RESEARCH PAPER

Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients

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ABSTRACT

Aim We tested whether the species–energy and species–human relationships vary between native and both naturalized and casual alien species richness when other environmental variables had been taken into account.

Location Trento Province, a region (*c.* 6200 km^2) on the southern border of the European Alps (Italy), subdivided into 156 contiguous (*c.* 37.5 km^2) cells and ranging in elevation from 66 to 3769 m.

Methods Data were separated into three subsets, representing richness of natives, naturalized aliens and casual aliens and separately related to temperature, human population and various environmental correlates of plant species diversity. We applied ordinary least squares and simultaneous autoregressive regressions to identify potential contrasting responses of the three plant status subsets and hierarchical partitioning to evaluate the relative importance of the predictor variables.

Results Variation in alien plant species richness along the region was almost entirely explained by temperature and human population density. The relationships were positive but strongly curvilinear. Native species richness was less strongly related to either factor but was positively related to the presence of calcareous bedrock. Native species richness had a decelerating positive relationship with temperature ($R^2 = 55\%$), whereas naturalized and casual aliens had a positive accelerating relationship explaining 86% and 62% of the variation in richness, respectively. Native species richness had a positive decelerating relationship with population density ($R^2 = 42\%$), whilst both alien subsets had a positive accelerating relationship.

Main conclusions Alien species richness was higher in areas with the most rich and diverse assemblages of native species. Areas at high altitudes are not especially prone to alien invasion due to energy constraints, low propagule pressure and disturbance, even considering a potential increased in temperature. Thus, if we consider future environmental change, we should expect a stronger response of aliens than natives in the currently warm, urbanized, low-altitude areas than in cold, high-altitude areas where human population density is low.

Keywords

Biological invasion, climate change, disturbance, elevation, exotic, homogenization, land-use change, propagule pressure, urbanization, weeds.

INTRODUCTION

The invasion of alien plants frequently alters the community dynamics of native species, imposing economic costs, enhancing local extinction rates and promoting biological homogenization (Hulme, 2003; McKinney, 2006; Lambdon *et al.*, 2008a). Recent advances in biogeographical research indicate that the likelihood of biological invasions at the macro scale might be reasonably well predicted simply from knowledge of availability of environmental energy and human impact, although the

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interaction between these two sets of drivers remains unclear (Evans & Gaston, 2005; Evans *et al.*, 2005). As current global change is characterized by general temperature warming and increasing human pressure on many natural ecosystems in temperate countries (Gaston, 2005), the question of whether native and alien plant species respond differently to these processes is crucially important for gaining insights into future trends in plant invasions at the macro scale. In this context, altitudinal gradients in species richness are a suitable model template for large-scale studies, as over relatively short distances they encompass several clines in climatic (energy) and environmental factors, such as land-cover dynamics, net primary productivity and geometric constraints (Rahbek, 2005; Nogués-Bravo *et al.*, 2008; Pauchard *et al.*, 2009).

A positive correlation between environmental energy availability and native plant species richness has been frequently observed along latitudinal (Currie, 1991; Hawkins *et al.*, 2003) and altitudinal gradients (Lomolino, 2001; Moser *et al.*, 2005; Marini *et al.*, 2008). The number of alien plant species in temperate regions often shows similar general patterns (Becker *et al.*, 2005; Pyšek & Richardson, 2006; Lambdon *et al.*, 2008b; Pauchard *et al.*, 2009). However, it is not clear whether the shape and the strength of the species–energy relationship differ between native and alien species. Such knowledge is essential to predict the scope of future floristic homogenization as a result of climate change. Few studies have either documented such comparisons or investigated the potential for humans to alter them (but see Chown *et al.*, 2005; Evans & Gaston, 2005; Evans *et al.*, 2005). Those studies that have done so have primarily considered birds, whereas none has yet dealt with plant invasions.

In addition, human population density may act to increase propagule pressure as well as environmental disturbance and is recognized as a key factor in alien plant invasions since it augments the chances of alien plant establishment, persistence and invasion (Rouget & Richardson, 2005). The propagule pressure and the species pool of alien species depend strongly on the distribution, activities and movements of humans (Becker *et al.*, 2005; Hulme *et al.*, 2008; Hulme, 2009a). Disturbance is also a key factor providing suitable ecological niches for establishment after propagule arrival (Woitke & Dietz, 2002). However, human population distribution is strongly related to energy availability (Gaston, 2005) and thus these two environmental drivers need to be analysed simultaneously.

