

Altitudinal distribution of alien plant species in the Swiss Alps

Thomas Becker^{a,b}, Hansjörg Dietz^{a,*}, Regula Billeter^a, Holger Buschmann^{a,c},
Peter J. Edwards^a

^a*Geobotanical Institute, Swiss Federal Institute of Technology, Universitätsstrasse 18, ETH Zentrum CHN H64, 8092 Zürich, Switzerland*

^b*Plant Ecology, Philipps University, Karl-von-Frisch-Strasse, 35032 Marburg, Germany*

^c*Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Grisebachstrasse 1a, 37077 Göttingen, Germany*

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Abstract

In summer 2003 we recorded the presence and abundance of alien plant species at 232 sites (107 railway stations and 125 road sites) along mountain passes in the Swiss Alps. The altitudinal distribution of species was related to the current abundance of the species in Switzerland and time since introduction. A total of 155 alien taxa were recorded. Numbers of species per site declined exponentially with altitude, and only a few species were found in the alpine zone (>2000 m). In contrast, species richness among comparable native taxa appeared to be nearly independent of altitude over the range investigated. Maximum altitude reached by alien species was related positively to both total area occupied in Switzerland and to time since introduction. A comparison of the results with earlier records suggests that many species, particularly those previously restricted to low or intermediate altitudes, have advanced their altitudinal limits over the past few decades. Various hypotheses are presented to explain the declining abundance of alien species with altitude: low-altitude filter effects, low propagule pressure, and genetic swamping of peripheral populations at higher altitudes. However, at present we do not have sufficient evidence to determine the relative importance of these effects. We conclude that invasion into mountain areas such as the Swiss Alps tends to proceed rather slowly, though the process may be accelerated by climatic warming. For this reason, further research to investigate the processes determining how plants invade mountain areas is urgently needed. And more generally, investigations into the distribution of alien species along strong altitudinal gradients may provide valuable insights into the mechanisms driving the spread of alien organisms.

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Introduction

Despite intensive research into the causes and consequences of biological invasion (Dietz and Steinlein, 2003), we are still far from understanding the full

complexity of the phenomenon. This is partly because so many different aspects – phylogenetic groups, communities, habitats – must be considered in developing a general theory (cf. Mack et al., 2000; Lambrinos, 2002). Faced with this situation, it seems prudent to concentrate our efforts on systems that may serve as models for a more general understanding of biological invasions. Particularly suitable are systems that are threatened but

*Corresponding author.

E-mail address: hansjoerg.dietz@env.ethz.ch (H. Dietz).

not yet heavily invaded by alien species, since these are most likely to reveal the early, dynamic stages of invasion. This is an important condition in the search for a mechanistic understanding of plant invasions, a goal that would be much harder to achieve by studying the more stable conditions after the invasion has occurred (Dietz, 2004; H. Dietz and P.J. Edwards, unpublished data). From a practical point of view, moreover, management to contain further invasions may be worthwhile in such systems, whereas it may be difficult or impossible in already heavily invaded areas (e.g. Mack, 1986; Thompson et al., 1987; Meekins and McCarthy, 1999; Sheley et al., 2000; Mack et al., 2000, and references therein; Sheley and Krueger-Mangold, 2003; Simberloff, 2003).

High mountains offer a variety of steep environmental gradients over relatively short distances (Peterson et al., 1997; Körner, 2003), and almost all alien organisms reach their distribution limits somewhere along these gradients. For this reason, mountains – especially those extending to the alpine zone – provide a useful model system for investigating invasion processes (H. Dietz and P.J. Edwards, unpublished data). However, there has been little research into plant invasions into high mountain systems, and the few studies that have been published show high variability between mountain areas in the altitudinal distribution of alien plants. For example, Wester and Juvik (1983) found a decrease in the number of both introduced and native plant species with increasing altitude in roadside habitats on Hawaii, and Tassin and Riviere (2003) note the same trend for introduced plant species in the upper part of an altitudinal transect on the tropical island of La Réunion. In contrast, Johnston and Pickering (2001) observed a high number (175) of alien plant species at subalpine altitudes above 1500 m a.s.l. in the Australian Alps. Kanehiro and Mueller-Dombois (1995) reported that in less disturbed habitats on Maui (Hawaiian Islands) alien plant species occurred mainly in more open areas at both low and high altitudes, these areas being separated by a less invaded zone of wet montane cloud forest at intermediate altitudes.

The studies that report on plant invasions into higher mountains (Wester and Juvik, 1983; Kanehiro and Mueller-Dombois, 1995; Johnston and Pickering, 2001; Tassin and Riviere, 2003; Godfree et al., 2004; Pauchard and Alaback, 2004; Underwood et al., 2004) have mostly been in Mediterranean or tropical regions. In mountainous regions of the temperate zone, growth conditions tend to become increasingly harsh with altitude, especially because of long, cold winters and short growing seasons (Imhof, 1965–1978; Körner, 2003), and we might therefore expect such regions to be less invadable.

The aim of this study was to assess the present distribution of alien plant species along altitudinal

gradients in the Swiss Alps. We go beyond the scope of most previous work in attempting both to relate the observed altitudinal patterns to potential predictor variables and to develop causal hypotheses. We ask, in particular, whether the upper altitudinal limits of introduced species can be related to (i) time of introduction, and (ii) the general abundance of the species in the region. In addition, drawing on previously published data for comparison, we ask (iii) whether alien plant species have progressed towards higher altitudinal limits during the last century. With these approaches we hoped to attain an insight into the recent progress of introduced plants in the European Alps and assess the risks of further invasion in the future.

We recorded the alien species growing at sites beside roads over mountain passes and at selected railway stations throughout Switzerland. Roadsides and railways provide favourable conditions for both dispersal and establishment of alien plant species (Wilson et al., 1992; Milton and Dean, 1998; Trombulak and Frissell, 2000; Johnston and Pickering, 2001; Pauchard and Alaback, 2004), and so offer convenient sites for investigating the altitudinal distribution of particular species.

