

Alien plant species distribution in the European Alps: influence of species' climatic requirements

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Abstract The paper provides the first estimate of the role of abiotic and anthropogenic variables driving both alien plant species richness and composition covering the whole region of the European Alps. To establish and spread in a new area, alien plants must be able to tolerate the prevailing climatic conditions. We therefore tested the hypothesis that climatic requirements modified by bioclimatic origin and elevational distribution influence the distribution of alien plants in the Alps. Despite most alien plant species showing a

relatively restricted distribution in the Alps, some regions, however, were already more strongly invaded. Most of these species were adapted to warmer conditions, probably constrained by climatic factors. Environmental heterogeneity was the most important predictor of alien plant species richness, followed by anthropogenic disturbance. Due to the political/artificial delineation of the administrative districts in the Alps (i.e., ignoring ecological conditions) we did not find a direct influence of climatic constraints on alien distribution. Anyway, northern Holarctic alien species showed a broader climatic tolerance and the capability to grow across a wide environmental range. Our results also reveal a strong

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influence of human pressure on warmer tropical species, despite their low adaptability to anthropogenic habitats. To this aim, managers would profit from early warnings to prevent future invasions. Considering bioclimatic origin, our study can aid in identifying potentially invasive species in a more regional setting.

Keywords Assemblage differentiation · Climate matching · Disturbance · Mountain ecosystems · Urbanization · Temperature

Introduction

Plant invasion in mountain regions have recently attracted the interest of ecologists (Alexander et al. 2011; Dainese and Bragazza 2012; Pauchard et al. 2009). Mountain ecosystems are generally less invaded than surrounding lowland ecosystems (McDougall et al. 2011a), however, an increased invasion risk and management challenge may be expected in the near future due to climate and land use change (McDougall et al. 2011b; Pauchard et al. 2009). Particularly in the European Alps, most of the alien plant species occur only at low elevations and none is known to threaten biodiversity at high elevations (Kueffer 2010). Nevertheless there is a relatively large pool of alien species naturalized in the lowlands that may indicate the presence of a pool of species potentially able to invade temperate mountains in the future (Marini et al. 2013).

Although several factors driving invasion patterns were proposed, generalizations on the mechanisms producing observed alien species distribution in mountain ecosystems are still not well recognized (McDougall et al. 2011a). For instance, Pauchard et al. (2009) indicated four main drivers that can promote or constrain plant invasions in mountain regions: (1) environmental barriers, (2) disturbances (especially anthropogenic disturbance), (3) biotic resistance of native plant communities, and (4) propagule pressure. Considering the environmental barrier, Alexander et al. (2011) proposed directional ecological filtering as a general process of invasion, where cold temperatures limit alien species invasion towards high-elevation sites (i.e., few invaders possess the necessary adaptations to succeed under extreme environmental conditions). Anthropogenic disturbance is a further

driver of alien plant invasions due to direct land-use changes that create niche opportunities for invaders, as pointed out in the ‘novel niche hypothesis’ (Shea and Chesson 2002), but also because it may enhance the chances of alien plant colonization, persistence and invasion by increasing propagule pressure to suitable sites (Chytrý et al. 2008). However, successful invaders must overcome biotic resistance, i.e., the reduction in invasion success caused by the resident community (Elton 1958; Levine et al. 2004). Long-established temperate forests, in particular, often have few alien plant species, suggesting that forests are somehow resistant to invasion (Matlack and Schaub 2011; Rejmánek et al. 1989; Von Holle et al. 2003).

In order to establish and spread in a new area alien plants must be able, however, to tolerate the prevailing climatic conditions, i.e., the greater the degree of climate matching between the invaded region and the species’ native region, the higher is the likelihood of establishment (‘climate matching hypothesis’; Williamson 1996; Wiens and Graham 2005). Although previous studies (de Albuquerque et al. 2011; Haider et al. 2010; Jakobs et al. 2010) showed contrasting results about the role of climate in facilitating alien species spread, recently, a large-test carried out by Petitpierre et al. (2012) confirmed that climatic niche requirements of invasive species largely match between their native and invaded ranges. Therefore, combining species that share the same ecological properties (e.g., bioclimatic origin or elevational distribution) and that might respond in a similar way to global change, can improve our prediction of invasion risk in specific regions.

To date, studies on plant species distribution in the European Alps are mainly based on local elevational gradients (Barni et al. 2012; Becker et al. 2005) or only valid for in limited regions of the Alps (Dainese and Poldini 2012; Marini et al. 2012, 2009). To the best of our knowledge, there are no studies covering the complete European Alps or any other large mountainous region. Moreover, while some studies have investigated potential drivers of alien plant species richness in mountain regions, few studies have assessed the drivers determining community differentiation, or beta diversity among sites (Alexander et al. 2011; Marini et al. 2013; Seipel et al. 2012).

In this study, we used the alien flora of the European Alps (Aeschimann et al. 2004) to fill that gap and to assess the influence of abiotic and anthropogenic

factors driving alien species richness and composition across the whole mountain region. The problem with such species lists, however, is that their extent is determined by administrative criteria, so they do neither meet the constant grain size assumption of diversity analyses nor homogeneity of ecological or environmental conditions. For this reason the level of invasion should change with increasing sample area (Hulme 2008). Despite this species-area relationship, it has been shown for many groups in Europe that variation in area has little effect in the explanatory models for species richness (Keil and Hawkins 2009; Nogués-Bravo and Araújo 2006). Anyway, we expected a great influence of area on alien species distribution as found by others studies (Lambdon et al. 2008; Pyšek et al. 2010a). Such results should confirm the ‘spatial heterogeneity hypothesis’ (Davies et al. 2005; Melbourne et al. 2007), whereby alien species richness increases with the surveyed area since environmental heterogeneity also increases with spatial scale (i.e., if there are more different types of resources in an area, there will be more niche opportunities). We also expected a strong influence of anthropogenic disturbance on alien plant invasion, while environmental barriers and biotic resistance should instead limit.

Second, we tested the hypothesis that climatic requirements of alien plants influence their distribution in the Alps. We selected two ecological plant properties characterizing alien species on the basis of their climatic pre-adaptation (i.e., using biogeographic origin as proxy for bioclimatic origin) and elevational distribution. By discerning the effects of abiotic and anthropogenic factors on alien plant distribution, according to the ecological requirements of the species, we expected to better understand the distribution of alien plants in the European Alps. Distinct responses among different climatic requirements of alien plants should allow identifying whether filtering of species assembly is driven by climatic constraints, anthropogenic disturbance and/or spatial heterogeneity.

Methods

Study area

The study area corresponds to the European Alps as geographically delimited by Aeschimann et al. (2004)

(Fig. 1). With c. 300 km at its widest N–S extension between Munich and Verona, and with an East–West extension of c. 1,000 km, the study area covers a total of c. 171,000 km². The area extends through seven states: Austria (31.5 %), Italy (28.5 %), France (19.2 %), Switzerland (14.6 %), Slovenia (3.3 %), Germany (2.9 %), and Liechtenstein (0.1 %). The highest peaks, well above 4,000 m a.s.l., are situated in western Switzerland, north-western Italy, and south-eastern France (highest peak of the Alps: Mt Blanc, 4,810 m a.s.l.). Further East, the characteristic altitude remains generally below 2,000 m a.s.l., with the highest peaks reaching around 3,000 m a.s.l. The population is about 15 million and mostly concentrated in low-lying valleys which are often quite densely populated. Moreover, increased population is recorded on the fringe areas of the Alps. With about 60–80 million visitors per year, the Alps are one of the most popular touristic destinations in the world (Agrawala 2007). Still, tourism does not cover extensive areas (Bätzing 2005).

