes and noting life forms, origin, invasive status (CAS, casual; NAT, naturalized; INV, invasive) and elevation range

Plant species	Life form	Origin	Status	Elev. range (m a.s.l.)	Frequency (%)					
					Elev. classes (m a.s.l.)					
					I	II	III	IV	V	VI
<i>Acer negundo</i> L.	Tree	N-America	INV	95–380	1	0	0	0	0	0
<i>Ambrosia trifida</i> L.	Annual	N-America	NAT	130	1	0	0	0	0	0
<i>Apios americana</i> Medicus	Perennial	N-America	NAT	267	1	0	0	0	0	0
<i>Symphyotrichum novi-belgii</i> (L.) G.L. Nesom	Perennial	N-America	NAT	110	1	0	0	0	0	0
<i>Symphyotrichum squamatum</i> (Spreng.) G.L. Nesom	Annual	S-America	NAT	200	1	0	0	0	0	0
<i>Commelina communis</i> L.	Perennial	Temperate Asia	NAT	187	1	0	0	0	0	0
<i>Datura stramonium</i> L.	Annual	N-America	NAT	360–380	1	0	0	0	0	0
<i>Juncus tenuis</i> Willd.	Perennial	N-America, S-America	INV	370	1	0	0	0	0	0
<i>Lindernia dubia</i> (L.) Pennell	Annual	N-America, S-America	INV	255	1	0	0	0	0	0
<i>Panicum miliaceum</i> L.	Annual	Temperate Asia	NAT	215	1	0	0	0	0	0
<i>Pueraria lobata</i> (Willd.) Ohwi	Woody vine	Temperate Asia	INV	196	1	0	0	0	0	0
<i>Spiraea japonica</i> L. fil.	Shrub	Temperate Asia	INV	409	1	0	0	0	0	0
<i>Chamaesyce prostrata</i> (Aiton) Small	Annual	S-America	INV	100–215	1	0	0	0	0	0
<i>Ulmus laevis</i> Pallas	Tree	Temperate Asia, Europe	NAT	120	1	0	0	0	0	0
<i>Erigeron sumatrensis</i> Retz.	Annual	S-America	INV	170–269	2	0	0	0	0	0
<i>Chamaesyce maculata</i> (L.) Small	Annual	N-America	INV	125–268	2	0	0	0	0	0
<i>Humulus japonicus</i> Siebold & Zucc. I+N	Annual	Temperate, Tropical Asia	INV	103–110	2	0	0	0	0	0
<i>Lonicera japonica</i> Thunb.	Shrub	Temperate Asia	NAT	290–345	2	0	0	0	0	0
<i>Setaria italica</i> (L.) Beauv.	Annual	Tropical Africa and Asia	NAT	142–266	2	0	0	0	0	0
<i>Sicyos angulatus</i> L.	Annual	N-America	INV	104–218	2	0	0	0	0	0
<i>Artemisia annua</i> L.	Annual	Temperate Asia	INV	95–380	3	0	0	0	0	0
<i>Cuscuta scandens</i> Brot. ssp. <i>cesatiana</i> (Bertol.) Greuter & Burdet	Annual	?	NAT	115–185	3	0	0	0	0	0
<i>Dysphania ambrosioides</i> (L.) Mosyakin & Clemants	Annual	N-America, S-America	NAT	130–275	3	0	0	0	0	0
<i>Cyperus microiria</i> Steudel	Annual	Temperate Asia	INV	142–275	4	0	0	0	0	0
<i>Oenothera fallacoides</i> Soldano e Rost.	Perennial	Uncertain	NAT	100–185	5	0	0	0	0	0
<i>Oenothera pedemontana</i> Soldano	Perennial	Uncertain	NAT	275–320	5	0	0	0	0	0
<i>Panicum dichotomiflorum</i> Michx.	Annual	N-America, S-America	INV	125–310	5	0	0	0	0	0
<i>Populus canadensis</i> L.	Tree	Hybrid	CAS	100–294	5	0	0	0	0	0
<i>Senecio inaequidens</i> DC.	Annual	S-Africa	INV	103–350	5	0	0	0	0	0
<i>Oenothera sesitensis</i> Soldano	Perennial	Uncertain	INV	196–328	6	0	0	0	0	0
<i>Sorghum halepense</i> (L.) Pers.	Perennial	Tropical Africa and Asia	INV	103–316	6	0	0	0	0	0
<i>Cyperus esculentus</i> L.	Perennial	?	NAT	102–270	7	0	0	0	0	0
<i>Helianthus tuberosus</i> L.	Perennial	N-America	INV	109–370	8	0	0	0	0	0
<i>Oenothera stuechii</i> Soldano	Perennial	Hybrid	INV	108–294	8	0	0	0	0	0
<i>Amorpha fruticosa</i> L.	Shrub	N-America	INV	100–337	12	0	0	0	0	0
<i>Ambrosia artemisiifolia</i> L.	Annual	N-America	INV	95–370	15	0	0	0	0	0