Temperate mountain areas characterized by marked elevation gradients provide suitable model systems for disentangling the effects of energy availability and human impact on alien and native plant species richness, and the results might help to shed light on ecological processes acting at larger spatial scales such as along latitudinal gradients. Ambient energy (quantified as temperature) is expected to change along altitudinal gradients at a spatial scale that is often comparable to the dispersal abilities of plant species (Willis & Hulme, 2002; Ross *et al.*, 2008). Furthermore, mountain areas are becoming more urbanized across the globe with increasing settlements and transport networks at higher elevations (Price, 2006). The expected consequence of these processes is to increase propagule pressure and human disturbance, and to provide more favourable thermal conditions and, as a result, enhance the likelihood of alien plant invasions (Pauchard *et al.*, 2009). However, it is not clear which part of the gradients might be more or less affected by these changes (e.g. low-altitude versus high-altitude areas) or at which scale these processes might work.

At both regional (Hulme, 2008) and national (Hulme, 2009b) spatial scales, similar environmental drivers can influence alien and native plant species richness differently and thus these taxa are not expected to respond similarly to current environmental change. As we expect that the establishment and persistence of alien plants will reflect the interaction between energy availability (Willis & Hulme, 2002) and human impact (Becker *et al.*, 2005; Botham *et al.*, 2009), we tested whether the species–energy and species–human relationships vary between native and alien species along altitudinal gradients. Along with these two sets of predictors we also tested several environmental variables known as potential drivers of plant species diversity at the biogeographical scale.

METHODS

Study area

The study area was the Province of Trento (north-east Italy), an area of 6207 km^2 (WGS84: N 45°43.8′–46°28.3′, E 10°31.9′–11°53.4′) on the southern border of the European Alps. The elevation range varies from 66 to 3769 m a.s.l. The local climate depends primarily on altitude (Table 1), and only secondarily on latitude, varying from sub-Mediterranean conditions in the southern and central parts to continental conditions in the inner valleys.

Data on alien and native plant species distributions

Information on the distribution of plant species was extracted from a floristic inventory of the Province of Trento (CFT project; Prosser & Festi, 1993), which contained over 600,000 records in 2006. The province was subdivided into a regular grid of 228 cells (sampling units for the surveys), each of 3′ × 5′ (arcmin), corresponding to *c.* 35.7 km^2. The sampling effort in the different cells was related to the saturation level of the species accumulation curves, i.e. a cell was explored until the number of species tended to saturation. As with all taxonomic inventories, the counts are inevitably incomplete due to the subjectivity of botanists involved in the inventory, but we assumed that this error should be negligible and similar in each cell. For the purpose of this study, we omitted obvious edge cells and used only the 156 cells with more than 80% of their area within the borders of the Province of Trento. The species richness data were gathered between 1991 and 2005 and separated into three plant status subsets following the definition of Richardson *et al.* (2000). The first subset comprised alien naturalized species, defined as those which invaded the study area after 1500 and that reproduce consistently to sustain populations over many life cycles without (or despite) human intervention. The

Table 1 Descriptive statistics and abbreviations of the explanatory variables calculated for each of the 156 cells in the Province of Trento (Italy), and used in the analyses.

Variables name and explanation		Unit	Mean	Min	Max
Environmental energy					
TEM	Annual average of mean temperatures	°C	6.55	–0.15	12.65
RAD	Cumulative radiation in May	kWh m^{-2}	170.6	154.3	191.8
Propagule pressure and disturbance					
POP	Number of inhabitants		3069	20	80,946
ROAD	Road density	km	25.25	0	94.39
RIVER	River density	km	43.61	6.17	106.53
URB	Total area covered by built-up elements	%	3.44	0	34.46
AGR	Area covered by agricultural area	%	6.13	0	50.10
Other environmental factors					
CAL	Area covered by calcareous bedrock	%	44.0	0	100
GRA	Area covered by grasslands	%	13.3	0.1	46.6
FOR	Area covered by forests	%	61.2	7.0	89.3
PRE	Mean annual precipitation	mm $year^{-1}$	1010	769	1277
SLO	Mean slope	%	24.87	12.0	35.30
TWI	Topographical wetness index	–	7.19	6.38	8.37
ELE-H	Elevation range (maximum-minimum)	m	1529	650	2230
LC-H	Shannon index of land-cover types	–	0.95	0.38	1.42
BED-H	Shannon index of bedrock types	–	0.545	0	1.27

second subset included casual alien plant species that invaded the study area after 1500 without forming self-reproducing populations and thus rely on repeated introductions for their persistence. The remainder were considered as comprising native species.