The Alps offer different climates ranging from Mediterranean and Atlantic influences in the South and West to continental characteristics in the East, and from low-elevation plains, valleys and basins to high-elevation mountain climate in regions above the tree-line and above the snow-line (Böhm et al. 2001). Annual precipitation sums along the northern and southern fringe are rather similar, but due to the topographic barriers in the North and South the inner Alpine valleys are usually rather dry (Frei and Schär 1998). Along an altitudinal gradient across the Alps the following vegetation belts can be described (with corresponding major habitats): colline (thermophilous and temperate broadleaf forests), montane (beech and coniferous forests), subalpine (dwarf shrub heaths), alpine (closed grasslands), and subnival (patchy grasslands, screes, and rocky slopes) (Nagy 2006).

Species database

Information on the occurrence of the alien plant species ($n = 509$) were extracted from Aeschimann et al. (2004), i.e., the most complete flora available for the European Alps region. Doubtful alien plant species ($n = 55$) sensu Aeschimann et al. (2004) were excluded from the analysis. The occurrence of each species was compiled at an administrative level (e.g., Province in Italy, Départments in France, Bundesländer in Austria,

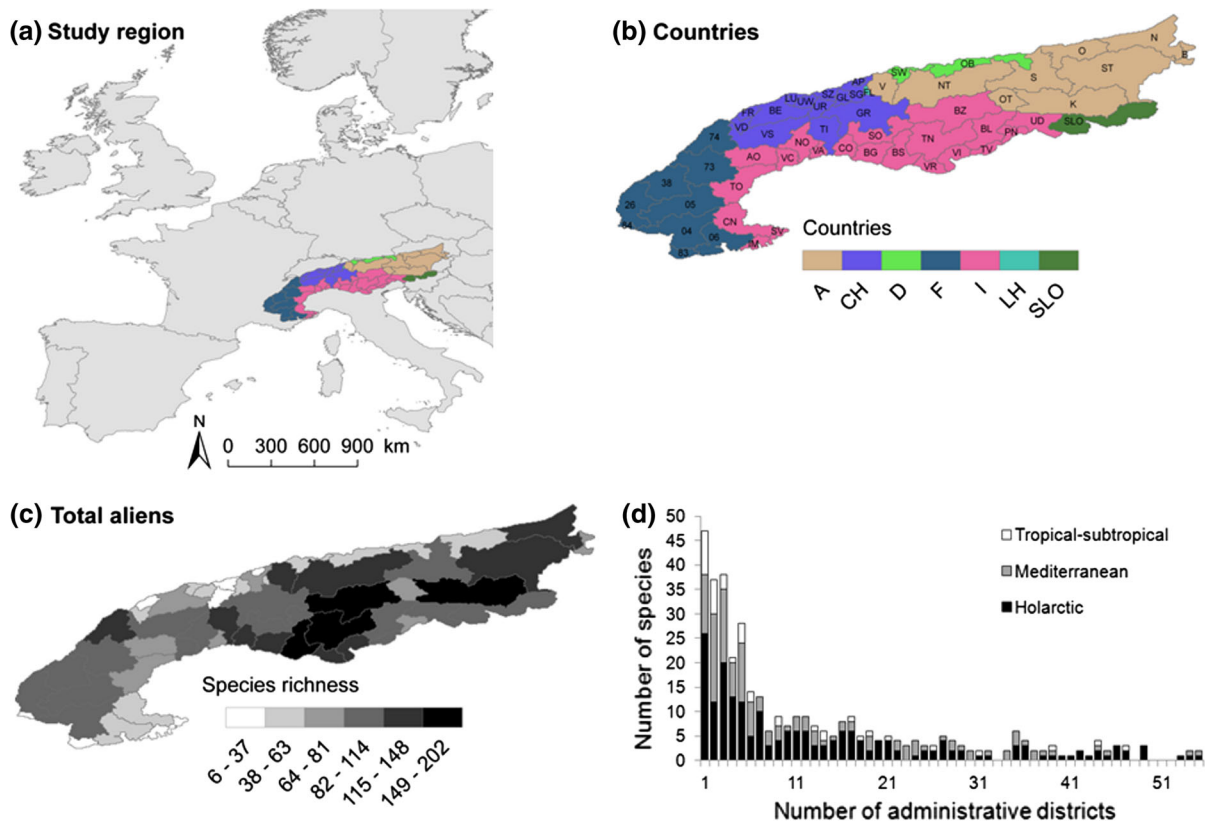


Fig. 1 Delimitation of the European Alps **a**, subdivision by countries **b**, total alien plant species richness distribution in the 55 administrative districts **c**, and frequency distribution of range sizes of European Alps alien plant species **d**. Each *bar* represents the number of northern Holarctic (*black*), Mediterranean (*grey*),

and tropical-subtropical (*blank*) alien plants that are recorded from a given number of administrative districts. *A* Austria, *CH* Switzerland, *D* Germany, *F* France, *I* Italy, *LH* Liechtenstein, *SLO* Slovenia

Kanton in Switzerland) with a total of 55 administrative districts (Fig. 1). We also excluded 75 alien plant species (e.g., mainly cultivated species) for which the occurrence within the administrative districts is not specified. In total, 379 alien plant species were used in the present study.

Aeschimann et al. (2004) also provided information about the biogeographical origin of species and we classified alien plant species into three bioclimatic origins (de Albuquerque et al. 2011): (1) northern Holarctic alien plants, comprising those species whose centres of origin are in extra-Mediterranean Europe, in extra-tropical Asia, or in North America (203 species); (2) Mediterranean alien plants, which originated either in southern Europe, northern Africa, or the Middle East (129 species); and (3) tropical–subtropical alien plants, which originated in the Neotropics, Afrotropics, or Indo-Pacific region (40 species). The

biogeographical origin was not available for seven plant species, which were then excluded from the respective analysis. We further classed the species into groups with different elevational and thermal centres of distribution using information from Landolt (2010) as follows: (1) subalpine alien plants (9 species); montane alien plants (30 species); colline alien plants (55 species); warm colline alien plants (149 species); and very warm colline alien plants (136 species).

Environmental data

For each administrative division, seven environmental variables were recorded according to the hypotheses formulated above (Table 1). The administrative area in km² (AREA) was determined in order to account for the species–area relationship. In addition, the elevation range (ELE-R) at administrative level was used as a

Table 1 Descriptive statistics of the environmental variables of the European Alps included in this study

Variable name and description		Unit	Mean	Min	Max
AREA	Area of each administrative division	km ²	3,182	164	12,478
TEMP	Minimum temperature of the coldest month	°C	−5.93	−10.55	1.30
PREC	Precipitation of the driest month	mm	221	116	383
HUM	Number of inhabitants		247,185	6,589	998,130
URB	Area cover by urban elements	%	4.59	0.24	30.99
FOR	Area covered by forests	%	40.3	5.7	67.6
ELE-R	Elevation range	m	2,437	334	4,165

measure of environmental heterogeneity. Area was included as a covariable because the use of residuals in multiple regression models can lead to biased parameter estimates (Freckleton 2002).

Minimum temperature of the coldest month (TEMP) and the amount of precipitation of the driest month (PREC) were selected as proxies of environmental barrier to plant invasion (Alpert et al. 2000; Pauchard et al. 2009). The climatic parameters were obtained from the WorldClim database at a resolution of 30'' (Hijmans et al. 2005).

The number of inhabitants (HUM) and the degree of urbanisation (URB) (i.e., the coverage of buildings, streets, and other artificial land uses) were calculated as a proxy for anthropogenic disturbance (Pauchard et al. 2009). HUM was obtained from the Gridded Population of the World (urban mapping project, version 3 produced by the Center for International Earth Science Information Network (CIESIN) and available at: <http://sedac.ciesin.columbia.edu/gpw>). We used the land-use variables derived from the CORINE 2006 land cover (raster data with 250 × 250 m resolution, version 16/2012, from the European Environment Agency) to calculate URB. The proportion of each land-use class in the administrative districts was computed and then the classes related to artificial surfaces were merged.

The proportion of forest (FOR) was used as a proxy of environmental barrier to alien plant invasion (Martin et al. 2009) and obtained from the CORINE 2006 land cover.