<i>Xanthium orientale</i> L. subsp. <i>italicum</i> (Moretti) Greuter	Annual	N-America	INV	95-421	27	0	0	0	0	0
<i>Galinsoga parviflora</i> Cav.	Annual	S-America	INV	620	0	2	0	0	0	0
<i>Rudbeckia hirta</i> L.	Annual	N-America	CAS	660	0	2	0	0	0	0
<i>Veronica persica</i> Poiret	Annual	Temperate Asia	INV	591	0	2	0	0	0	0
<i>Amaranthus cruentus</i> L.	Annual	N-America, S-America	NAT	740	1	2	0	0	0	0
<i>Galega officinalis</i> L.	Perennial	?	NAT	260-523	1	2	0	0	0	0
<i>Solanum lycopersicum</i> L.	Annual	N-America, S-America	CAS	103-490	1	2	0	0	0	0
<i>Ailanthus altissima</i> (Miller) Swingle	Tree	Temperate Asia	INV	167-450	2	2	0	0	0	0
<i>Amaranthus hybridus</i> L.	Annual	N-America, S-America	NAT	102-620	2	2	0	0	0	0
<i>Amaranthus retroflexus</i> L.	Annual	N-America	INV	109-740	3	3	0	0	0	0
<i>Galinsoga quadriradiata</i> Ruiz & Pav.	Annual	N-America, S-America	INV	270-660	3	5	0	0	0	0
<i>Phytolacca americana</i> L.	Perennial	N-America	INV	108-474	4	2	0	0	0	0
<i>Eragrostis pectinacea</i> (Michx.) Nees	Annual	N-America, S-America	INV	185-470	4	3	0	0	0	0
<i>Parthenocissus quinquefolia</i> (L.) Planch	Woody vine	N-America	INV	123-490	4	3	0	0	0	0
<i>Impatiens balfourii</i> Hooker fil.	Annual	TROPICAL Asia	INV	200-665	7	12	0	0	0	0
<i>Oenothera suaveolens</i> Pers.	Perennial	N-America	INV	103-700	8	3	0	0	0	0
<i>Amaranthus powellii</i> S. Watson	Annual	N-America	NAT	254-704	8	14	0	0	0	0
<i>Panicum capillare</i> L.	Annual	N-America	INV	95-740	14	9	0	0	0	0
<i>Cyperus glomeratus</i> L.	Perennial	Temperate Asia	INV	100-470	19	2	0	0	0	0
<i>Artemisia verlotiorum</i> Lamotte	Perennial	Temperate Asia	INV	103-704	27	16	0	0	0	0
<i>Robinia pseudoacacia</i> L.	Tree	N-America	INV	118-740	35	22	0	0	0	0
<i>Bidens frondosa</i> L.	Annual	N-America	INV	95-635	48	19	0	0	0	0
<i>Matricaria discoidea</i> DC.	Annual	Temperate Asia	INV	1085	0	0	4	0	0	0
<i>Potentilla indica</i> (Andrews) Th. Wolf	Perennial	Temperate Asia	INV	294-925	1	7	4	0	0	0
<i>Lepidium virginicum</i> L.	Annual	N-America, S-America	INV	95-1085	8	0	4	0	0	0
<i>Solidago gigantea</i> Aiton	Perennial	N-America	INV	95-845	57	12	7	0	0	0
<i>Buddleja davidii</i> Franchet	Shrub	Temperate Asia	INV	158-925	24	50	21	0	0	0
<i>Erigeron annuus</i> (L.) Pers.	Annual	N-America	INV	95-925	25	16	14	0	0	0
<i>Impatiens glandulifera</i> Royle	Annual	Tropical Asia	INV	196-1250	8	9	7	17	0	0
<i>Impatiens parviflora</i> DC.	Annual	Temperate Asia	INV	196-1278	9	17	21	17	0	0
<i>Reynoutria japonica</i> Houtt.	Perennial	Temperate Asia	INV	103-1380	36	41	7	17	0	0
<i>Erigeron canadensis</i> L.	Annual	N-America	INV	95-1109	38	38	14	6	0	0

