Invasive Alien Plants in Protected Mountain Summer Pastures

Drivers of Invasion Risk in the Austrian Alps

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Abstract

Invasive alien plant species (IAPS) are increasingly encroaching into alpine summer pastures in the Austrian Alps, even inside protected areas, where they potentially threaten unique, biodiversity-rich cultural landscapes. This study surveyed 260 sites in three large protected areas (Naturpark Karwendel and the Salzburg and Tyrol sections of Hohe Tauern National Park) to quantify IAPS richness, occurrence frequency and cover, and to identify the main environmental and management drivers of invasion risk. Using a standardized T-shaped plot design based on the MIREN road survey protocol and logistic regression, we related neophyte presence to road proximity, grazing intensity, vegetation type, climate and geochemical conditions. Five different IAPS were detected in study plots (*Juncus tenuis, Matricaria discoidea, Erigeron annuus, Solidago canadensis, Galinsoga quadriradiata*), with an overall proportion of invaded plots of 7.7%, but notable differences among regions, elevational belts and road proximity and low cover values in most invaded plots. Plots directly adjacent to roads showed by far the highest invasion levels, and the odds of IAPS occurrence declined strongly with distance from roads, confirming access roads as key dispersal corridors. Trampling-induced disturbance significantly increased invasion likelihood, whereas excrement density and vegetation type per se were not significant, indicating that disturbance intensity rather than biotic resistance is the critical driver. Climatic conditions further modulated invasion risk: longer growing seasons and relatively dry summers were associated with higher IAPS occurrence, whereas aspect had no detectable effect, highlighting climate as an important but non-exclusive filter. Overall, our results suggest that invasion pressure in alpine pastoral systems is still moderate but clearly non-negligible, with invasions tightly linked to human infrastructure, disturbance and climatic conditions. Effective protection measures in these areas should therefore focus on prevention and early detection along roads, integrate biosecurity into planning of new development projects, and promote less intensive, disturbance-aware agricultural practices in collaboration with landowners and park administrations.

Zusammenfassung

Gebietsfremde invasive Pflanzenarten (IAPS) dringen zunehmend in Almgebiete der österreichischen Alpen ein. Diese Entwicklung betrifft selbst Naturschutzgebiete, wo sie besonders wertvolle, artenreiche Kulturlandschaften potenziell gefährden. Diese Studie untersuchte 260 Standorte in drei großen Schutzgebieten (Naturpark Karwendel sowie die Salzburger und Tiroler Teile des Nationalparks Hohe Tauern), um den IAPS-Reichtum, die

Auftretenshäufigkeit und Bedeckung zu quantifizieren sowie die wichtigsten Umwelt- und Managementfaktoren für das Invasionsrisiko zu identifizieren. Unter Verwendung eines standardisierten T-förmigen Layouts der Untersuchungsflächen nach dem ‚MIREN-Road Survey Protocol‘ und logistischer Regression wurde das Vorkommen von Neophyten mit Distanz zu Wirtschaftswegen, Beweidungsintensität, Vegetationstyp, Klima und geochemischen Bedingungen in Beziehung gesetzt. Fünf verschiedene IAPS wurden in den Untersuchungsflächen nachgewiesen (*Juncus tenuis, Matricaria discoidea, Erigeron annuus, Solidago canadensis, Galinsoga quadriradiata*) mit einem Gesamtanteil von 7,7% befallenen Flächen, jedoch deutlichen Unterschieden zwischen Regionen, Höhenstufen, Straßendistanz und meist niedrigen Bedeckungsgraden in den betroffenen Flächen. Direkt an Straßen angrenzende Flächen zeigten deutlich die höchsten Invasionsgrade, wobei die Wahrscheinlichkeit für IAPS-Vorkommen stark mit zunehmender Straßenentfernung abnahm – dies bestätigt Wirtschaftswege als zentrale Ausbreitungskorridore. Trittschäden erhöhten signifikant die Invasionswahrscheinlichkeit, während Kotdichte und Vegetationstyp selbst nicht signifikant waren, was darauf hindeutet, dass Störungsintensität wichtiger ist als biotische Resistenz. Klimatische Bedingungen modulierten das Invasionsrisiko zusätzlich: längere Vegetationsperioden und relativ trockene Sommer waren mit höherem IAPS-Vorkommen assoziiert, während die Exposition keinen nachweisbaren Effekt hatte – dies unterstreicht das Klima als wichtigen, aber nicht exklusiven Filter. Insgesamt zeigen unsere Ergebnisse, dass der Invasionsdruck in alpinen Weidesystemen noch moderat, aber nicht zu vernachlässigen ist und eng mit menschlicher Infrastruktur, Störungen und klimatischen Bedingungen verknüpft bleibt. Schutzmaßnahmen sollten daher auf Prävention und Früherkennung entlang von Straßen fokussieren, Präventionskonzepte in die Planung neuer Entwicklungsprojekte integrieren und weniger intensive, störungsbewusste landwirtschaftliche Praktiken in Zusammenarbeit mit Landwirten und Parkverwaltungen fördern.