Statistical analyses

Species richness

The relative roles of the environmental variables in explaining the observed variation in alien species

richness were assessed using ordinary least squares (OLS) regression. Since species richness does not follow a normal distribution but ranges between zero and the maximum species number of the species pool, we logit-transformed species richness in order to make the spread of the data approximately symmetric. We performed backward manual selection starting from the full model (based on error probability with $\alpha = 0.05$). The residuals of our non-spatial ordinary least-square regression (OLS) model did not exhibit significant spatial autocorrelation (Moran's $I = 0.09$; $P = 0.110$), so we only fitted non-spatial OLS model to these variables. The model residuals approximated a normal distribution and exhibited homogeneity of variance after visual inspection of model residuals. We also extracted standardized partial regression coefficients from this model using the 'lm.beta' function of the 'QuantPsyc' package (Fletcher 2010) for R v. 2.15.2 (R Development Core Team 2012).

Since one of the aims of our study is to test whether plant properties modify the relationships between alien species richness and environmental variables, we examined the interactions between environmental variables and plant properties using a linear mixed effects model (i.e., environment × bioclimatic origin, environment × elevation, environment × bioclimatic origin × elevation). Bioclimatic origins were coded as categorical fixed factors with three levels (northern Holarctic, Mediterranean and tropical-subtropical), elevational distribution as a five-level ordered fixed factor (subalpine < montane < colline < warm colline < very warm colline), and environmental variables as continuous fixed factors. The number of species for each combination of plant properties was considered the response variable, at each administrative division; that is, there were 15 species richness values (one for each combination of plant properties) for each

administrative division. As the number of species was quantified in the same administrative division, we included the administrative division as a random factor to account for this nesting. Starting from the full models described above, we simplified the model by manual backward selection ($\alpha = 0.05$). First we removed the non-significant interaction terms and then the non-significant main effects (unless part of a significant interaction). Using elevation as ordered factor allowed testing both linearised and quadratic contrasts. The mixed model was performed using the function ‘lmer’ in the ‘lme4’ package in R (Bates et al. 2011). The P values of fixed effects were obtained from 10,000 Markov chain Monte Carlo (MCMC) simulations based on the posterior distribution of the parameters, using the ‘pvals.fnc’ and ‘aovlmer.fnc’ functions in the ‘languageR’ package in R (Baayen 2011). Post-hoc comparisons were further used to test whether the slopes differed from zero and to compare the regression curves of the significant interaction terms, using the ‘glht’ (general linear hypothesis test) function in the ‘multcomp’ package in R (Hothorn et al. 2008).

Species composition

We also examined the factors explaining assemblage differentiation in alien plants using Constrained Analysis of Principal Coordinates (CAP) (Anderson and Willis 2003; Legendre and Anderson 1999) followed by forward selection of environmental variables. Compared with traditional canonical ordination (e.g., RDA and CCA) this approach has the advantage of accommodating any dissimilarity measure through the use of principal coordinates analysis (PCoA) as an intermediate step, while taking into account the correlation structure among variables in the response data. We used the Jaccard index based on presence/absence data to compute the species dissimilarity matrix. The analysis was performed using the function ‘capscale’ in the ‘vegan’ package (Oksanen et al. 2011) implemented in R. Forward selection of environmental factors was run to select those variables that significantly contributed ($\alpha = 0.05$ after 999 random permutations) to explain the variation in species composition. We used the function ‘ordiR2step’ in the ‘vegan’ package for R (Oksanen et al. 2011). After that, CAP was also used to describe and visualise the relations between environmental variables and alien species composition. All the

environmental variables recorded were included in the CAP diagram to get an overview of the relations.

Finally, an analysis of variance was performed to test whether the first two CAP axes mean scores significantly differed among the species grouped according their bioclimatic origin and elevational distribution. Tukey contrasts were calculated from the models to test for differences within plant properties, using the function ‘glht’ in R package ‘multcomp’ (Hothorn et al. 2008).

Results

Austria and Italy included the administrative districts with higher numbers of alien plant species (Fig. 1c): Kärnten (K: Carinthia; 202 species), Steiermark (ST: Styria; 148 species), Voralberg (V; 133 species), Tirol (NT: Tyrol, 131 species) in Austria, and Bolzano (BZ, 177 species), Brescia (BS, 160 species), Trento (TN, 159 species), Verona (VR, 142 species), Bergamo (BG, 141 species) in Italy. The alien species recorded from more than a half of the administrative districts were 59. The most common alien species was *Veronica persica* (native to Asia) and *Medicago sativa* (native to Mediterranean region), occurring in all the districts. Other species occurring in more than 80 % of regions were *Aster novi-belgii*, *Conyza canadensis*, *Juncus tenuis*, *Oenothera biennis*, *Oxalis stricta*, *Robinia pseudoacacia*, *Solidago gigantea* (native to North America), *Amaranthus retroflexus*, *Lepidium virginicum* (North and Central America), *Galinsoga ciliata* (Central and South America), *Galinsoga parviflora*, *Matricaria discoidea* (South America), *Hesperis matronalis*, *Onobrychis vicifolia*, *Tanacetum parthenium* (Mediterranean region), and *Artemisia verlotiorum*, *Buddleja davidii*, *Impatiens glandulifera* (Asia). Most alien species had a relatively restricted distribution in the European Alps (Fig. 1d and Appendix 1 in supplementary material).

The elevation distribution spectrum was mainly composed of thermophilic species (c. 70–90 %) for both bioclimatic origin groups. However, some differences were found ($\chi^2 = 23.86$, $df = 8$, $P = 0.002$). For instance, the northern Holarctic species pool was mainly composed of warm colline species (45 %), while the Mediterranean and tropical–subtropical species pool were mainly composed of very warm colline species (45 and 58 %, respectively). Subalpine and

montane species were under-represented (c. 10 %) for Holarctic and Mediterranean species pool, while not represented for tropical species pool.

Temperature, precipitation, and urban elements were significantly correlated with elevational range (see Appendix 2 in supplementary material). Specifically, temperature and urban elements showed a negative correlation with elevation range, while precipitation had an opposite pattern. The distribution of forest showed instead a hump-shaped relationship with elevational range.

Species richness

The pattern of alien species richness was significantly related to area, temperature, precipitation, urban elements and forest cover (Table 2). As expected, area was the most important factor and was positively related with alien species richness. Hence, controlling for area, a positive but weaker relationship was also found for urban elements. Temperature, precipitation and forest cover had instead a negative relationship with alien species richness.

Significant interactions were found between bioclimatic origin, elevational distribution and environmental variables (Table 3). The model showed that elevational distribution modified the response of species richness of all the environmental variables except for forests, while bioclimatic origin modified the response of species richness to area, temperature and urban elements. Concerning bioclimatic origin, the species-area relationship was flatter for tropical-subtropical alien plants than for Holarctic and

Mediterranean alien plants (Fig. 2a). The influence of temperature was only significant for northern Holarctic (post hoc comparisons test; $\chi^2 = -3.73$, $P < 0.001$) with alien plants showing a negative relationship (slope = -0.105), while not significant for Mediterranean ($\chi^2 = -1.43$, $P = 0.153$) and tropical-subtropical ($\chi^2 = -0.88$, $P = 0.380$) alien plants (Fig. 2b). A significant interaction was also found between bioclimatic origin and elevational distribution showing a quadratic relationship with northern Holarctic and Mediterranean alien plants (i.e., the number of species had a decelerating positive pattern from subalpine to warm colline species, followed by a reduction in species passing to very warm colline species) while a positive linear relationship with tropical-subtropical alien plants (Fig. 2c). Notably, there was higher species richness of subalpine and montane species for northern Holarctic alien plants. Considering the elevational distribution, the relationship between environmental variables and species richness showed a steeper species-area (Fig. 3a) for thermophilic species. The relationship with temperature indicated a negative trend except for very warm colline species which had a neutral pattern (Fig. 3b). The relationship with precipitation showed a neutral trend with subalpine and mountain species, a slightly positive trend with colline species, while a negative trend for thermophilic species (Fig. 3c). Finally the three-way interaction between urban elements, bioclimatic origin, and elevational distribution indicated an increasing influence of urban elements on species richness for thermophilic species of northern Holarctic and tropical-subtropical origin (Fig. 4).