Elevation classes: I = 100-450 m; II = 450-800 m; III = 800-1,150 m; IV = 1,150-1,500 m; V = 1500-1850 m; VI = 1850-2100 m. Origin: the symbol "?" means that the origin is uncertain.

A great majority of the species are invasive in Piedmont and in Italy (71%), while 25% are naturalized and only 4% are casual species. All the species which occurred in more than 25% plots are invasive. Concerning life forms, there was a prevalence of annual species (56%) while among perennials (44%), there was a prevalence of herbaceous species (28% of the total) while shrubs formed 6%, trees only accounted for 7% and woody vines for 3%.

As for the origin of the species, they came mainly from N-America (33.8%), N- and S-America (14.5%), S-America (5.8%) and from Temperate Asia (25%) (Table I).

Pattern and distribution of non-native species with relation to elevation

The number of non-native species per plot strongly decreased with increasing elevation (Figure 2) following a reversed j-shaped distribution as shown by the simple Poisson regression model developed (Table II). This outlined relationship accounted for 62% of total variation in the distribution of the number of non-native species (Table II).

Table II. Summary for the regressive Poisson model between number of non-native species and elevation

Model parameters	Coefficient	p (χ^2)	SE	Explained variance (D^2 adj)
Intercept	2.288		0.054	0.618
Elevation	-0.002	***	>0.001	