Introduction

Alpine summer pastures represent some of the Alps most beautiful cultural landscapes and harbour a high species and ecosystem diversity. Historically, these mountain ecosystems, particularly in the European Alps, have largely remained free from biological invasion (Kueffer et al. 2013, Alexander et al. 2016), while invasive alien plants around the world cause serious consequences to ecological, economic and social systems (Vitousek et al. 1996, Williamson 1996). Although this semblance of resistance is currently crumbling, as propagule pressure from lowland areas increases, human land-use intensifies and a rapid change in climate creates new opportunities for the invasions of alien plant species into higher elevations (Pauchard et al. 2009, Dainese et al. 2017). The Alps constitute one of the most intensively agriculturally used yet biodiversity-rich mountain regions worldwide, where traditional land-use created a fine-grained mosaic of agriculturally shaped semi-natural habitats that host exceptional plant diversity. These extensive summer pastures are now recognized as both cultural heritage landscapes and European biodiversity hotspots (UNESCO 2023, Zulka et al. 2024). Over recent decades, several large protected areas have been established to safeguard these landscapes. Yet even within their boundaries ongoing changes in climate, land-use, land abandonment and expanding tourism continue to create conditions that may facilitate plant invasions (Foxcroft et al. 2013). At the same time, invasion biology in European mountain grasslands has historically received less attention than in lowland systems. This is partly because the number and impact of alien plant species at higher elevations have so far remained relatively low. However, concerns have been raised that the current management and agricultural policy may underestimate the substantial ‘invasion debt’ building up in these landscapes (Essl et al. 2011, Foxcroft et al. 2013).

Mountain ecosystems are not inherently more resistant than other ecosystems, and their low levels of neophyte richness mainly reflects historically lower anthropogenic disturbance and propagule pressure at higher elevations, rather than true biotic resistance (Pauchard et al. 2009, Kueffer et al. 2013). Climate warming is expected to increase invasion risk also in higher elevated belts primarily by relaxing existing ecological filters. Rising temperatures, longer growing seasons and altered precipitation regimes will expand the area of climatically suitable habitat uphill (Petitpierre et al. 2016). This could allow climatic generalists, such as many lowland invaders are, to expand their suitable habitat into higher elevations (Steyn et al. 2017). The findings by Alexander et al. (2011) and Steyn et al. (2017) would suggest that invasion risk is higher where the local microclimate most closely resemble those of the valley bottom. As is often the case on warmer, south-facing slopes, with longer growing season. Although cold-tolerant neophytes are less common (Steyn et al. 2017), the risk posed by these neophytes, which are pre-adapted to high-elevation climates and are directly introduced into upper montane or alpine zones should not be neglected. Such invasions can have particularly far-reaching consequences for these ecosystems (Pauchard et al. 2009).

However, where and when neophytes actually establish is mainly determined by the local disturbance regime and resource availability (Davis et al. 2000). According to the fluctuating resource availability hypothesis by Davis et al.(2000), plant communities become more susceptible to invasion ('invasible') whenever peaks of unused resources arise. Either due to damage or removal of resident vegetation or due to an increase in the supply of limiting resources from external sources. Disturbance can also promote the establishment of alien species by reducing competition from native plants (Milbau et al. 2013, Lembrechts et al. 2016). In alpine summer pastures, such fluctuating resource availability can be caused by trampling and grazing, by fertilization and nutrient enrichment around huts, feeding and resting sites, and by mechanical disturbance during construction and use of access roads.

In addition, roads serve as the most important corridor for the spread of neophytes into isolated areas, with vehicles, hikers and the transport of building materials, animal feed and seed material contributing to the concentration of alien plants along roads and around alpine huts (Taylor et al. 2012, Lembrechts et al. 2017, Vorstenbosch et al. 2020). Pastoral management could further increase invasibility along transport corridors. For example, when livestock carry seeds between lowland and upland pastures and repeated trampling along the road margin maintains open microsites suitable for colonization. Together, these heavily anthropogenically influenced sites in and around farms, huts, parking areas and roads can potentially act as 'stepping stones' from which neophytes spread further into adjacent semi-natural communities. This emphasizes that propagule pressure and fluctuating resource availability due to disturbance from land use intensification can override any perceived resistance of mountain systems and reinforces the importance of prevention and early detection in these highly connected parts of the alpine landscape.