Table 2 Results of the selection of the environmental variables in the multiple regression models on alien plant species richness and composition

	Species richness				Species composition			
	β	t	P	R^2 model	R^2	F	P	R^2 model
Model				0.67				0.18
Area	0.708	7.818	<0.001		0.073	5.247	0.001	
Temperature	-0.374	-3.499	0.001		0.047	3.856	0.001	
Precipitation	-0.306	-2.769	0.008		0.024	2.438	0.002	
Urban	0.394	4.542	<0.001		0.021	2.302	0.001	
Forests	-0.198	-2.073	0.043		-	-	-	
Elevation range	-	-	-		0.014	1.878	0.005	

Predictors were tested using ordinary least squares (OLS) multiple regression models followed by backward selection for species richness and using Constrained Analysis of Principal Coordinates (CAP) followed by forward selection for species composition. Standardized regression coefficients (β) are presented in the species richness model

Species composition

Variation in alien species composition was significantly influenced by area, temperature, precipitation, urban elements and elevation range (Table 2). Considering the overall environmental variables (Fig. 5), the first axis accounted for 13 % of the species-environment variation and was mainly determined by area ($r = -0.65$), human population ($r = -0.52$), and precipitation ($r = 0.58$). The second axis captured 10 % of the species-environment variation and was mainly determined by temperature ($r = -0.84$).

Species which were grouped according to their bioclimatic origin did not significantly differ in their scores along CAP axis 1 (ANOVA; $F = 0.99$; $P = 0.371$) (Fig. 5a), which was most strongly associated with human impact. In contrast, bioclimatic origin showed a significant difference along CAP axis 2 (ANOVA; $F = 10.68$ $P < 0.001$) (Fig. 5a), which was most strongly associated with temperature. Specifically, temperature determined assemblage differentiation in alien plants separating northern Holarctic alien plants from Mediterranean (Tukey contrasts, $P < 0.001$) and tropical-subtropical (Tukey contrasts, $P = 0.025$) alien plants, while Mediterranean and tropical-subtropical alien plants did not significantly differ (Tukey contrasts, $P = 0.999$).

Considering the elevation distribution, CAP axis 1 (ANOVA; $F = 9.25$; $P < 0.001$) showed a significant differentiation between species occurred from subalpine to colline belt and species occurred on warmer belt (contrast, $P < 0.001$) (Fig. 5b). CAP axis 2 showed also a significant differentiation among the elevational distribution (ANOVA; $F = 11.76$; $P < 0.001$), with very warm colline having a greater association with temperature (significant differentiation with respect the other groups; Tukey contrasts, $P < 0.05$) (Fig. 5b).

Discussion

The most common alien species occurring in the European Alps are the same as reported by Lambdon et al. (2008) at the European continental-scale. Notably, almost all of them are aliens to Europe and originating from North or South America. In the Alps, alien plants have a relatively restricted distribution (i.e., half of all aliens species occur in six or fewer

districts), a result comparable to the continental-scale where half of all naturalized species occur in four or fewer European countries (Lambdon et al. 2008). This could suggest that the local distribution of so many aliens is strongly constrained by climatic and environmental factors. Similarly, local-gradient studies (Alexander et al. 2011; Becker et al. 2005; Marini et al. 2013; Seipel et al. 2012) showed that a great majority of alien species were introduced in the lowlands, and that only a subset of this lowland assemblage has spread up the mountains, in line with the directional ecological filtering hypothesis (Alexander et al. 2011). Local occurrences of alien plants could result in floristic differentiation with large species turnover between urbanized areas in the lowlands (Kühn and Klotz 2006; Lambdon et al. 2008; Marini et al. 2013).

Do climatic requirements determine different responses to environmental processes?

The alien species pool occurring in the European Alps is composed of a small number of mountain specialists. Indeed, we found a greater presence of species adapted to warmer and disturbed conditions that therefore may give support to the directional ecological filtering hypothesis to explain invasions of alien species in mountain regions (Alexander et al. 2011), although the spatial scale of our study is not appropriate. Therefore, as few invaders possess the necessary adaptations to succeed under extreme environmental conditions, species introduced into disturbed habitats at low elevations are progressively filtered out by the increasingly harsh climatic conditions along the elevational gradients, as suggested by previous studies (Alexander et al. 2011; Becker et al. 2005; Marini et al. 2013; Seipel et al. 2012).

According to our initial hypothesis, source regions climatically similar to the target region are more species rich. Similarly, alien plants grouped according to their elevational distribution show also different responses to environmental processes. However, we found no three-way interaction between environmental factors, bioclimatic origin, and elevational distribution, expected for urban elements. This suggests a consistent response to area and temperature across the elevational distribution for each bioclimatic origin, and a consistent response to area, temperature, precipitation, forests cover, and elevation range across the bioclimatic origin for each elevational distribution.

Table 3 Result of linear mixed effects model (REML method) testing the fixed effect of environmental variables, bioclimatic origin (northern Holarctic, Mediterranean and tropical-subtropical alien plants) and their interaction

	Estimate	SE	<i>t</i> value	<i>P</i> value
<i>Overall regression</i>				
Intercept	-6.4520	0.3141	-20.541	0.0002
Area	0.5961	0.0986	6.047	0.0002
Temperature	-0.0432	0.0129	-3.335	0.0002
Precipitation	-0.0018	0.0006	-2.957	0.0004
Urban	0.0292	0.0063	4.620	0.0004
Forests	-0.0053	0.0024	-2.241	0.0120
Elevation range	0.0001	0.0001	0.757	0.3964
Elevation distribution.L	-0.7903	0.3002	-2.632	0.0084
Elevation distribution.Q	-0.6799	0.3002	-2.265	0.0280
Origin				0.0001
Holarctic ^a	-6.1960	0.3589	-17.264	0.0002
Mediterranean ^b	-0.4838	0.3008	-1.608	0.1164
Tropical ^b	-0.2826	0.3008	-0.940	0.3376
<i>Interaction terms</i>				
Area × elevation distribution	0.8000	0.0942	8.490	0.0002
Temperature × elevation distribution	0.0416	0.0124	3.363	0.0012
Precipitation × elevation distribution	-0.0026	0.0006	-4.412	0.0002
Urban × elevation distribution	0.0482	0.0060	6.546	0.0002
Forests × elevation distribution	-0.0090	0.0023	-3.986	0.0002
Elevation range × elevation distribution	0.0002	0.0001	4.002	0.0002
Area × Origin				0.0001
Holarctic ^c	0.6183	0.1087	5.689	0.0002
Mediterranean ^d	0.2177	0.0792	2.747	0.0072
Tropical ^d	-0.2842	0.0792	-3.587	0.0008
Temperature × origin				0.0001
Holarctic ^c	-0.1048	0.0151	-6.948	0.0002
Mediterranean ^d	0.0977	0.0134	7.287	0.0002
Tropical ^d	0.0872	0.0134	6.499	0.0002
Urban × origin				0.0001
Holarctic ^c	0.0473	0.0073	6.489	0.0002
Mediterranean ^d	-0.0345	0.0063	-5.452	0.0002
Tropical ^d	-0.0200	0.0063	-3.156	0.0020
Elevation distribution × origin				0.0001
Elevation.L × holarctic ^c	-0.6852	0.3046	-2.250	0.0284
Elevation.Q × holarctic ^c	-1.1790	0.3046	-3.873	0.0002
Elevation.L × mediterranean ^d	0.2155	0.0887	2.431	0.0228
Elevation.Q × mediterranean ^d	0.3909	0.0887	4.409	0.0002
Elevation.L × tropical ^d	-0.5309	0.0887	-5.988	0.0002
Elevation.Q × tropical ^d	1.1080	0.0887	12.492	0.0002
Urban × elevation distribution × origin				0.0001
Holarctic ^c	0.0624	0.0095	6.546	0.0002