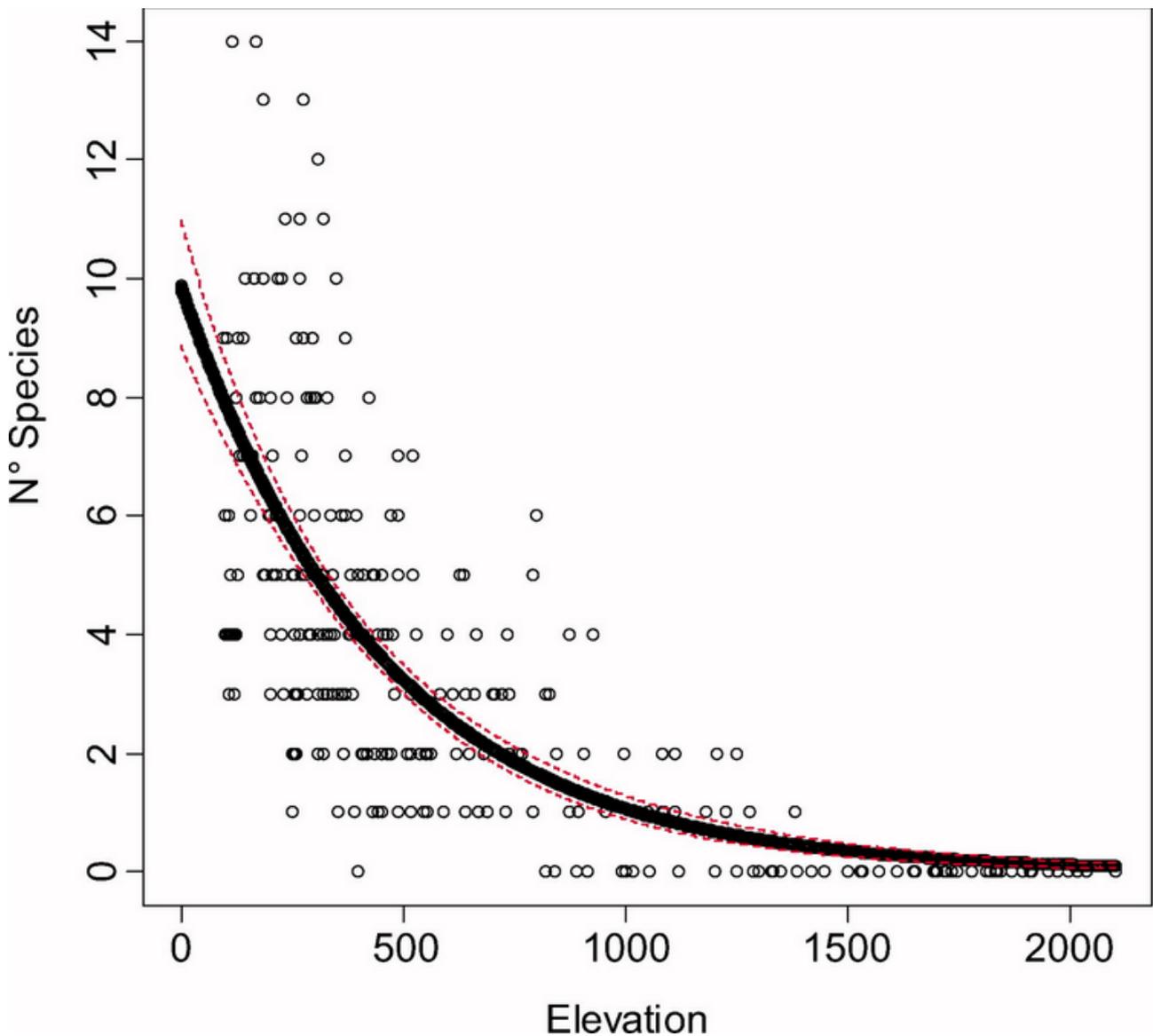


Figure 2. Estimated relationship for non-native plant species richness with respect to the elevation. Dotted lines represent 95% C.I.s.

Derived from the predictive model, the number of non-native species decreased as a function of elevation in the following way:

$$N^{\circ} \text{ non-native species} = 2.288 - 0.002 (\text{elevation})$$

considering both a Poisson distribution of residuals and a log-link function.

Consequently, it can be estimated that non-natives will result lower than 1 species for plots sampled above the 1028 m a.s.l. threshold.

Moreover, the data in Figure 2 displayed great variability in the number of non-native species per plot at lower altitudes where it ranged from very low (1–2) to very high values (12–14), while at higher elevation the number of species per plot was always very low (0–2).

Considering the frequency of each species (Table I) in each of the six elevation classes we found that many species occurred only in 1–2% of the plots at lower elevations, while some others occur more frequently, up to 27%. With increasing elevation the number of species per plot decreased but the total number of species in the elevation classes also decreased, from 64 (96%) in the lowest class, to 29 (42%) from 450 to 800 m, to 10 (15%) from 800 to 1150 m, and to 4 (6%) from 1150 to 1500 m (Table I, Figure 3). In the last two elevation classes (1500–1800 and 1800–2100 m) non-native species were totally absent. A large number of species, representing 54% of the total, grew only within the lowest elevation class, while three species occurred in the second class and *Matricaria discoidea* was sampled only in the third.