In our use of the term ‘invasive plant’ we follow the simple and relatively unambiguous definition of Daehler (2001), who classified non-native species as invasive if they were increasing in abundance in the new area.

Material and methods

Study area

In summer 2003 (July–September), we recorded the presence of introduced plant species at 232 sites (107 railway stations ranging between 200 and 2300 m a.s.l., and 125 road sites ranging between 320 and 2470 m a.s.l.) along the 28 most frequented mountain passes in the Swiss Alps (spanning an area of c. 100 × 300 km²; Fig. 1). The survey sites were either parking areas along trunk roads or railway stations. Roadside surveys of such ruderal habitats along mountain passes have the advantages of being easily accessible and providing relatively constant site conditions across a wide range of elevation (see also Arévalo et al., 2005). The sites were selected to ensure equal sampling intensity in each 200 m altitudinal band from the lowlands (200–400 m a.s.l.) to the alpine zone (at c. 1800–2500 m). Because there are few railway sites at higher altitudes, the upper altitudinal bands are represented disproportionately by road sites; thus the mean altitude of all railway sites is 960 m, and that of all road sites is 1480 m. The strong environmental gradients covered in our sample are reflected in the mean annual temperatures, which ranged

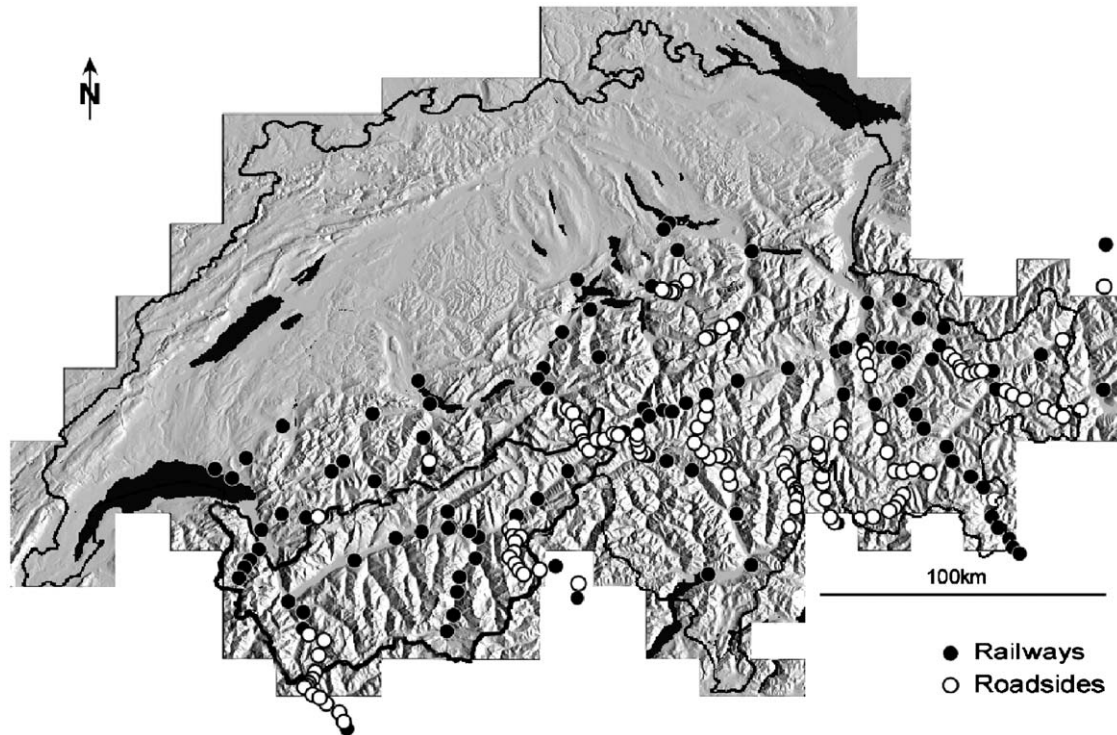


Fig. 1. Distribution of the study sites along railways and roads (mountain passes) in Switzerland. The border of the canton Wallis in the Southwest is delineated in bold. Subsequent sites along a mountain pass are spaced by steps of 200 m in altitude. The background relief image was created in the CD-ROM Atlas of Switzerland. Digital map data DHM25, reproduced by permission of Swisstopo (BA057333).

from 11.5 °C at the lowest site to −3.3 °C at the highest, and in the annual precipitation which increased from 550 mm in the low valleys of the Wallis in the southwest to 2700 mm at high altitudes in central Switzerland (Imhof, 1965–1978).

Species and data collection

At each site we recorded all alien vascular plant species (i.e. species introduced to the area after 1492) except for recent garden escapes that have not become naturalized (Lauber and Wagner, 1998). Some annual plant species may have escaped detection because they were not in flower, but we were able to identify most perennial and woody species from vegetative material. Due to the timing of the survey, in late summer and autumn, there were almost no seedlings present.

The area of the study sites ranged from 100 to 1000 m², and there was a significant decrease in site area with altitude (Spearman rank correlation; $r_s = -0.50$, $P < 0.001$). Each site, irrespective of its size, was searched for 30 min by two experienced botanists who subsequently combined their lists of species. The frequency of each species at a site was estimated using

three categories: low (1–10 individuals), intermediate (> 10–100 individuals) and high (> 100 individuals).

As a measure of the general abundance of the introduced plant species in Switzerland, we used percentage frequency values given in Lauber and Wagner (1998); these are based on the presence/absence data in floristic mapping units (Welten and Sutter, 1982). The time of first introduction of the alien species to Switzerland was compiled from various databases and floras, in particular Hegi (1964–1998), Sebald et al. (1990–1998) and Klotz et al. (2002).