Table 3 continued

	Estimate	SE	<i>t</i> value	<i>P</i> value
Mediterranean ^d	-0.0337	0.0128	-2.630	0.0112
Tropical ^d	-0.0091	0.0128	-0.711	0.4880

Administrative division was included as random factor to account for the fact that the numbers of species in each bioclimatic origin were quantified within the same administrative districts

Parameter estimates, standard error (SE) and *t* value for significant linear (.L) and quadratic (.Q) terms are reported. *P* value was obtained from 10,000 Markov chain Monte Carlo (MCMC) simulations

^a The intercept belongs to the factor level that comes first in the alphabet

^b Further categorical effects are differences to the first term

^c The slope belongs to the first factor level in the alphabet

^d Further interaction terms are differences to the first term

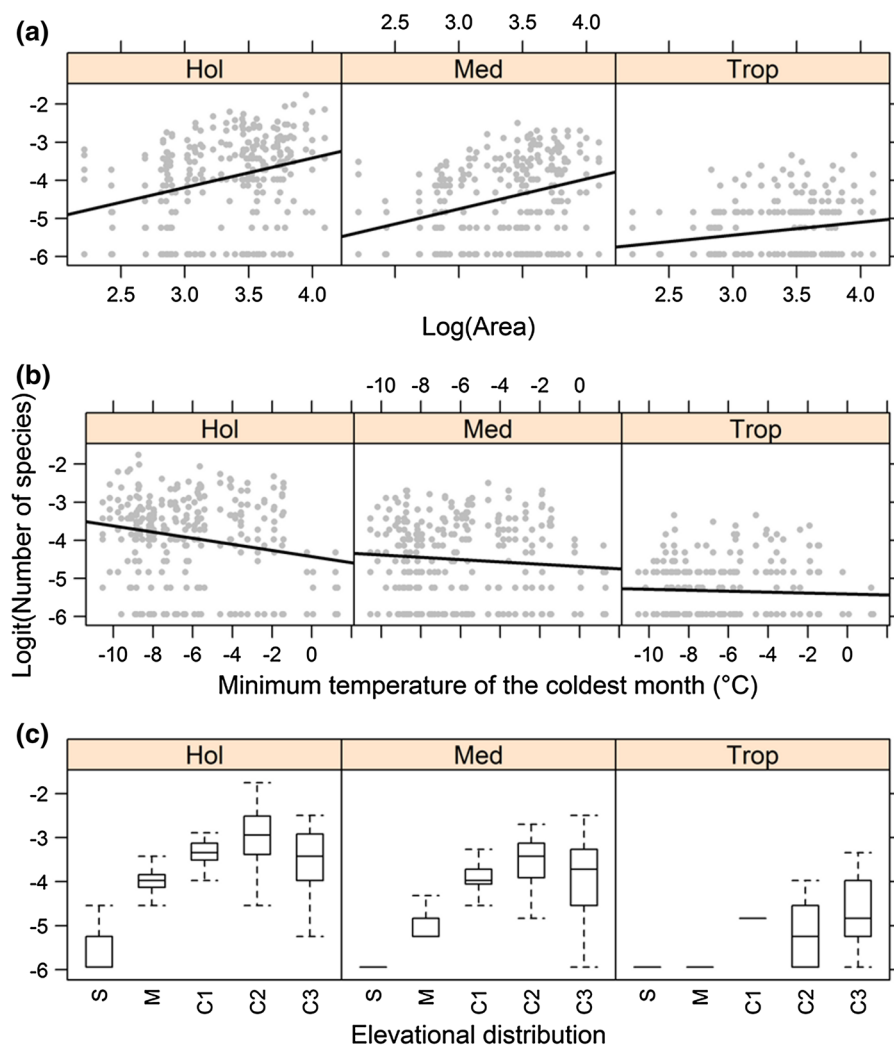


Fig. 2 The effect of bioclimatic origin (*Hol*, northern Holarctic; *Med*, Mediterranean; *Trop*, tropical-subtropical) on the response of alien species richness to **a** area, **b** temperature, and **c** elevational distribution

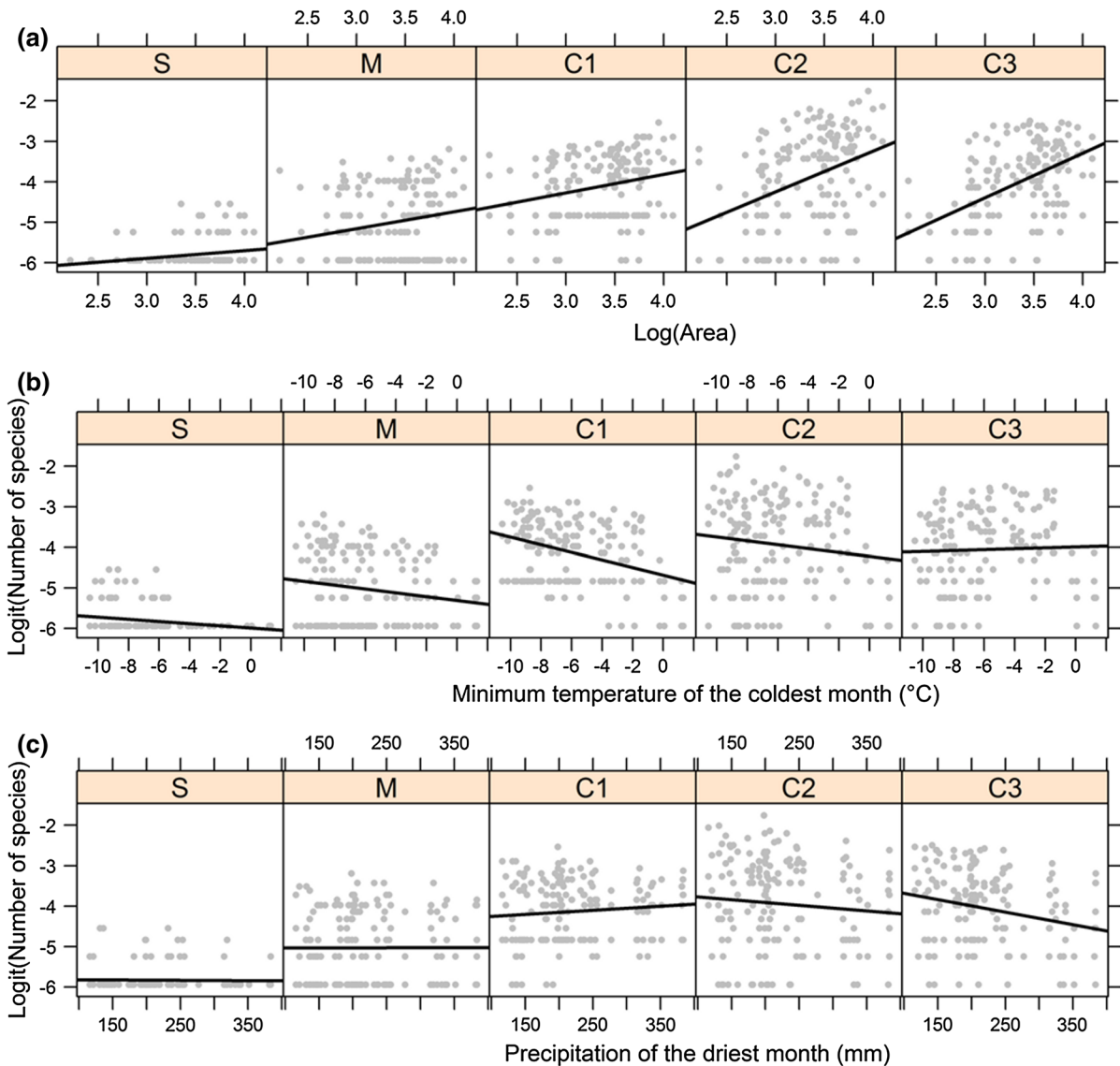


Fig. 3 The effect of elevational distribution (*S*, subalpine; *M*, montane; *C1*, colline; *C2*, warm colline; *C3*, very warm colline) on the response of alien species richness to **a** area, **b** temperature, and **c** precipitation