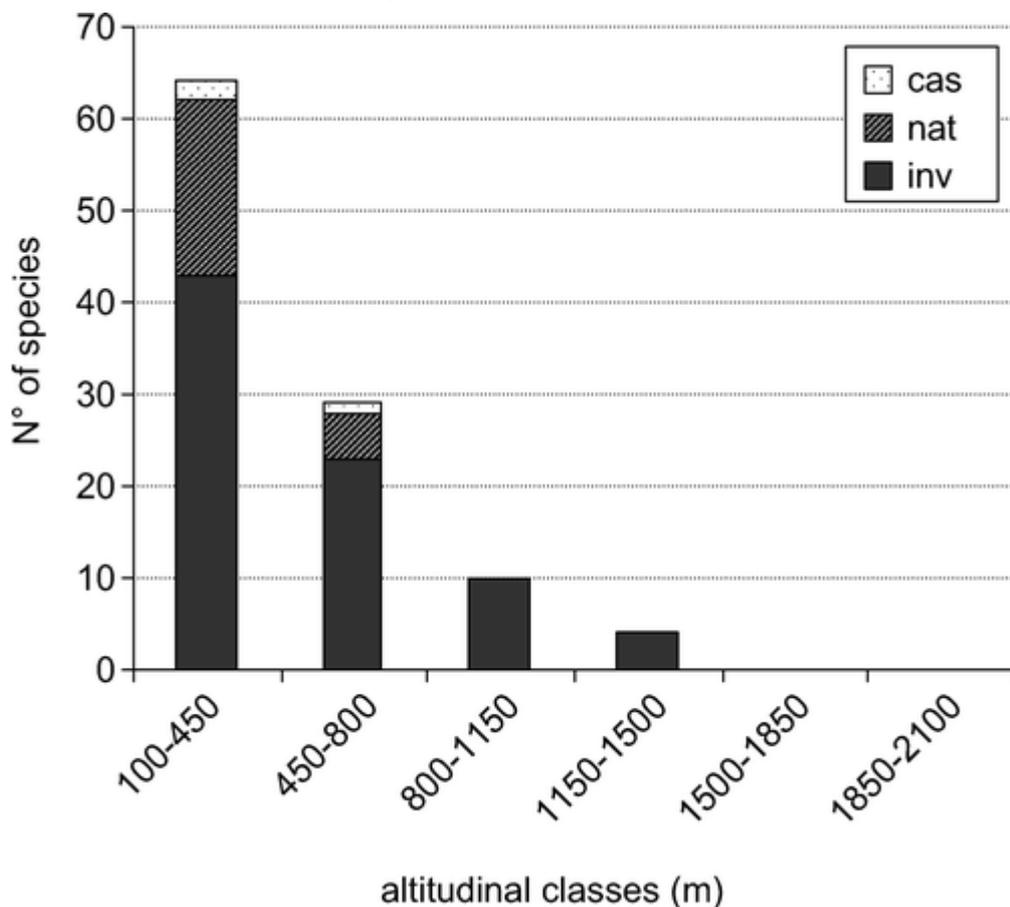


Figure 3. Number of casual, naturalized and invasive species in the elevation classes.

The species which reached higher elevations always displayed medium to high frequency values, from 6 to 17% of the plots.

The invasive species were always predominant: their proportion increased along the elevation gradient (Figure 3), while casual species were very uncommon even in the lowest elevation class, naturalized species occurred only up to 800 m a.s.l.

Clustering the species according to their frequencies in the different elevation classes (Figure 4a), we obtained the following four groups: (A) all the species occurring only at lower elevation with low or medium frequencies; they were annual, perennial herbaceous, trees and shrubs; (B) *Impatiens glandulifera* and *I. parviflora*, the only two species showing an increase in frequency from the lowest elevation class, to the second, third and fourth classes; they were annual species; (C) *R. japonica*, *E. (=Conyza) canadensis* and *B. davidii* which were very frequent at low elevations but continued to be common also in the second, third and fourth elevation classes, with a slightly decreasing trend; among these three species, only *B. davidii*, a shrub, showed its highest frequency at intermediate elevation, in the 450–800 m class; (D) the most frequent species occurring in the lowest class which did not maintain a high frequency at higher altitudes, showing a rapid decline. All the five species in this last cluster, *Erigeron annuus*, *Robinia pseudoacacia*, *Artemisia verlotiorum*, *S. gigantea* and *B. frondosa*, are among the most common non-native invasives in Italy and in most of Central Europe. Only *R. pseudoacacia* is a tree, while the others are annual or perennial herbs producing many seeds.