Data analysis

The influence upon species richness of altitude and site characteristics (road vs. railway) was investigated using residual regression. To allow for variation in the size of sites, we used the residuals from the regression of log species richness on site area when analysing these relationships. Differences in the relative frequency of individual species between railway and road sites were analyzed using χ^2 tests of independence (only for species present at ≥ 20 sites). The statistical analyses were performed using JMP 5.1 for Windows (SAS Institute) and SPSS 11 for Windows.

Determining the maximum altitude reached by a species is fraught with difficulties. One problem arises when species are relatively sparse and likely to be sampled only a few times. In such cases, the maximum observed altitude may have very little significance;

indeed, because of the sampling effect we would observe a maximum value even for a species that was entirely unaffected by altitude. Because of this problem, we only report the maximum altitudes for species that were recorded in at least 20 sites (Table 1). We also calculated

Table 1. Time of introduction, abundance and altitudinal distribution of the most common alien species in Switzerland

Plant species	Introduction (year)	Number of sites			Altitude (m a.s.l.)		
		Total	Rail	Road	Present (maximum)	50%/10% frequency	1895–1970 ^a (upper zone)
<i>Matricaria discoidea</i>	1850	158	76	82*	2300 ^b	—	1300–2000
<i>Bromus inermis</i>	c.1920	131	64	67*	2300 ^b	—	1300–2000
<i>Coryza canadensis</i>	1750	116	75	41	2010	1230/1720	1300–2000
<i>Trifolium hybridum</i>	?	105	37	68***	2470 ^b	—	1300–2000
<i>Erigeron annuus</i> ssp. <i>annuus</i>	1805	93	63	30	1790 ^b	1050/1470	700–1300
<i>Euphorbia peplus</i>	?	93	60	33	1470	1050/1520	1300–2000
<i>Veronica persica</i>	1840	86	59	27	1640	930/1880	1300–2000
<i>Galinsoga ciliata</i>	1889	85	58	27	1480 ^b	980/1520	700–1300
<i>Oxalis fontana</i>	?	82	57	25	1550 ^b	960/1400	700–1300
<i>Solidago canadensis</i>	1850	80	60	20	1650 ^c	950/1410	<700
<i>Amaranthus retroflexus</i>	1831	73	52	21	1620	820/1630	1300–2000
<i>Echinochloa crus-galli</i>	?	68	39	29	1600 ^b	810/1480	700–1300
<i>Portulaca oleracea</i>	?	64	47	17	1550 ^b	820/1280	700–1300
<i>Buddleja davidii</i>	1916	60	46	14	1030 ^b	820/1040	<700
<i>Eragrostis minor</i>	?	58	46	12	1360 ^b	780/1170	<700
<i>Impatiens parviflora</i>	1837	54	28	26	1620	470/1640	1300–2000
<i>Lepidium virginicum</i>	1912	54	43	12	1770	740/1200	1300–2000
<i>Robinia pseudoacacia</i>	1800	53	39	14	1420	720/1200	700–1300
<i>Oenothera biennis</i> agg.	1768	52	39	15	1220	730/1200	700–1300
<i>Amaranthus cruentus</i> s.l.	1850	44	26	18	1760 ^b	—	700–1300
<i>Juncus tenuis</i>	1841	32	15	17	1540 ^b	—	700–1300
<i>Panicum capillare</i>	1891	32	28*	4	1050 ^b	—	<700
<i>Solidago gigantea</i>	1850	31	20	11	1540 ^c	—	<700
<i>Heracleum mantegazzianum</i>	1884	30	18	12	1940	—	>2000
<i>Reynoutria japonica</i>	1825	29	17	12	1650 ^b	—	700–1300
<i>Diplotaxis tenuifolia</i>	?	29	20	9	1650 ^b	—	700–1300
<i>Tanacetum parthenium</i>	?	27	16	11	1650 ^b	—	700–1300
<i>Oxalis corniculata</i>	?	27	16	11	1040 ^b	—	<700
<i>Artemisia verlotiorum</i>	1902	26	12	14	1550 ^b	—	700–1300
<i>Lupinus polyphyllus</i>	?	25	14	11	2110 ^b	—	700–1300
<i>Amaranthus blitum</i>	?	24	15	9	1140	—	700–1300
<i>Helianthus tuberosus</i>	1900	23	17	6	1250 ^b	—	<700
<i>Cynodon dactylon</i>	?	23	16	7	1080	—	700–1300
<i>Cerastium tomentosum</i>	?	23	16	7	1940 ^b	—	700–1300
<i>Aurinia saxatilis</i>	1916	22	14	8	1640 ^b	—	700–1300
<i>Helianthus annuus</i>	?	22	11	11	1650 ^c	—	<700
<i>Rhus typhina</i>	?	21	13	8	1220 ^b	—	<700
<i>Syringa vulgaris</i>	≤1918	20	14	6	1430 ^b	—	700–1300

Logistic regression (altitude at 50% or 10% species frequency) calculated only for species with frequency >50 sites, and only for species which decline in abundance with altitude.

Species are ordered after decreasing abundance; see text for further explanation.

?, Unknown.

^aHighest altitudinal zone based on records taken 1895–1970; Becherer (1956) and Hess et al. (1967–1972).

^bHigher altitudinal limits than in the previous records (one zone).

^cMuch higher altitudinal limits than in prior records (two zones; see Methods).

*Indicates significant ($P < 0.05$).