Interestingly, the slope of the species-area relationships for urban elements differ between bioclimatic origins and elevational distribution. Both warmer alien species of northern Holarctic and tropical-subtropical origin appear more positively affected by the degree of urbanisation than alien plants of Mediterranean origin. However, we are not able to ascertain whether this pattern is due to a direct effect of urbanization or just the indirect consequence of urban areas being situated at the lowest elevations and thus climatically most suitable for warmer species. Despite this, the available

species pool (Zobel 1997) of tropical alien plants that preferably occupy anthropogenic habitats in their native range is much lower than that for Mediterranean and Holarctic species. Those few species that are capable of surviving and reproducing under anthropogenic habitats seem, however, to perform disproportionately well. The question remains whether tropical species thrive through import into gardens (Dehnen-Schmutz 2011) and how many of these were supported by propagule pressure from surrounding gardens (Hanspach et al. 2008; Hulme 2011). Likewise, anthropogenic

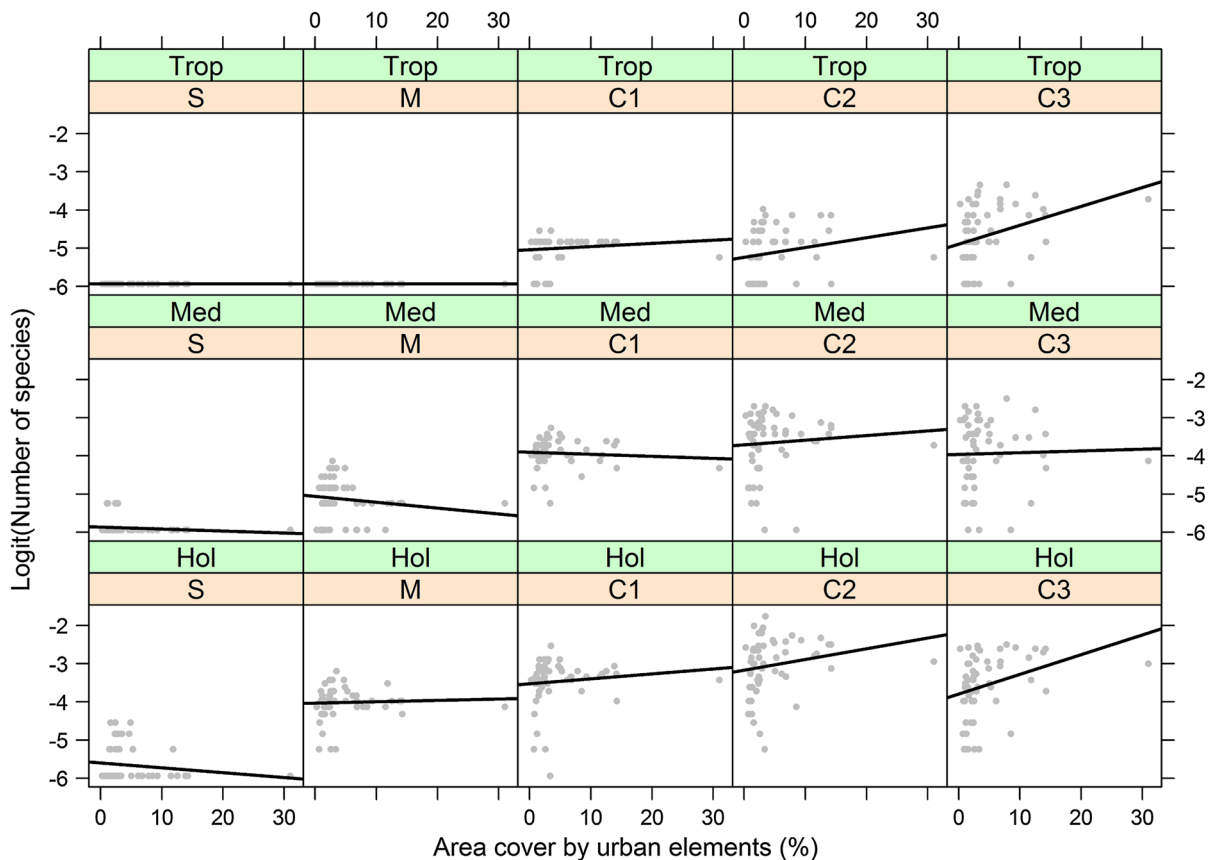


Fig. 4 The relationship between species richness and urban elements within different elevational distributions (**a–e**) (S, subalpine; M, montane; C1, colline; C2, warm colline; C3, very

warm colline) separately for bioclimatic origins (*Hol*, northern Holarctic; *Med*, Mediterranean; *Trop*, tropical-subtropical)

disturbance determines assemblage differentiation in alien plants separating warmer species from the other groups. Conversely, species differentiation in their bioclimatic origin responds similarly along the human population gradient (Fig. 3, CAP axis 1) and the associated drivers (Essl et al. 2011; Pyšek et al. 2010b).

The interpretation of our results (e.g., temperature effect), limited by potential source of error due to the coarse and unequal grain size of our study units, was improved by comparing the separate species-temperature relationship for each climatic requirements group. To this aim, only northern Holarctic alien plant species show a significant negative relationship with temperature. The contrasting influence of temperature is also supported by the analysis of species composition. Temperature affects assemblage differentiation in alien plants, separating northern Holarctic alien plant species from Mediterranean and tropical-subtropical alien species. Since temperature may be

considered as proxy for spatial heterogeneity (i.e., lower temperature indicates higher spatial heterogeneity and then habitat diversity), administrative districts having a broader elevational gradient show a greater number of northern Holarctic alien plants. Among them, subalpine and montane species had higher richness than in other bioclimatic origins (Fig. 2). Holarctic species, besides being better adapted to colder environment than Mediterranean and tropical species, seem to show a wider distribution along the elevational gradient, a broader climatic tolerance and the capability to grow across a wide environmental range. For instance, Seipel et al. (2012) showed a broad climatic plasticity for Eurasian alien species (i.e., a subset of northern Holarctic alien plants) that they observed not only in several mountains around the world but also along the entire elevational gradient within those regions. Indeed, most potentially invasive plants of higher elevations in