Explanatory variables

Environmental energy

Environmental energy was quantified as the mean annual temperature (TEM) (Currie, 1991). The mean value was obtained by averaging the values within the cells. The data were retrieved from continuous raster-based climatic maps with a resolution of 100 × 100 m (1990–99). The climatic data were interpolated using 64 stations located throughout the province by Sboarina & Cescatti (2004). We also quantified radiation (RAD) using a digital elevation model (DEM) with a grid size of 25 × 25 m.

Human impact variables

We quantified the number of inhabitants within each cell (POP) using the human population density data from CORINE 2000 (http://www.eea.europa.eu/). We measured the degree of urbanization as the cover of built-up area (URB) (buildings, streets and other artificial land uses), and quantified road density (ROAD) and river density (RIVER) as further predictors. We also determined the proportion of agricultural land (AGR) as a further predictor of human disturbance and the proportion of grasslands (GRA) and forest (FOR). These land-cover variables were derived from a vector-based land-use map (SIAT, Servizio Urbanistica e Tutela del Territorio, Trento, Italy; http://www.territorio.provincia.tn.it/).

Further environmental predictors

Using the DEM we quantified mean slope (SLO) and elevation (ELE) within each cell. Bedrock variables were retrieved from the geological map (1:200.000) of the province. We classified each bedrock type into four main classes: (1) sedimentary calcareous bedrock (CAL), (2) volcanic and metamorphic acid bedrock (ACI), (3) volcanic basic bedrock (BAS), and (4) mixed debris (DEB). Due to high collinearity between these bedrock variables, we included only CAL in further analyses. Along with temperature, we included the total precipitation (PRE) as an indicator of water availability using data from Sboarina & Cescatti (2004). As plant–water relationships are strongly dependent on the availability of soil water, we quantified soil moisture using the topographic wetness index (TWI). The TWI was calculated from the DEM using SAGA GIS (version 1.2, available at http://www.saga-gis.org/). To provide measures of environmental heterogeneity within each cell, we derived habitat heterogeneity as the Shannon diversity index calculated on the land-cover classes (LC-H) and on the bedrock types (BED-H). The Shannon index was computed using FRAGSTATS version 3.3 (http://www.umass.edu/landeco/index.html). We further calculated topographical heterogeneity (ELE-H) as the elevation range (the difference between the maximum and the minimum altitude).

Data analysis

We examined correlations between all the variables chosen in this study to evaluate the degree of collinearity. In order to detect the shape and the strength of the relationships between species richness and both temperature and human population density, we performed general linear models [ordinary least squares (OLS) regression] of species richness of the three plant status guilds and the overall level of invasion (ratio between total aliens and natives) against TEM and POP, separately. Subsequently, we tested all the environmental variables in a multiple regression model to account for other important correlates of species richness. In all cases, quadratic terms were tested along with the linear terms to detect nonlinear relationships. We log-transformed POP and URB to improve model error distributions. In the multiple models, we performed a backward selection of the variables following the procedure suggested by Crawley (2007). The residuals of our OLS models exhibited low and slightly significant spatial autocorrelation, indicating the presence of a spatially structured process not explained by the variables included in the model. To examine the potential influence of residual spatial autocorrelation on parameter estimates, we used simultaneous autoregressive models (SAR) and the resulting standardized SAR coefficients are presented along with the OLS coefficients (Kühn, 2007). The SAR was performed in the SAM package (version 3.0; Rangel *et al.*, 2006). In all analyses, we standardized the response variables to mean 0 and standard deviation 1 to make the parameter estimation comparable. We omitted one cell from the analysis as an outlier (Cook's distance > 1.5).