***Highly significant deviation ($P < 0.001$) in proportional species frequency between road and railway sites.

the expected mean maximum altitude for samples of different sizes on the assumption that plants are distributed at random amongst the study sites. To do this we calculated the probability that a species would be present at any particular site; this given by n/N , where n is the number of times the species was recorded in the survey, and N is the total number of sites (i.e. 232). We then ranked the sites according to altitude, and for different values of n calculated the cumulative values of this probability, starting with the highest site. For a particular value of n , the mean maximum altitude is the site at which the cumulative probability is closest to 0.5. From this null model, it is easily seen whether the majority of species are distributed at random or whether they are probably limited by altitude.

A second problem with observed maximum altitudes is how to eliminate extreme values due to the freak occurrence of an individual plant outside the normal range of the species. To avoid this problem we calculated logistic regressions of presence/absence against altitude for those species recorded more than 50 times (>21% of all sites). We then calculated the altitude at which the probability of occurrence of the species had declined to 50% or 10% of its maximum, respectively. The latter value provides a conservative estimate of the maximum altitude that takes account of the entire data set rather than being determined by the chance presence of the species at a single point.

Few exact data are available on the altitudinal distributions of introduced plant species in Switzerland. However, [Becherer \(1956\)](#) provides information on the highest recorded altitudes of several of the introduced species in the Wallis, based on records collected between 1895 and 1954. In addition, [Hess et al. \(1967–1972\)](#) contains information on the altitudinal ranges of all introduced species in Switzerland, classified into the following zones: colline (<700 m), montane (700–1300 m), subalpine (1300–2000 m) and alpine (>2000 m). We combined both information sources to find the highest altitudinal zone from which the species was known to occur before 1970 (see [Table 1](#)). It is problematic to compare maximum altitudes with the generalized information given in a flora because the latter tends to exclude exceptional values. For this reason we used the altitudes at 10% species frequency as a conservative estimate of the upper distribution limits of the species at the time of our survey (logistic regressions, see above). As altitude at 10% species frequency was, on average, 120 m lower than the maximum recorded altitude for each species, we used this difference to adjust the maximum altitudes downward before comparing with the previous altitudinal classification. We then determined whether this adjusted maximum altitude for a species corresponded to a higher altitudinal zone than that reported between 35 and 100 years ago ([Table 1](#)).

Results

Altitudinal patterns of species richness

A total of 155 species were recorded at 232 sites (107 railway stations and 125 road sites; [Fig. 1](#)). The four most abundant species – *Matricaria discoidea*, *Bromus inermis*, *Conyza canadensis* and *Trifolium hybridum* – were found at more than 100 sites ($\geq 43\%$ presence), and a further 15 species occurred at more than 50 sites ($\geq 21\%$ presence). However, the majority of species were recorded less often, and over half of them were recorded at less than five sites.

The numbers of alien species per site declined strongly with increasing altitude ([Fig. 2a](#)). For example, at sites <500 m a.s.l. there were 12–32 species while only 0–4 species were recorded at sites >2000 m. The residual regression analysis, intended to eliminate any confounding effects due to variation in site area, shows that the trend with altitude was highly significant ($P < 0.001$; [Table 2](#), [Fig. 2](#)). In contrast, there was no difference in species richness between road and railway sites, but there was a significant interaction with elevation ($P < 0.05$; [Table 2](#)); this is reflected in the different slopes of the regression lines for railway and road sites ([Fig. 2](#)).

The proportion of alien species showing low abundance of individuals within sites increased consistently from 25% at the lowest sites to >50% at intermediate altitudes. In contrast, the percentages of species with intermediate and high abundance of individuals declined from 47% and 28%, respectively, at the lowest sites to 40% and 9% at intermediate altitudes ([Fig. 3](#)). At altitudes above 1250 m a.s.l., further changes in these percentages were mostly weak and less consistent.

Distribution of individual species

Of the 39 species recorded at 20 or more sites, only four deviated significantly in their proportional occurrence along roads and railways from the expected values (χ^2 test; [Table 1](#)). As two occurrences of significant results at $P < 0.05$ can be expected by chance if 40 tests are performed, the only strong support for non-random deviation was found for *Trifolium hybridum*, which together with *M. discoidea* and *B. inermis* were relatively more frequent at road sites than almost all other species.

As expected, the observed maximum altitude was positively related to the number of times that the species was recorded ([Fig. 4](#), $r^2 = 0.43$, $P < 0.001$). However, for most species, this altitude was well below that predicted by a null model based on the assumption that plants were distributed at random. *Trifolium hybridum* and *M. discoidea* were amongst the few species that did reach the predicted altitude. There were also significantly