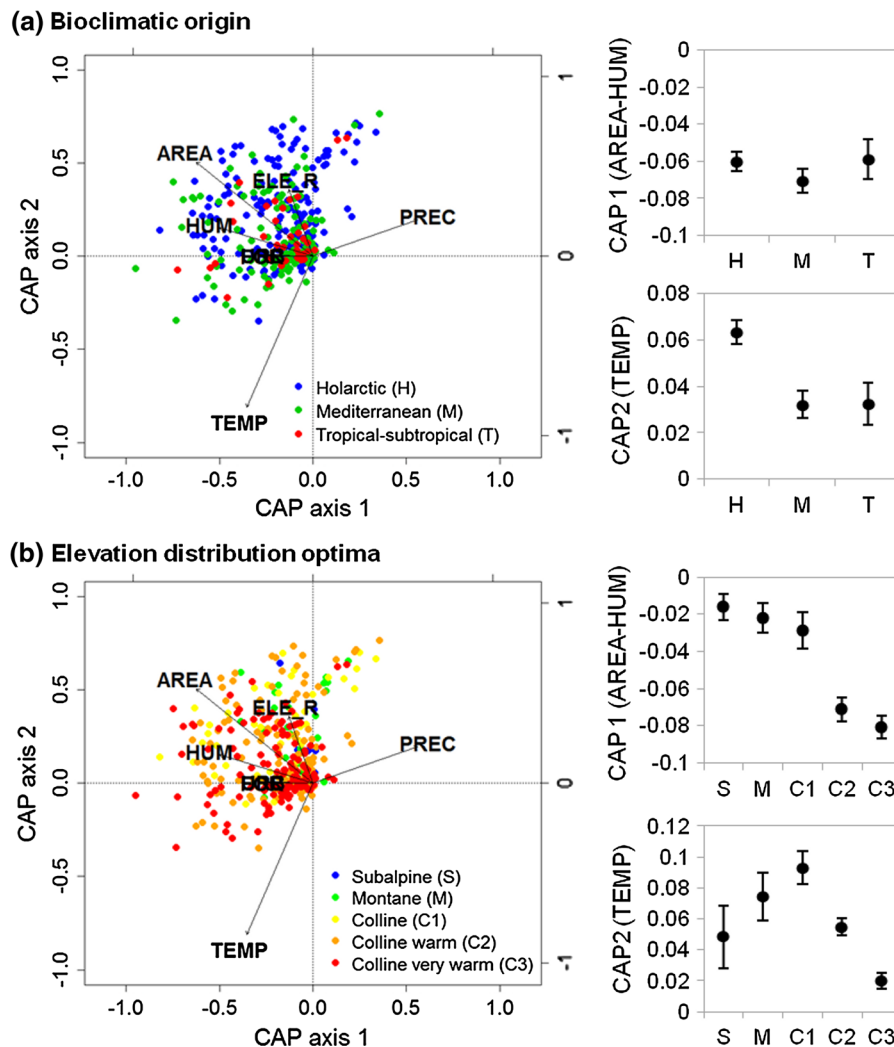


Fig. 5 Constrained Analysis of Principal Coordinates (CAP) ordination for the alien species composition, based on Jaccard dissimilarity index: **a** species are grouped according their bioclimatic origin and **b** according their elevational distribution. CAP axes 1 and 2 explain 13.1 and 10.1 % of the floristic variance, respectively. Explanatory variables are indicated by arrows, while species scores by dots. Plots on the right illustrate

score mean (\pm SE) distribution of alien species grouped according (a) bioclimatic origin (*H*, northern Holarctic; *M*, Mediterranean; *T*, tropical-subtropical) and (b) elevational distribution (*S*, subalpine; *M*; montane; *C1*, colline; *C2*, warm colline; *C3*, very warm colline) along CAP axes 1 and 2. CAP axis 1 was strongly associated with area and human population, while CAP axis 1 with temperature

the European Alps are almost all northern Holarctic species (c. 80 %; Kueffer 2010). Preventive regulation of these potentially mountain invaders should be taken in order to avoid their dispersal (Alexander et al. 2011; Marini et al. 2013; McDougall et al. 2011a, b). Alien plant species introduced from warmer regions, though, show no dependence to spatial heterogeneity (i.e., neutral pattern with temperature), despite having a significant species-area relationship. This could confirm that human pressures become more important in

determining the distribution of these alien plants, especially tropical species.

Precipitation has a negative influence on thermophilic alien species, in contrast to observations at the European level (Lambdon et al. 2008), even though the same trend has been reported as well, with more non-native species in warmer and drier sectors (Gassó et al. 2009). This suggests that thermophilic species are more successful invaders where environmental conditions are not excessively harsh (e.g. at low

elevations), which are also those most urbanized, such as the Southern Alps.

General patterns

Our models indicate that alien plant species distribution is affected by spatial heterogeneity, anthropogenic disturbance and climatic constraints, with area as the most important predictor of alien plants distribution. Surprisingly, we found a negative relationship between temperature, precipitation and alien species richness. Previously local-scale gradient studies (Alexander et al. 2011; Dainese and Poldini 2012; Marini et al. 2009) found instead that cold temperatures limit alien species invasion in mountain regions. At continental-scale, Lambdon et al. (2008) found that the number of naturalized neophytes in European countries was determined mainly by the interaction of temperature and precipitation and it increased with increasing precipitation, but only in climatically warm and moderately warm regions. Our contrasting pattern may be due to an artefactual delineation of the administrative districts in the Alps that could hide a species-area relationship, but also a species-habitat diversity relationship. On one hand, area and temperature are negatively correlated and this is due to the distribution of temperature/elevation across the different administrative districts (i.e., larger administrative districts tend to have a smaller percentage of warm/lowland territory, but a higher percentage of cold/highland territory than smaller districts; see Appendix 3 in supplementary material). On the other hand, we found a negative correlation between temperature and urbanisation with elevational range, while a positive correlation was found between precipitation and elevation range. This indicates that lower temperature, less urbanisation, and higher precipitation do not characterize districts at higher elevation, but districts that are situated in the central Alps where they include valleys up to high above the treeline. Instead the districts on the fringe areas of the Alps (i.e., especially the southern) are those most urbanized and have lower elevational gradients. This means that districts with lower temperature include broader elevational gradient and thus higher habitat diversity. Therefore, our study suggests that spatial heterogeneity has a direct influence on the distribution of alien species in the Alps. Hence, heterogeneous environments would provide more niche opportunities

for invaders (i.e., promoting both establishment and species coexistence), than homogeneous environments where the invader would need to be a superior competitor to outcompete the resident species (Melbourne et al. 2007).

Also, our study confirms the importance of anthropogenic disturbance in driving alien plants, as already found at local scale (Dainese and Poldini 2012; Marini et al. 2012, 2009) and continental-scale (Essl et al. 2011; Pyšek et al. 2010b). However, such studies highlighted a strong covariation between climate and human factors that makes it difficult to separate their individual effects. This correlation among the abiotic and anthropogenic factors was found also in our study, although partly due an artefactual delineation of the administrative districts. Anyway, the results confirm the importance of human-impact factors and environmental filtering to drive the distribution of alien plant species in mountain regions (Marini et al. 2012, 2013; Seipel et al. 2012).

Furthermore, our results confirm that forests may act as a potential constrain of alien plant invasion in the Alps (Martin et al. 2009; Matlack and Schaub 2011). Indeed, most alien species are shade-intolerant weedy species unsuited to forest communities (Martin et al. 2009), while the shade-tolerant examples are often propagule-limited in the early stages of invasion (Martin and Marks 2006). However, not all the alien plants are unsuited to forest communities. For instance, the same authors indicated some alien plant species that are likely to colonize and persist under a closed canopy in temperate forests, such as *Impatiens glandulifera*, *I. parviflora*, and *Reynoutria japonica* already well established in the Alps (Siniscalco et al. 2011).

However, one potential limitation of our study is the coarse and unequal grain size of our study that could affect in the explanatory models, although previously studies have shown little effect (Keil and Hawkins 2009; Nogués-Bravo and Araújo 2006). In particular, Keil and Hawkins (2009) found similar results comparing the parameters estimated by models using unequal sampling units (countries) compared to grids of comparable sample size. All this evidence could be context dependent, due to the artificial configuration of European Alps administrative districts, but also because many invasive species are not in equilibrium with the environment in the invaded range (Guisan and Thuiller 2005; Gassó et al. 2012).

For instance, the stage of the invasion process may have a profound influence on species distribution by affecting the extent to which occurrence observations match the species environmental niche (Václavík and Meentemeyer 2012; Gassó et al. 2012). To this aim, residence time (i.e., the time since the introduction of a taxon to a new area) could be used to account for non-equilibrium spatial distribution of alien plants (Dainese and Poldini 2012; Pyšek and Jarosik 2005; Williamson et al. 2009). However, differences in the residence time of individual species in the study region could not be accounted for at the scale studied because of data availability issues. Despite these potential limitations, we consider our results reasonable useful to obtain a first picture of the distribution of alien plants and the related drivers in the whole region of the European Alps.

Conclusion

Although alien plants in the European Alps show a relatively restricted distribution and most of them are adapted to warmer climatic conditions, their relative restricted distribution may increase in the future. However, some regions in the Alps are already more invaded (e.g., the Southern Alps where the nearby Po Plain can act as further source of alien plants). Other regions, therefore, would profit from early warnings to prevent future invasions (McDougall et al. 2011a, b). Considering bioclimatic origin, our study can aid in identifying potentially invasive species in a more regional setting. This is even more important given that the prevention of invasions was recognized as more cost-effective than eradication or control (Leung et al. 2002).