In addition to OLS and SAR models, hierarchical partitioning (HP) was also used to determine the relative importance of the variables most likely to affect variation in species richness (Chevan & Sutherland, 1991). HP allows the joint consideration of all the possible models in a multiple regression attempting to identify the most likely causal factors. This analysis splits the variation explained by each explanatory variable into a joint effect with the other explanatory variables and an independent effect not shared with any other variable. HP was conducted using the 'Hier.Part' package (version 0.5–1; Mac Nally & Walsh, 2004) implemented in R version 2.5.1 (R Development Core Team, 2004). As HP needs monotonic relationships between response variables and explanatory variables, we transformed the explanatory variables when appropriate to improve the linearity of the relationships. We tested for independent effects using a randomization routine ($n = 200$), which gives Z-scores for the generated distribution of randomized independent contributions and a level of statistical significance (P) based on this score.

RESULTS

The mean number of species per cell was 801, 33 and 3 for natives, naturalized aliens and casual aliens, respectively. The level of invasion varied between 0 and 14%, with a mean of 4%. The number of native species was correlated positively with the number of both naturalized ($r_s = 0.66$, $P < 0.01$) and casual alien species ($r_s = 0.43$, $P < 0.01$). We found relatively high collinearity between temperature and the human-related variables (Table 2). High positive correlation occurred between temperature, human population density, proportion of urban elements, road density and agricultural land, i.e. human settlements and agricultural land were mainly concentrated in the lowland areas with high energy availability.

Native and alien species richness were strongly related to TEM, although the shape and the strength of the relationships were different (Fig. 1a–c). All relationships were nonlinear. Native species richness had a decelerating positive relationship with TEM which explained 55% of the total variation. Naturalized and casual alien species richness had a positive accelerating relationship with temperature, explaining 86% and 63% of the total variation, respectively. As a result, the level of invasion also had a positive accelerating relationship with temperature (Fig. 1d), thus it was higher in warmer climes. Considering POP, we found similar patterns to those observed for temperature (Fig. 1e–h). Although POP was log-transformed, the relationship between alien species richness and POP was still nonlinear with a positive accelerating trend (i.e. if POP was not transformed, the relationship would be exponential). The proportion of variation explained by POP was always lower than that explained by TEM.

On testing TEM and POP in a multiple regression model with all the environmental predictors, the two factors remained highly significant for natives, naturalized aliens, casual aliens and the level of invasion, although with some important differences between the three different plant status subsets (Table 3). The model for native species richness explained less variation (70%) than that for naturalized alien species richness (90%), while the model for casual aliens explained the least variation (67%). For natives, the model retained CAL along with POP and TEM. For naturalized aliens, the model included TEM, POP and SLO. For casual aliens, the model included POP, TEM and AGR. Finally, the level of invasion was significantly related to POP, TEM, CAL and SLO, explaining 90% of the total variation. Results from OLS and SAR models were very similar in terms of selected variables, parameter estimates and proportions of explained variation (Table 3).

The results of the HP analysis confirmed that TEM and POP were the most important variables explaining large fractions of variation for all plant status subsets, although with contrasting results between natives and aliens. For natives, the relative importance of TEM, POP and CAL was very similar with equal independent effects (*c.* 17%). For naturalized aliens, TEM showed the largest independent effect (> 40%), followed by POP (*c.* 25%), while SLO had a small independent effect. For casual aliens, the patterns for TEM and POP were similar to those found for naturalized aliens; AGR had smaller relative importance (Fig. 2c). For the degree of invasion, the relative importance of the variables was very similar to that found for naturalized aliens; CAL had a very small independent effect (Fig. 2d).

DISCUSSION

The distribution of alien plant species and the level of invasion along our alpine elevation gradient were mainly determined by

Table 2 Pearson correlations between species richness of alien naturalized, alien causal and native species with the factors tested in this study.