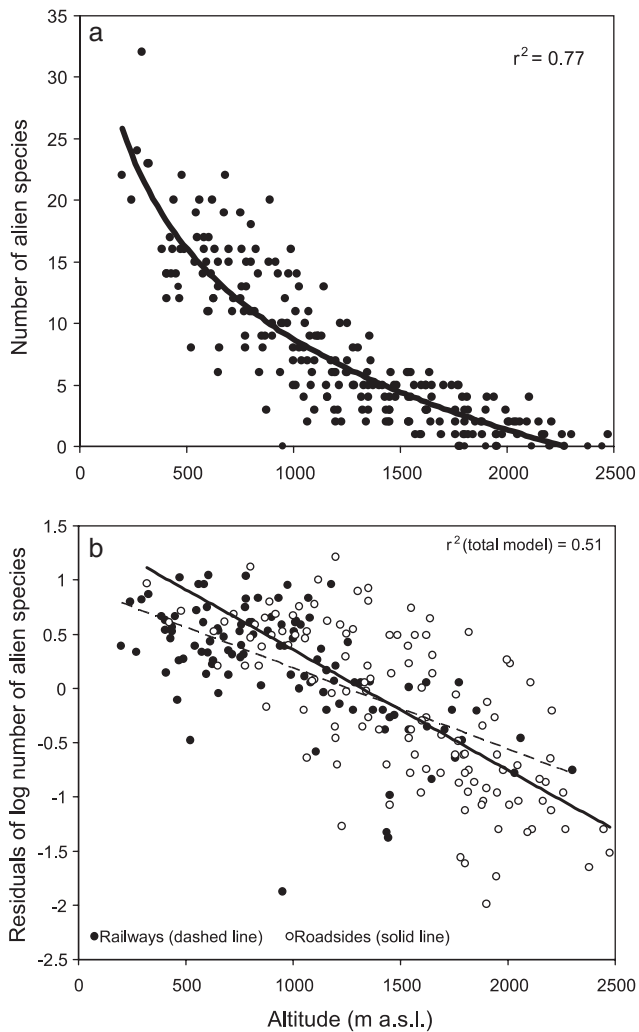


Fig. 2. (a) Relationship between number of alien species per site and altitude (logarithmic fit), (b) residuals from the regression of log species number against site area shown separately for roadsides and railways (with linear regression lines). See Table 2 for regression statistics.

Table 2. Results of residual regression analysis with site elevation and type (i.e. roadside or railway) as the main factors and using the residuals from the regression of log species number against site area

Source of variation	DF	Sum of squares	F ratio	Prob > F
Elevation	1	41.94	178.9	<0.001
Rail/road	1	0.26	1.1	0.30
Rail/road × elevation	1	1.57	6.7	0.01

positive relationships between the maximum altitude recorded for a species and both the general abundance of the species in Switzerland ($r^2 = 0.54$, $P < 0.001$;

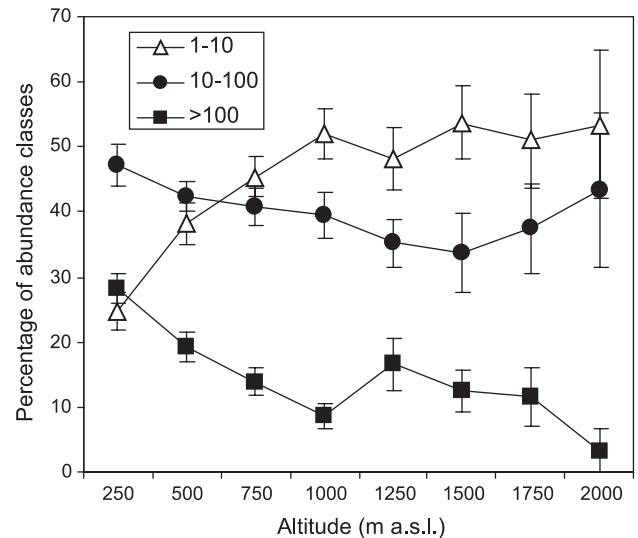


Fig. 3. Change of within-site abundance of alien species with altitude. Data points are means of three abundance classes (individuals site⁻¹) for 250 m steps in altitude (\pm 1 SE).

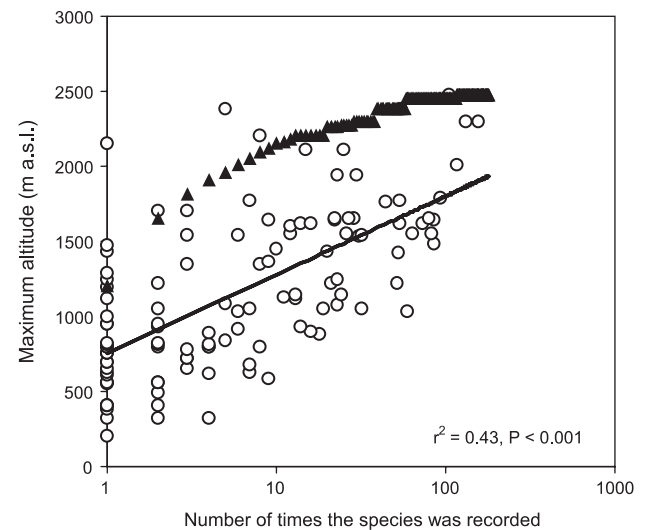


Fig. 4. Maximum observed altitude for alien plant species in relation to the number of times they were recorded (circles). The upper curve (triangles) represents the expected mean maximum altitude assuming that the individuals are randomly distributed amongst the sites.

Fig. 5a) and the time since it was introduced ($r^2 = 0.22$, $P < 0.01$; Fig. 5b). These two variables were themselves significantly correlated ($r = 0.63$, $P < 0.001$).

Further information on the distribution of individual species with respect to altitude was provided by the logistic regressions, calculated for the 19 species present in more than 20% of the sites (Table 1; Fig. 6). A few species, notably *M. discoidea*, occurred across the full