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References

- Aeschmann D, Lauber K, Moser DM et al (2004) Flora alpina. Zanichelli, Bologna
- Agrawala S (2007) Climate change in the European Alps: adapting winter tourism and natural hazards management. Organisation for economic Co-operation and development (OECD), Paris
- Alexander JM, Kueffer C, Daehler CC et al (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proc Natl Acad Sci USA* 108:656–661
- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3:52–66
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511–525
- Baayen RH (2011) languageR: Data sets and functions with “Analyzing Linguistic Data: A practical introduction to statistics”. R package version 1.4. <http://CRAN.R-project.org/package=languageR>
- Barni E, Bacaro G, Falzoi S et al (2012) Establishing climatic constraints shaping the distribution of alien plant species along the elevation gradient in the Alps. *Plant Ecol* 213:757–767
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using Eigen and S4 classes. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>
- Bätzing W (2005) Die Alpen: Geschichte und Zukunft einer europäischen Kulturlandschaft, 3rd edn. Beck, Munich
- Becker T, Dietz H, Billeter R et al (2005) Altitudinal distribution of alien plant species in the Swiss Alps. *Perspect Plant Ecol Evol Syst* 7:173–183
- Böhm R, Auer I, Brunetti M et al (2001) Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. *Int J Climatol* 21:1779–1801
- Chytrý M, Jarosik V, Pyšek P et al (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541–1553
- Dainese M, Bragazza L (2012) Plant traits across different habitats of the Italian Alps: a comparative analysis between native and alien species. *Alp Bot* 122:11–21
- Dainese M, Poldini L (2012) Does residence time affect responses of alien species richness to environmental and spatial processes. *NeoBiota* 14:47–66
- Davies KF, Chesson P, Harrison S et al (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86:1602–1610
- de Albuquerque FS, Castro-Diez P, Rueda M et al (2011) Relationships of climate, residence time, and biogeographical origin with the range sizes and species richness patterns of exotic plants in Great Britain. *Plant Ecol* 212:1901–1911
- Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. *J Appl Ecol* 48:1374–1380
- Elton CS (1958) The ecology of invasions by plants and animals. Methuen, London
- Essi F, Dullinger S, Rabitsch W et al (2011) Socioeconomic legacy yields an invasion debt. *Proc Natl Acad Sci USA* 108:203–207
- Fletcher TD (2010) QuantPsyc: quantitative psychology tools. R package version 1.4. <http://CRAN.R-project.org/package=QuantPsyc>

- Freckleton RP (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J Anim Ecol* 71:542–545
- Frei C, Schär C (1998) A precipitation climatology of the Alps from high-resolution rain-gauge observations. *Int J Climatol* 18:873–900
- Gassó N, Sol D, Pino J et al (2009) Exploring species attributes and site characteristics to assess plant invasions in Spain. *Divers Distrib* 15:50–58
- Gassó N, Thuiller W, Pino J et al (2012) Potential distribution range of invasive plant species in Spain. *NeoBiota* 12:25–40
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Haider S, Alexander J, Dietz H et al (2010) The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. *Biol Invasions* 12:4003–4018
- Hanspach J, Kühn I, Pyšek P et al (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspect Plant Ecol Evol Syst* 10:241–250
- Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Hulme PE (2008) Contrasting alien and native plant species–area relationships: the importance of spatial grain and extent. *Glob Ecol Biogeogr* 17:641–647
- Hulme PE (2011) Addressing the threat to biodiversity from botanic gardens. *Trends Ecol Evol* 26:168–174
- Jakobs G, Kueffer C, Daehler CC (2010) Introduced weed richness across altitudinal gradients in Hawai'i: humps, humans and water-energy dynamics. *Biol Invasions* 12:4019–4031
- Keil P, Hawkins BA (2009) Grids versus regional species lists: are broad-scale patterns of species richness robust to the violation of constant grain size? *Biodivers Conserv* 18:3127–3137
- Kueffer C (2010) Alien plants in the Alps: status and future invasion risks. In: Price MF (ed) *Europe's ecological backbone: recognising the true value of our mountains*. European Environment Agency (EEA), Copenhagen, pp 153–154
- Kühn I, Klotz S (2006) Urbanization and homogenization—comparing the floras of urban and rural areas in Germany. *Biol Conserv* 127:292–300
- Lambdon PW, Pyšek P, Basnou C et al (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80:101–149
- Landolt E (2010) *Flora indicativa: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Verlag Haupt, Bern
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- Leung B, Lodge DM, Finnoff D et al (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc R Soc Lond B Biol Sci* 269:2407–2413
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol Lett* 7:975–989
- Marini L, Gaston KJ, Prosser F et al (2009) Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Glob Ecol Biogeogr* 18:652–661
- Marini L, Battisti A, Bona E et al (2012) Alien and native plant life-forms respond differently to human and climate pressures. *Glob Ecol Biogeogr* 21:534–544
- Marini L, Bertolli A, Bona E et al (2013) Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Glob Ecol Biogeogr* 22:450–460
- Martin PH, Marks PL (2006) Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). *J Ecol* 94:1070–1079
- Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front Ecol Environ* 7:142–149
- Matlack GR, Schaub JR (2011) Long-term persistence and spatial assortment of nonnative plant species in second-growth forests. *Ecography* 34:649–658
- McDougall KL, Alexander JM, Haider S et al (2011a) Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. *Divers Distrib* 17:103–111
- McDougall KL, Khuroo AA, Loope LL et al (2011b) Plant invasions in mountains: global lessons for better management. *Mt Res Dev* 31:380–387
- Melbourne BA, Cornell HV, Davies KF et al (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol Lett* 10:77–94
- Nagy L (2006) European high mountain (alpine) vegetation and its suitability for indicating climate change impacts. *Proc R I Acad* 106:335–341
- Nogués-Bravo D, Araújo MB (2006) Species richness, area and climate correlates. *Glob Ecol Biogeogr* 15:452–460
- Oksanen J, Blanchet F, Kindt R et al (2011) *vegan: community ecology package*. R package version 2.0-2. Available at <http://CRAN.R-project.org/package=vegan>
- Pauchard A, Kueffer C, Dietz H et al (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Front Ecol Environ* 7:479–486
- Petitpierre B, Kueffer C, Broennimann O et al (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science* 335:1344–1348
- Pyšek P, Jarosik V (2005) Residence time determines the distribution of alien plants. In: Inderjit S (ed) *Invasive plants: ecological and agricultural aspects*. Birkhäuser Verlag, Basel, pp 77–96
- Pyšek P, Bacher S, Chytrý M et al (2010a) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Glob Ecol Biogeogr* 19:317–331
- Pyšek P, Jarošík V, Hulme PE et al (2010b) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proc Natl Acad Sci USA* 107:12157–12162

- Rejmánek M et al (1989) Invasibility of plant communities. In: Drake J, diCastrì F, Groves R (eds) *Biological invasions: a global perspective*. Wiley, New York, pp 369–388
- Seipel T, Kueffer C, Rew LJ et al (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. *Glob Ecol Biogeogr* 21:236–246
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Siniscalco C, Barni E, Bacaro G (2011) Non-native species distribution along the elevation gradient in the western Italian Alps. *Plant Biosyst* 145:150–158
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/>
- Václavík T, Meentemeyer RK (2012) Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Divers Distrib* 18:73–83
- Von Holle B, Delcourt HR, Simberloff D (2003) The importance of biological inertia in plant community resistance to invasion. *J Veg Sci* 14:425–432
- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Ann Rev Ecol Evol Syst* 36:519–539
- Williamson M (1996) *Biological invasions*. Chapman & Hall, London
- Williamson M, Dehnen-Schmutz K, Kühn I et al (2009) The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Divers Distrib* 15:158–166
- Zobel M (1997) The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol Evol* 12:266–269