	Natives	Naturalized aliens	Casual aliens	Aliens/natives	TEM	RAD	Log[POP]	ROAD	RIVER	log(URB)	AGR	CAL	GRA	FOR	PRE	SLO	TWI	ELE-H	LC-SH
Naturalized aliens	0.66																		
Casual aliens	0.43	0.81																	
Aliens/natives	0.55	0.98	0.84																
TEM	0.68	0.90	0.67	0.89															
RAD	–0.34	–0.44	–0.33	–0.41	–0.50														
Log[POP]	0.67	0.86	0.67	0.85	0.88	–0.32													
ROAD	0.48	0.80	0.66	0.80	0.82	–0.25	0.82												
RIVER	0.34	0.59	0.38	0.61	0.60	–	0.67	0.58											
Log[URB]	0.55	0.84	0.68	0.85	0.82	–0.25	0.94	0.88	0.66										
AGR	0.32	0.70	0.59	0.71	0.70	–0.34	0.64	0.69	0.51	0.68									
CAL	0.55	0.23	–	–	0.36	–0.45	–	–	–	–	–								
GRA	–0.23	–0.51	–0.42	–0.52	–0.55	0.61	–0.37	–0.38	–0.26	–0.37	–0.51	–							
FOR	0.45	–	–	–	0.36	–	0.32	–	–	–	–0.22	–	–						
PRE	–	–0.30	–0.30	–0.33	–0.29	–	–0.36	–0.29	–	–0.37	–0.37	–	–	–					
SLO	–0.31	–0.62	–0.57	–0.65	–0.65	–	–0.70	–0.73	–0.50	–0.77	–0.66	–	–	–	0.46				
TWI	0.24	0.52	0.38	0.51	0.38	–0.32	0.46	0.42	0.49	0.53	0.45	–	–0.31	–	–	–0.31			
ELE-H	–0.26	–	–	–	–	–	–	–	–0.21	–	–	–	–	–	–	–	–0.14		
LC-SH	0.21	0.44	0.44	0.43	0.32	–	0.42	0.42	0.24	0.49	0.56	–	0.06	–0.49	–0.29	–0.47	0.48	–0.32	
BED-SH	0.35	0.33	0.23	0.32	0.32	–	0.50	0.37	0.34	0.51	0.29	–	–	–	–0.29	–0.38	0.33	–0.32	0.31

Only significant values are shown ($P < 0.01$). See Table 1 for variable definition.