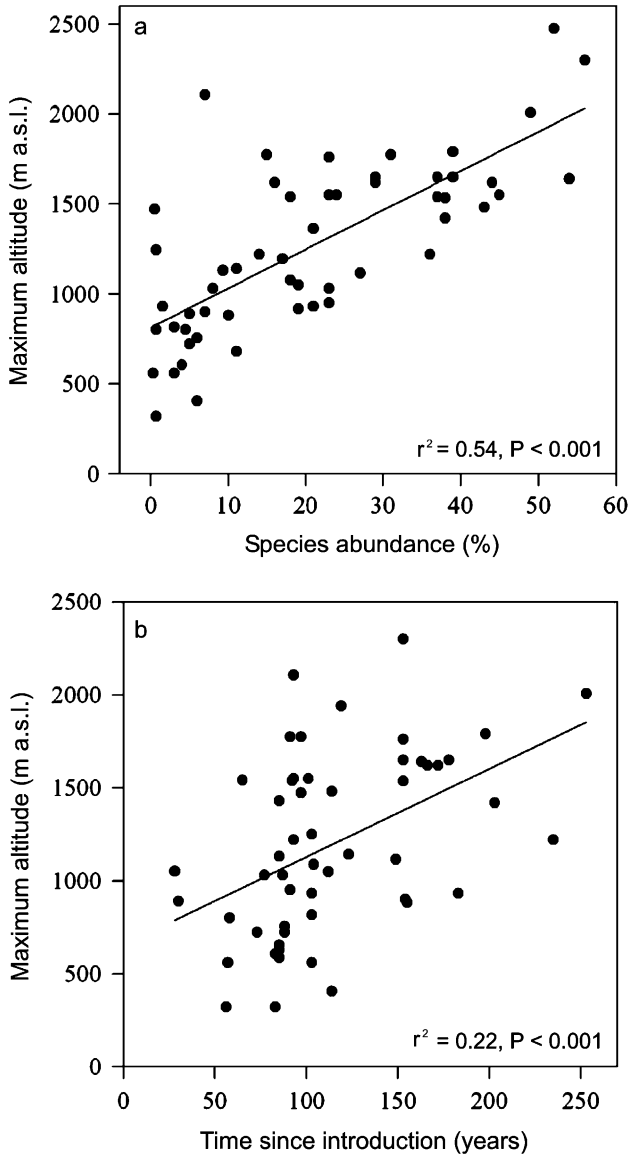


Fig. 5. Relationship between maximum altitude recorded for the alien species and (a) their abundance in Switzerland, (b) time since first recorded in Switzerland. See Methods for details.

altitudinal range (400–2400 m). This species and *B. inermis* showed no significant variation in presence across the altitudinal gradient ($\chi^2 \leq 0.65, P \geq 0.42$). *Trifolium hybridum* was the only species which occurred with increasing frequency at higher altitudes ($\chi^2 = 30.7, P < 0.001$). However, most species showed a strong decline in frequency with altitude ($\chi^2 \geq 26.6, P < 0.001$: thus, *Erigeron annuus*, *C. canadensis*, *Oxalis fontana* and several other species had very similar distributions, with a decline to approximately 50% frequency between 700 and 1100 m, and to 10% frequency at 1200–1600 m. *Impatiens parviflora* showed a similar but less well defined decline with altitude ($\chi^2 = 4.8, P < 0.03$).

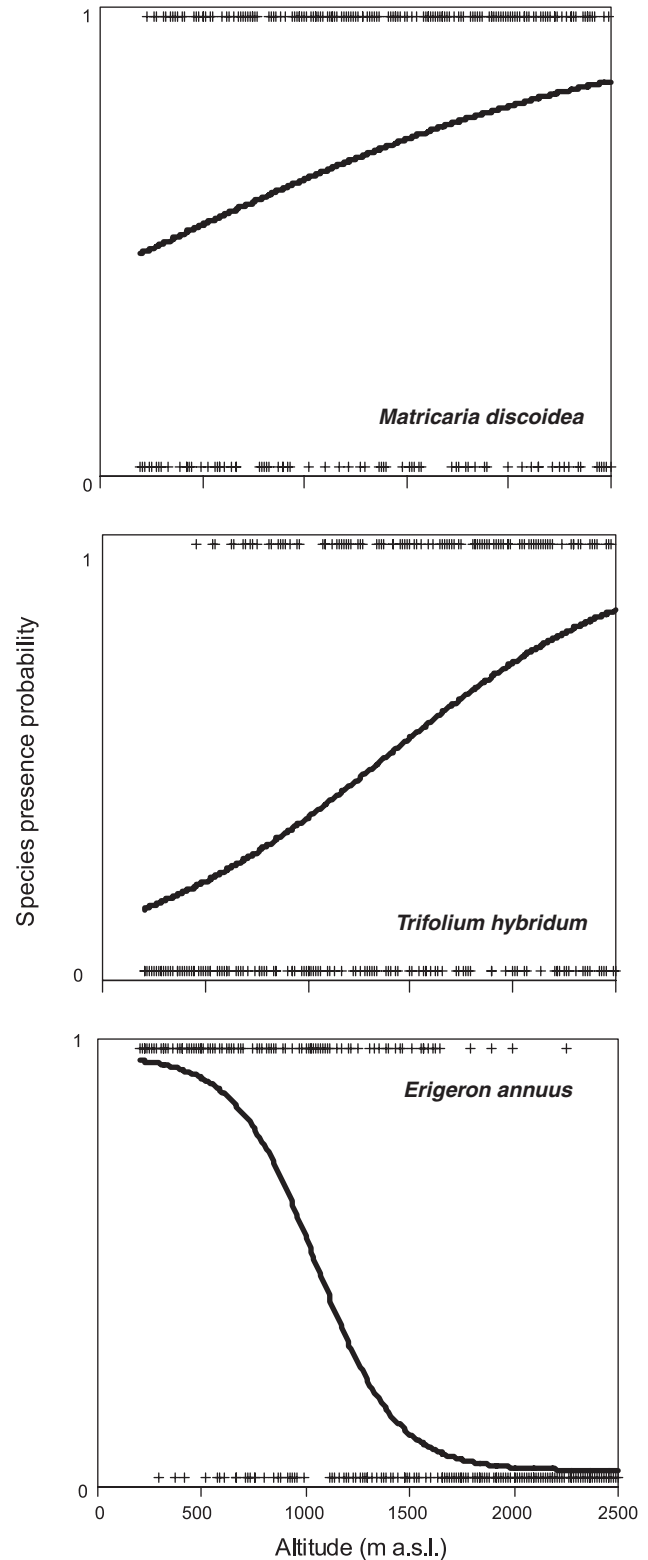


Fig. 6. Logistic regressions for presence/absence of selected species against altitude. Few species showed a very wide altitudinal range (e.g. *Matricaria discoidea*) or increasing abundance with altitude (*Trifolium hybridum*). Most species declined rapidly above mid-altitudes (*Erigeron annuus*). See text and Table 1 for further information.