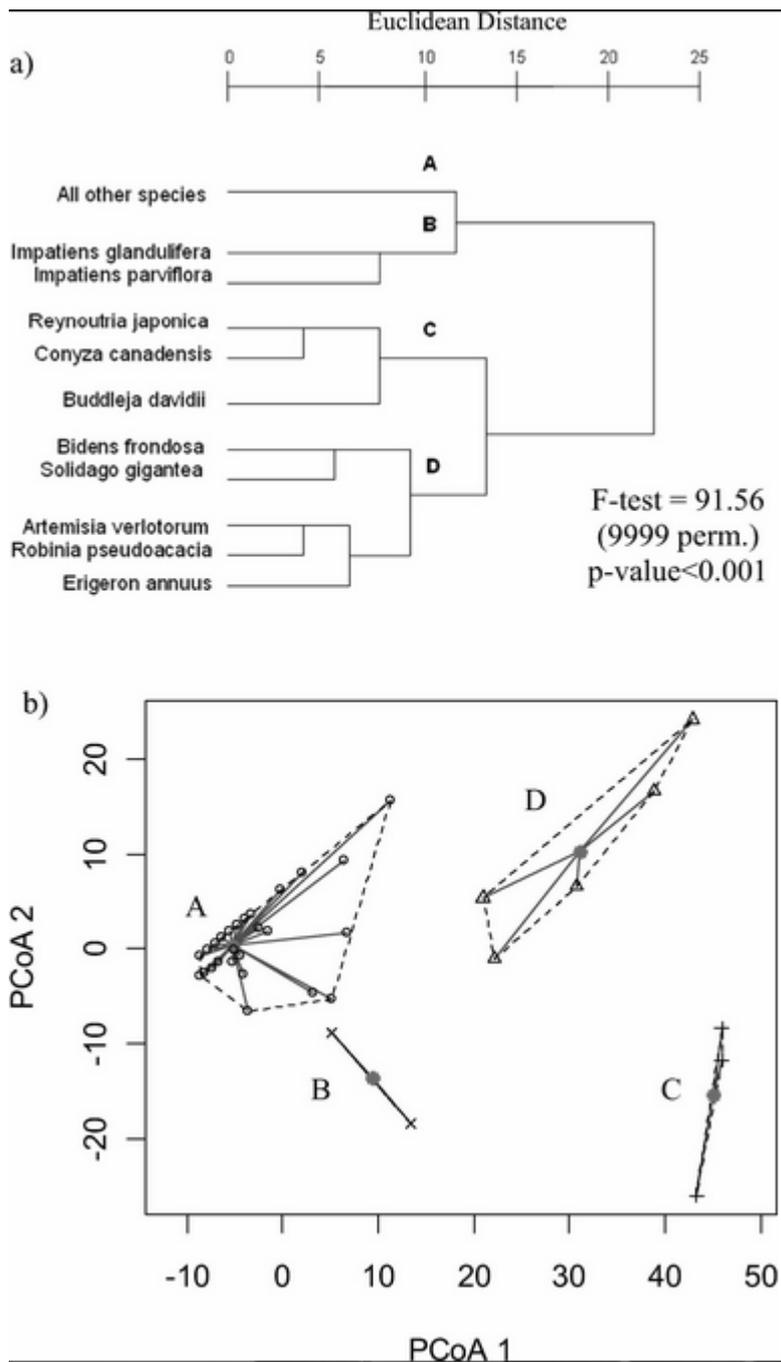


Figure 4. (a) Cluster analysis grouping non-native species with similar frequency along the gradient (option for clustering: Euclidean distance; resemblance coefficient: centroid). Test for cluster adequacy (F -test and its related p -value) was also described. (b) graphical display of cluster centroids on a PCoA biplot and single observation distance (species) from centroids.

The same four groups were also obtained using Euclidean distance and complete linkage, and very similar grouping resulted with other clustering methods (not showed here). Moreover, test for cluster adequacy resulted highly significant ($F = 91.52$, p -value < 0.001; Figure 4a and b).

Discussion

The rapid and abrupt decrease of non-native species occurrence along the elevation gradient confirms that elevation is a key factor restricting plant invasion (Pauchard et al. 2009). This result can be interpreted considering that in the studied valleys, river geomorphological features and consequently disturbance levels, naturally or artificially induced, do not change notably among the elevation classes considered, where the highest abrupt falls in non-native species number were registered. Moreover the structure of riparian plant communities, mainly scattered along the whole river course, does not offer resistance to invasion (Planty-Tabacchi et al. 1996). So we think that in the study area, climate harshness may play a major role in affecting the non-native species decline with elevation.