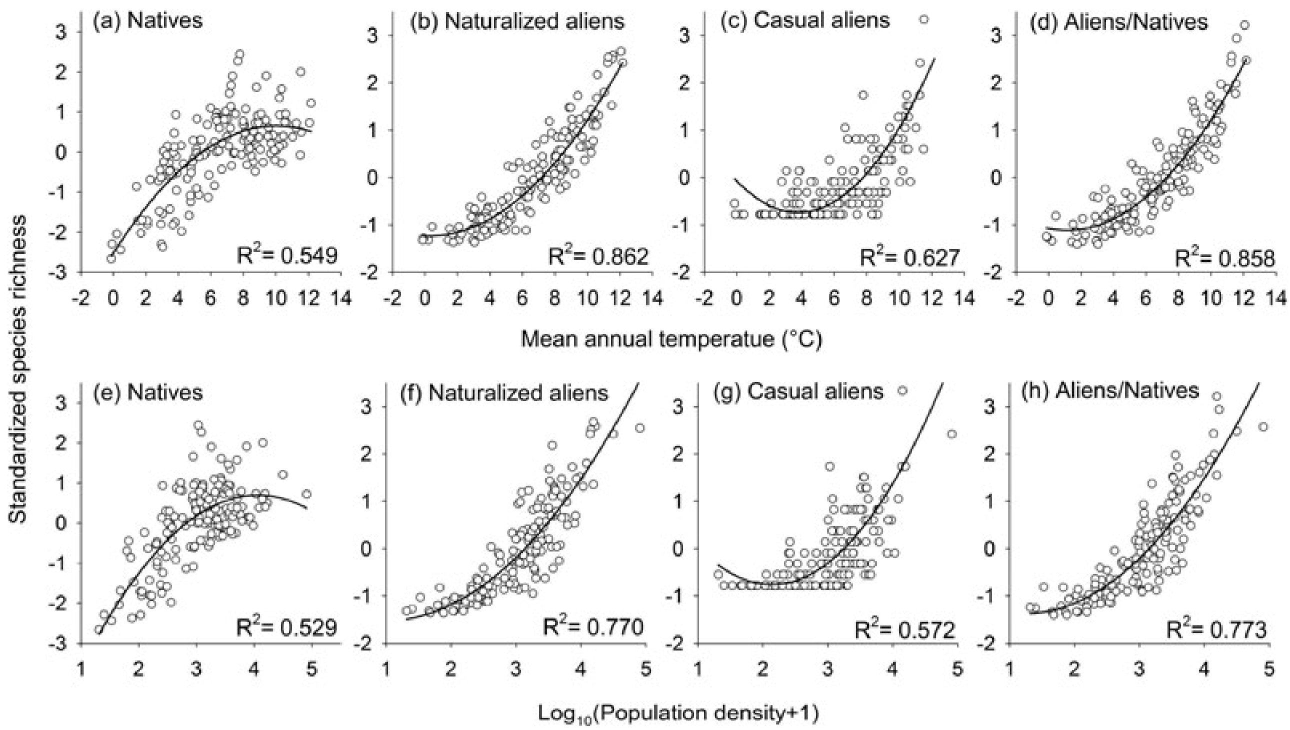

Figure 1 Relationship from ordinary least squares (OLS) regression between energy availability and species richness of (a) natives, (b) naturalized aliens, (c) casual aliens, and for (d) the level of invasion. Relationship between human population and (e) natives, (f) naturalized aliens, (g) casual aliens, and for (h) the level of invasion. All the values were standardized to mean = 0 and SD = 1. The fitted lines were obtained from a polynomial regression testing linear and quadratic terms ($P < 0.05$). One cell was excluded as an outlier (Cook's distance > 1.5).

temperature and by human population density, with a very low proportion of unexplained variation (*c*. 10%). This suggests that temperature and human population density are the key correlates of alien plant invasion, and that other environmental factors such as water availability, bedrock, habitat heterogeneity and topography do not contribute directly to shaping alien distribution at our spatial scale. The response of native species was weaker, and *c*. 30% of the variation remained unexplained suggesting that different mechanisms contribute to determining native species distribution along our elevation gradient. The shape of these relationships was also different between native and alien species richness. The level of invasion drastically increased both with temperature and human population density, posing serious conservation concerns regarding the protection of native communities in urbanized, low-elevation areas (see also McKinney, 2006). The relationships were strongly curvilinear, indicating that along the elevation gradient aliens and natives responded differently to temperature and humans according to altitude. Although naturalized and casual alien species showed similar patterns (shape of the relationships), the explained variation for casual aliens was always lower than for naturalized aliens. This result was probably caused by the transitory and sporadic occurrence of casual species whose populations can disappear after a short period of time. OLS and SAR models presented very similar results, indicating that the variables included in the OLS models almost completely removed residual spatial autocorrelation. Thus, the ecological interpretation of the models did not differ between spatial and non-spatial models.

Energy and human population density covaried strongly, as urban settlements and agricultural land were concentrated in the most thermally favourable areas. However, both factors had large independent effects suggesting the presence of separate processes controlling species richness. Our results concur with those of several authors (Chown *et al.*, 2003; Kühn *et al.*, 2004; Gaston, 2005; Pautasso, 2007; Pautasso & McKinney, 2007; Pautasso & Chiarucci, 2008) who concluded that the broad-scale positive correlations between human population, plant species richness and energy (productivity) suggest that people have preferentially settled and generally flourished in areas of high biodiversity and productivity and/or have contributed to species pools with species introductions and habitat diversification. However, these relationships are much more complex if we consider invasion dynamics and may have important consequences for understanding plant invasion in regions with steep energy gradients such as the European Alps.

The areas least vulnerable to plant invasion from the perspective of energy availability were those with a mean annual temperature below 6.0°C (areas above *c*. 1500 m), while the level of invasion drastically increased above this temperature threshold. The shape of the relationship was quite similar to that found by Becker *et al.* (2005) for alien plants in anthropogenic habitats in

Table 3 Multiple regression models [ordinary least squares (OLS) and simultaneous autoregressive models (SAR)] for native, alien naturalized and alien casual plant species richness (values standardized to mean = 0 and SD = 1) testing all the environmental predictors.