Recent changes in the altitudinal limits of alien species

Of the 38 species recorded in at least 20 sites, 24 (63%) were found to occur one altitudinal zone higher than had been previously reported (cf. Becherer, 1956; Hess et al., 1967–1972; Table 1), and three species were present two zones higher. All of the species classified as colline (<700 m) by 1970 were found at least one zone higher in the present study. Similarly, most of the species (15 out of 19) described before 1970 as extending into the montane zone (700–1300 m) were found in the subalpine zone (>1300 m). However, only three out of nine species occurring before 1970 in the subalpine zone were found at a higher level (i.e. the alpine zone) in our study.

Discussion

Distribution of alien plants in the Swiss Alps

In this study we focused on species growing in disturbed, ruderal habitats along major traffic corridors in the Swiss Alps. Our results indicate that this region is not wholly protected against invasion; a considerable proportion of the alien flora in Switzerland can be observed up to mid-altitudes, and a few introduced species are even able to cope with the harsh climatic conditions of the alpine zone (>2000 m a.s.l.). However, most alien species, including some that were very abundant in the lowlands, were absent or rare at sites above c. 1000 m. The few invasive species that did not show a marked decline with altitude include some that are well known as having a wide ecological amplitude in their native range (e.g. *M. discoidea*), and others that have been deliberately introduced at higher altitudes (e.g. *B. inermis*; Conert, 1998); yet others are garden escapes that originate from other mountain areas (e.g. *Papaver croceum*).

An analysis of relevé data for annual weed communities in the Swiss canton of Wallis (Fig. 1; Waldis, 1986) revealed a decline in the number of introduced plants with altitude similar to that in our survey ($r^2 = 0.28$, $P < 0.001$). In marked contrast, the number of native weed species in the same relevés was nearly independent of altitude ($r^2 = 0.01$; data not shown). This analysis strongly suggests that plant species native to the Swiss Alps are less restricted by altitude than alien species with a similar growth form and life history.

The fact that the altitudinal gradient in alien species richness was similar at road and railway sites suggests that both types of transport corridor are effective as routes for the dispersal of introduced plants. The less steep regression line for railway sites (Fig. 2b) could be

because site conditions at railway stations change less with altitude than they do at roadsides, particularly in terms of soil conditions and vegetation. However, none of the species we recorded showed a particular association with either road or railway sites. The few species that were proportionally more abundant at road sites, particularly *Trifolium hybridum* and *M. discoidea*, are also those that increased in abundance with altitude, and their higher frequency at road sites may simply reflect the fact that most high altitude sites were along roads. In addition, *B. inermis* was often sown along roads in order to protect slopes against soil erosion (Conert, 1998).

It may be argued that we would have obtained a different picture had we studied longer-lived species in more closed habitats. The propagules of many such species are not readily dispersed by road or rail traffic but depend upon vectors such as birds (e.g. the palm *Trachycarpus fortunei*; Walther et al., 2002); they might therefore have more (or possibly less) difficulty in reaching high altitude sites than the ruderal species we recorded. However, very few introduced species in Switzerland are confined to less disturbed habitats, and even species that can be also found in semi-natural habitats, e.g. *Heracleum mantegazzianum*, *Reynoutria japonica*, *Robinia pseudoacacia* and *Solidago* spp., were present at our study sites. Thus, while our study clearly focuses on humans as the dominant vector for the dispersal of introduced species, this appears to reflect closely the present situation of plant invasions in the Swiss Alps.

Comparisons between our data and previous records of the altitudinal limits of alien plants in Switzerland (Becherer, 1956; Hess et al., 1967–1972) are complicated because of differences in the way that altitude is reported. For this reason we deliberately used a conservative estimate of the present maximum altitude. From these comparisons it appears that several species, and particularly those that were previously restricted to low or intermediate altitudes, have expanded their range into the montane or subalpine zones during the past few decades. Hence, our results suggest that, while all altitudes appear to have received and will continue to receive more alien species, this will affect mostly low to intermediate altitudes. High altitudinal zones appear to be less affected, though we suppose that further species may spread from the montane and subalpine zones into the alpine zone.

Factors influencing the altitudinal distribution of alien species

Two contrasting hypotheses can be proposed to explain the rather low altitudes reached by most plant species in our survey – poor adaptation to conditions at

higher altitudes and low propagule pressure. If poor adaptation were the major constraint to the spread of plants into mountain areas, we would rather expect a relatively long lag-phase before significant numbers of introduced plant species became naturalized at higher altitudes. Alternatively, the process of plant invasions into higher mountains may be driven mainly by propagule pressure; that is, when existing populations of a species become sufficiently abundant close to their current altitudinal limit, they increase propagule pressure beyond the threshold level necessary to successfully colonize new habitats at the next altitudinal level. If this process – involving the build up of sufficiently large populations at the invasion front – was the main determinant of mountain invasions we might expect more rapid invasion than would be the case if genetic adaptation was necessary.

Probably both mechanisms play a role in determining the distribution of invasive plant in the Alps (Fig. 7). Propagule pressure is likely to be low in most alpine valleys, especially those that are not associated with alpine passes and therefore carry only local traffic. This may explain the almost complete absence of invasive plants in many valleys, even at relatively low altitudes (H. Dietz, pers. observ.). However, our study sites were mainly located along heavily used transport corridors that have been important for centuries. We suppose, therefore, that propagule pressure was not the most important factor determining the distribution of at least the most common alien species, but rather that these

species have reached their physiologically determined altitudinal limits.