Although some general principles of invasion biology are now well known, there is still limited empirical evidence on how neophyte invasions unfold specifically within Alpine agricultural systems, especially inside protected areas where conservation priorities are highest. In the European Alps, historically low invasion pressure and research focus on lowland ecosystems mean that local-scale data on invasion patterns in mountain grasslands remain scarce, making it difficult to assess whether the European approach of "No Problem Yet, and No Active Management" (Kueffer et al. 2013) is still justifiable in these landscapes. This creates a challenging situation in protected mountain regions, where agricultural areas are simultaneously valued as cultural assets and potential invasion gateways embedded in otherwise strictly protected surroundings. Understanding invasion processes at an early stage and in the context of the local land-use is particularly important because prevention and early detection are most effective and least costly when alien species are still rare and spatially restricted (González-Moreno et al. 2014).

Based on these circumstances we tried to find out to what extent invasive alien plant species (IAPS) have already invaded alpine pastoral systems within protected areas in the Austrian Alps, and which environmental and management factors facilitate their establishment and spread. Building on the insight of past studies by Lembrecht et al. (2017), Pauchard et al. (2009) and Davis et al. (2000) we developed the following hypotheses:

1. Access roads serve as primary dispersal corridors, with IAPS occurrence and cover decreasing with distance from these infrastructures.
2. Intensive grazing in terms of both trampling and dung density facilitates IAPS establishment in comparison to sites that are either managed less intensively or abandoned.
3. Warmer, south-facing sites with longer growing season exhibit a higher probability of IAPS occurrence compared to cooler, north-facing sites.

To test the hypothesis, we analyse the current IAPS occurrence over a wide spectrum of mountain grassland sites crossing a large part of the Alpine arc with the aim to elucidate the relative importance of road proximity, management practices and abiotic site conditions, to determine invasion patterns and to identify strategies to minimize the invasibility of these mountain ecosystems and the negative impacts of IAPS on them. The results help us to understand the current and future threat posed by IAPS to mountain ecosystems in the context of a rapidly changing climate and land use patterns. Additionally, they can assist in finding solution-oriented approaches to neophyte management and raising the awareness of landowners as well as of protected area administrations and practically contributes to early detection and prevention efforts.