Variables	d.f.	OLS estimate	SE	*P*	OLS R^2	SAR estimate	SE	*P*	SAR R^2
Natives	**149**				**70.1**				**71.3**
Intercept		−3.607	0.312	–		−3.654	0.316	–	
TEM		0.362	0.078	< 0.001		0.400	0.078	< 0.001	
TEM^2		−0.026	0.005	< 0.001		−0.029	0.005	< 0.001	
Log[POP]		0.648	0.153	< 0.001		0.640	0.150	< 0.001	
CAL		0.025	0.005	< 0.001		0.025	0.005	< 0.001	
CAL^2		-1.62×10^{-4}	5.27×10^{-5}	0.002		-1.61×10^{-4}	5.25×10^{-5}	0.001	
Naturalized aliens	**150**				**89.5**				**90.8**
Intercept		−3.095	0.334	–		−3.041	0.343	–	
TEM		−0.168	0.045	< 0.001		−0.170	0.046	< 0.001	
TEM^2		0.031	0.003	< 0.001		0.031	0.003	< 0.001	
Log[POP]		0.613	0.091	< 0.001		0.617	0.092	< 0.001	
SLO		0.030	0.008	< 0.001		0.028	0.008	< 0.001	
Casual aliens	**150**				**66.8**				**69.0**
Intercept		−0.960	0.321	–		−0.972	0.327	–	
TEM		−0.545	0.082	< 0.001		−0.556	0.083	< 0.001	
TEM^2		0.056	0.007	< 0.001		0.057	0.007	< 0.001	
Log[POP]		0.586	0.150	< 0.001		0.599	0.151	< 0.001	
AGR		−0.019	0.008	0.020		−0.019	0.008	0.019	
Total aliens/natives	**149**				**90.0**				**91.2**
Intercept		−2.657	0.327	–		−2.615	0.333	–	
TEM		−0.153	0.046	< 0.001		−0.153	0.047	< 0.001	
TEM^2		0.032	0.003	< 0.001		0.032	0.003	< 0.001	
Log[POP]		0.524	0.091	< 0.001		0.524	0.092	< 0.001	
CAL		−0.004	0.0004	< 0.001		−0.004	0.0004	< 0.001	
SLO		0.024	0.008	0.002		0.024	0.008	0.004	

Quadratic terms were also tested to detect nonlinear relationships. One cell was excluded as an outlier (Cook's distance > 1.5).
TEM, annual average of mean temperatures; POP, number of inhabitants; AGR, area covered by agricultural area; CAL, area covered by calcareous bedrock; SLO, mean slope.

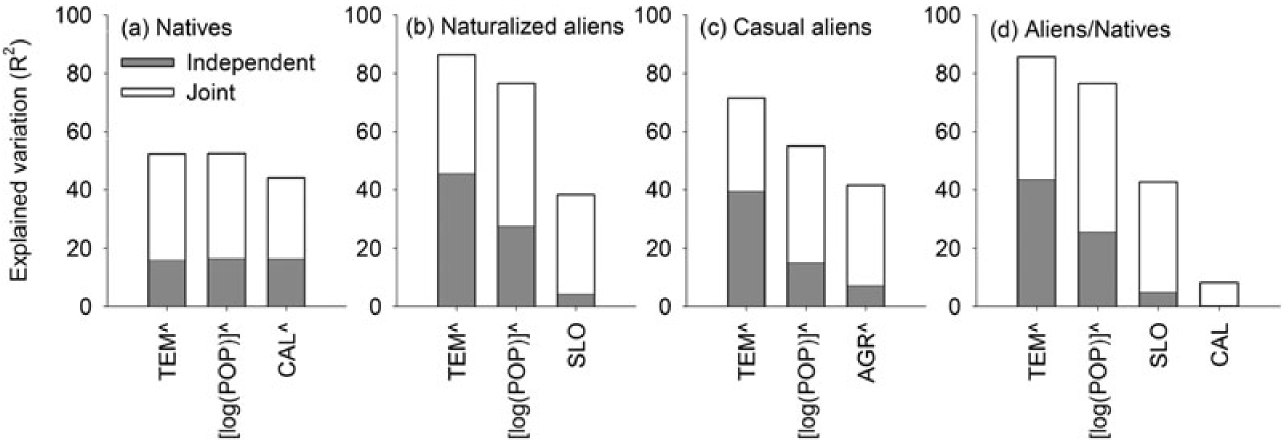

Figure 2 The independent and joint contributions (given as the percentage of the total explained variation) of each explanatory variable selected in the multiple regression model (OLS) for the species richness of (a) natives, (b) naturalized aliens, (c) casual aliens, and for (d) the overall level of invasion as estimated from hierarchical partitioning. All the variables showed significant independent effects ($P < 0.05$), resulting from the *z*-randomization procedure ($n = 999$). ^ Indicate a power transformation to increase the linearity of the relationships. TEM, annual average of mean temperatures; POP, number of inhabitants; AGR, area covered by agricultural area; CAL, area covered by calcareous bedrock; SLO, mean slope.