The finding that species abundant in Switzerland tend to reach higher altitudes would therefore indicate that these species, or at least certain genotypes, are better adapted to high altitude conditions than less common species. Furthermore, the significant positive correlations between the time since introduction and both species abundance in Switzerland and maximum observed altitude are consistent with the suggestion that it takes time for introduced species to adapt to a broader range of local conditions (including altitude). However, other explanations are also possible: the abundance of a species in the new area could reflect its ecological amplitude and abundance in the native range (Scott and Panetta, 1993; Rejmánek, 1995; Maillet and Lopez-Garcia, 2000; Weber, 2001) and therefore the likelihood of it being picked up and transported to a new area (Alpert et al., 2000). In addition, species that are abundant in the native range may have traits such as high phenotypic flexibility that contribute to their invasiveness and also enable them to spread into high altitude areas.

General features of plant invasions into temperate high mountains

Our results indicate that, while many species of alien plants have been introduced into the Swiss Alps, their ecological impact has been mainly small, especially at higher altitudes. We hypothesize that the processes of plant invasion into mountain regions differ in several important respects from those in lowland areas.

1. *The low altitude filter effect*: Because of the harsher climate and more difficult access, land at higher altitudes is usually used less intensively than in the lowlands. This in turn means that high altitude species or genotypes are much less likely to be transported to new areas than those from low altitudes; and those genotypes that are transported to new regions are likely to arrive at low altitude sites to which they may be poorly adapted. Thus the chances of a high-altitude genotype being transported directly to a new region where conditions are similar to those of the source habitat are small. It is more likely for a lowland ecotype of a potential invader to establish a population in the vicinity of a mountainous region, from which propagules may be dispersed to different altitudes (Fig. 7).
2. *Limited connectivity*: In lowland regions suitable habitats for invading species may occur anywhere in the landscape, and the patterns of roads and railways may facilitate the spread of propagules in any direction. In contrast, in mountainous regions suitable low altitude sites occur only in valleys, and

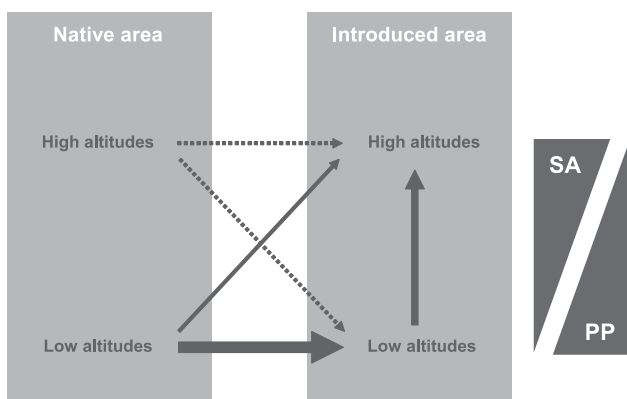


Fig. 7. Conceptual diagram on probable routes by which alien species enter an high-mountain region (relative importance of the routes indicated by arrow thickness). Because the principal transport routes connect lowland areas, most introduced populations may lack adaptations to higher mountain areas. Therefore, specific adaptation (SA) is likely to increase in importance with altitude as a constraint for invasion. Conversely, propagule pressure (PP) is likely to decrease in importance relative to environmental effects and partly as a result of increasing distance from large source populations in the lowland. See text for further information.

neighbouring sites are often separated by impassable mountain ridges. This very different pattern of connectivity and the lower number and smaller size of anthropogenic habitats at higher altitudes is likely to reduce local seed abundance and restrict the rate at which invasive plants spread into a mountainous region. In addition, it may restrict gene flow in the form of pollen and seeds, and thus reduce the opportunities for genetic adaptation.

3. *Genetic swamping of peripheral populations*: In mountain regions, climatic conditions change rapidly over short distances, especially with increasing altitude. Genetic models have shown that gene flow from areas where a species is abundant can be a strong force that inhibits peripheral populations from evolving to their local ecological optima (Garcia-Ramos and Kirkpatrick, 1997). It seems plausible, therefore, that gene flow from low altitude populations of invasive species may often hinder adaptation to high elevation conditions. This may be especially the case in regions where traffic is heavy, for example along the main north-south transport corridors across the Alps, and large numbers of diaspores are dispersed by human activities (e.g. Wester and Juvik, 1983; Tyser and Worley, 1992; Wilson et al., 1992).

Because of these special features of mountain systems, invasions into mountain areas appear to proceed rather slowly, and the higher altitudes in the Alps are at present strongly ‘unsaturated’ with alien plants, i.e. they are not yet in a steady-state situation with respect to the distribution of alien plants but offer space for further colonization as a result of increasing propagule pressure or ongoing adaptation. In addition, most of the species present at lower altitudes are plants of ruderal habitats and it may be argued that they pose little threat to mountain ecosystems. However, for various reasons it would be a mistake simply to assume that temperate mountain regions are not vulnerable to invasion. Firstly, our study suggests that many introduced plants are extending their altitudinal range, perhaps as a result of local adaptation to growth conditions at higher altitudes. Secondly, many types of disturbance are common at higher altitudes in temperate mountains, including freeze–thaw processes, solifluction, avalanches, activities of burrowing animals, trampling by cattle and various human activities (Chambers, 1993, and references therein; Zwinger and Willard, 1996; Grabherr, 1997). It may be, therefore, that adapted genotypes of ruderal species will increasingly find suitable habitats at high altitudes. Thirdly, the spread of invasive species could be accelerated both by increased use of remote mountain areas by humans and by climatic warming. Evidence that climatic changes, and especially warmer winter temperatures, are already having an effect is provided by the rapid spread of alien evergreen tree species in parts

of southern Switzerland since the 1950s (Walther et al., 2002). There are also predictions that alien plants will spread into alpine areas of the Australian Alps as a response to climate warming (McDougall et al., 2005). For all these reasons, further research to investigate the processes determining how plants invade mountain areas is urgently needed. Such information will be essential if we are to ensure that these biologically diverse and ecological sensitive areas remain protected from the effects of biological globalization.

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