The observed pattern seems to depend on the pool of non-native species that can be transported along the valleys and invade higher elevations. Some of their traits, such as low density of propagules with low dispersal capabilities and a narrow climatic tolerance, may explain the decrease of casual and naturalized species, which rapidly disappear with increasing elevation. In the study area, high numbers of propagules are introduced due to proximity to the Po Plain, widely invaded by many non-native species (Celesti-Grapow et al. 2010), to the proven role of rivers as vectors (Stohlgren et al. 1999), and to the proximity of the roads running parallel to the rivers (Hood & Naiman 2000; Gelbard & Belnap 2003). These processes promote the spread of invasive species which exert a higher propagule pressure than casual and naturalized plants since they are widespread in the plain, have a high output of seeds, often wind-dispersed, and/or very efficient vegetative propagation. In fact invasive species were the most frequent among non-natives, in the whole study area (48 species representing 71% of the total); they were dominant at medium elevations and exclusive at the highest elevations reached. Selection for invasives is particularly evident if compared to the invasive status of the non-native flora of the whole region, in which only 62 species on 371 (17%) are invasive (Celesti-Grapow et al. 2010).

Cluster analysis of non-native plant frequencies within different elevation classes shows that the distribution of species and therefore their characteristics vary significantly along the altitudinal gradient; in this study the majority of non-natives only grow at low elevation, with low frequencies (1–5% of the total number of plots) and do not survive upwards. These species do not seem to be pre-adapted to mountain conditions, in company with others which are very frequent in the lowlands but do not reach higher elevation where conditions become harsher, like *S. gigantea* and *A. verlotiorum*. On the contrary, a very small number of species such as *R. japonica*, *E. canadensis* and *B. davidii*, all invasives, are pre-adapted to severe climate if we consider the latitudinal and elevation limits in their native range. For instance, *R. japonica*, native to temperate Asia, has an extremely wide ecological range, as already noted for north-western Europe (Beerling 1993). This species, living up to 2500 m on Mt. Fuji, can survive at an absolute minimum temperature of -30.2°C ; hybrids between *R. japonica* and *R. sachalinensis*, which are now becoming more frequent in Europe, due to the combination of successful vegetative propagation, hybridization and polyploidation, have more genetic variation than the progenitors and have a higher ecological amplitude (Tiébré et al. 2007).

B. davidii, native to central and south-western China, grows on mountain slopes between 800 and 3000 m and is found in very different climatic regions, from sub-continental to oceanic, showing a wide ecological range (Ebeling et al. 2008). Similarly, *E. canadensis* can grow at up to 2000 m in its native North American range.

In our study area there is a last group of species whose distribution differs from the others, having increasing frequencies from the lowlands to medium elevation: *Impatiens glandulifera* native of the Himalayas and *I. parviflora*, native of Central Asia and Siberia, are pre-adapted to live in cold regions, the first one living up to 2000–2500 m (Gupta 1989) and 4000 m (Polunin & Stainton 1984) and the second up to high latitudes. They are annuals, with initial rapid growth to reach the reproductive phase, and so they are not constrained by winter temperatures. They can produce many seeds, which need a period of chilling (Mumford 1990). Both species form monospecific communities, thus threatening native biodiversity.

All the listed invasive non-native species growing at higher elevations, adapted to both cold climate and disturbance, evolved probably in different situations with respect to the native alpine species which are not adapted to disturbance, so that they could be able to invade the disturbed areas of the Alps, although up to now their spread proceeded rather slowly. Analysis of these species populations looking at the mechanisms which make them harmful is required.

Moreover, the most invasive and harmful species should be listed in blacklists as prohibited from import and sale, following the recent European Commission communications (http://ec.europa.eu/environment/natura/pdf/council_concl0609.pdf).

An early warning and rapid response framework has to be urgently developed to tackle new invasions or to halt the ongoing ones and this seems to be more possible on mountain systems than elsewhere. Moreover the eradication and control of the most harmful non-native species is needed and possible in particular in protected areas, and should be focussed at peripheral populations, where they can better adapt to local conditions through micro-evolution (Maron et al. 2007).

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