the Swiss Alps, and by Pyšek *et al.* (2002) for aliens in temperate nature reserves. The stronger species–energy relationship of aliens than of natives has also been documented for plants in the Australian Alps (McDougall *et al.*, 2005) and birds in Britain (Evans & Gaston, 2005; Evans *et al.*, 2005). The latter authors also demonstrated that the strong correlation between temperature and urbanization did not contribute to the observed species–energy relationship. The shape of the species–energy relationship reported here was also different, with a steeper response of aliens than natives at the upper end of the energy gradient (i.e. lowland areas). Considering species–energy relationships of naturalized aliens versus natives, a 2°C temperature change at high elevations (where TEM is *c.* 0°C) will have relatively little impact on naturalized alien plant richness but a considerable impact on native plant richness. In contrast, at low elevations (where TEM is *c.* 10°C), the reverse is true, i.e. an increase in temperature by 2°C will have negligible or possibly negative effects on native plant richness, while it will strongly increase alien richness. The nonlinearity implies that the observed species–energy relationships cannot be generalized across the altitudinal gradient. Thus, if we consider future temperature warming, we should expect a stronger response of aliens than natives in warm, low-altitude areas and the reverse in cold, high-altitude areas.

Human population density used as a proxy for propagule pressure and disturbance (Becker *et al.*, 2005; Hulme *et al.*, 2008; Botham *et al.*, 2009) has been found to explain a large proportion of variation for both natives and aliens. However, the response of naturalized alien species to human impact was stronger than for native species with an exponential relationship between human population density and naturalized alien species richness. Thus, we may expect that increases in the human population in existing high-density urban areas will have a more marked effect on alien species richness and the level of invasion than a new area of low-density human settlement. Although the relationship between human population and species richness was weaker than that with energy availability, a large proportion of variation in alien species distribution explained by temperature was shared with population density, indicating that the interplay between suitable thermal conditions and humans largely determined the observed levels of invasion.

Cover of calcareous bedrock was a further key factor increasing native species richness (see also Wohlgemuth, 1998; Moser *et al.*, 2005; Marini *et al.*, 2008). This well-known broad pattern for the native European flora has been suggested to be the result of processes such as speciation and extinction dynamics related to the prevalence of basic substrates in Europe or other potential factors confounded with calcareous bedrock (Wohlgemuth & Gigon, 2003). Although bedrock composition was very important for natives, it played no role in the alien plant species richness.

The findings of our study support the hypothesis that, at the biogeographical scale, alien species richness is higher in areas with the most rich and diverse assemblages of native species (Pyšek *et al.*, 2002; Stohlgren *et al.*, 2003; Richardson *et al.*, 2005; Simonová & Lososová, 2008) and that locally (i.e. within a cell) alien species enhanced overall species richness (see also McKinney, 2002). In our system, alien species richness is increasing and probably enhancing biological homogenization of the areas harbouring some of the most valuable native communities; these lowland regions have witnessed a recent a loss of rare native species (Marini *et al.*, 2008). Although high-altitude alpine areas were not prone to high biological invasion due to energy constraints and low propagule pressure and disturbance, the different response between native and alien species to energy and human population density suggests that we might expect an increased level of invasion, particularly in the lowlands, if mountain areas become progressively warmer and more urbanized as a result of current global change.

As the maintenance of local, native species diversity is becoming a priority conservation goal (McKinney, 2006), it is crucial to also focus conservation activities in human-dominated ecosystems, particularly those in and around urban settlements (Kühn *et al.*, 2004; Richardson *et al.*, 2005). A full understanding of the risk of biological invasion and homogenization should be incorporated into urban development and planning in relatively poorly urbanized mountain regions, as changes in land use, from agriculture to tourism, are likely to test a new suite of alien species in the natural alpine environment. Thus, the high elevation of temperate mountain ranges cannot be considered as an impervious barrier to plant invasion in the face of climate warming and increasing human pressure in the Alpine zone (McDougall *et al.*, 2005).

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