Methods

Study Area

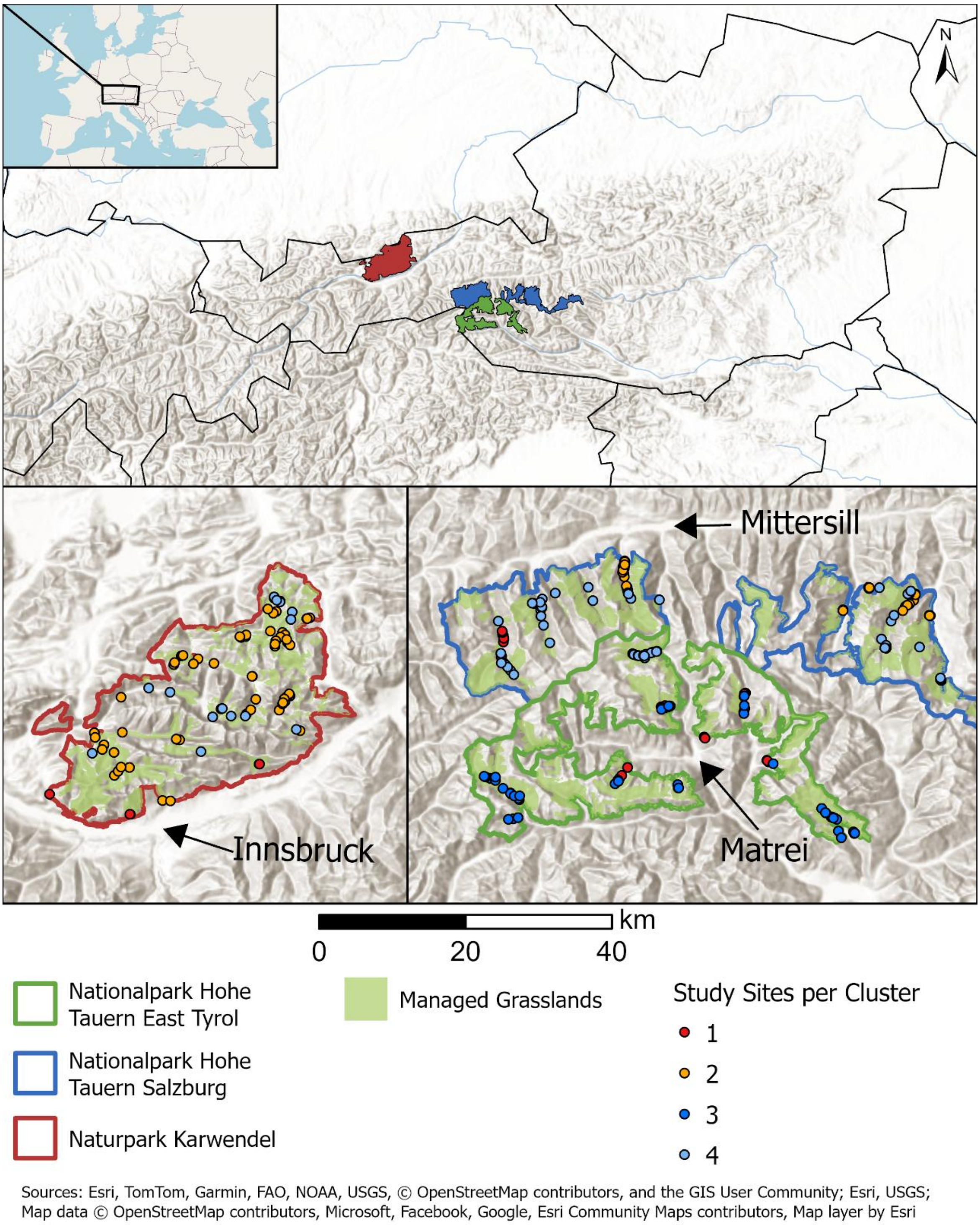

Figure 1: Distribution of the study areas over the Central to the Northern Alps as well as the distribution of study sites within the managed grasslands. Cluster 1 (red) represents all grasslands declared by the farmers (INVECOS) as meadows or occasionally grazed meadows, cluster 2 (orange) represents pastures at the lowest elevations with the longest growing season and moderate to large summer precipitation, cluster 3 (dark blue) represents high elevation pastures with a short growing season and medium to low summer precipitation and cluster 4 (light blue) represents pastures at intermediate elevation with high summer precipitation. (More details are provided in Figure A1 and A2)

Austria is an inland country in Central Europe. About two-thirds of its territory are covered by the mountains of the Eastern Alps. It is characterized by a temperate and humid climate with warm summers and cold winters at low elevations and increasingly harsher conditions at higher elevations. Austria also harbours a climatic transition zone across the main Alpine ridge, where Atlantic (maritime), continental, and Mediterranean weather systems meet. Due to climate warming, the mean temperature in Austria has risen already by ~2.0 °C between the 1980s and recent years (Geosphere Austria 2025). The vegetation forms clear altitudinal belts, from colline and montane mixed forests in the large valleys through subalpine conifer forests to alpine grass- and shrublands and nival pioneer communities. The climatic tree line is generally around 2,000 m in the northern outer ranges and up to 2,300 m in the central ranges (Pecher et al. 2011). Due to the long history of human settlement in the valleys, the Austrian Alps have become some of the most densely populated and highly developed mountain areas worldwide (Thornton et al. 2022).

The study was conducted in three protected areas in Austria, at a total of 260 sites using a standardized guideline and protocol (Figure 1). The first study area is the Naturpark Karwendel in the Northern Limestone Alps, north of the city of Innsbruck, with an area of 739 km². It is a Category V protected area according to the IUCN (International Union for Conservation of Nature), as well as an EU Natura 2000 site, and parts of it are protected under several strict Tyrolean state laws (EEA 2025). In the park, we surveyed 81 sites during August and September 2025, spanning an altitudinal gradient from 900 to 1,780 m.

The second and third protected areas are within the Hohe Tauern National Park (IUCN category II and EU Natura 2000 site) (EEA 2025). Because the park spans three federal states (Salzburg, Tyrol and Carinthia) and each state has its own legislation and administration, Hohe Tauern National Park effectively consists of three separately managed protected areas that share the same name and purpose. In the Salzburg part of Hohe Tauern, just north of the main Alpine ridge covers an area of 805 km². In close collaboration with the national park administration in Mittersill 90 sites were surveyed during August and September 2025 across an elevation range of 1,050–1,900 m. For logistical reasons, the easternmost section of the park was excluded.

The Tyrolean part of the Hohe Tauern National Park is located in East Tyrol on the south side of the main Alpine ridge and covers an area of 611 km². Between mid-July and mid-September 2025, the Tyrolean park administration in Matrei coordinated the survey of 89 sites along an elevation gradient from 1,570 to 2,070 m. The geology of the Hohe Tauern National Park is highly diverse, with zones of predominantly siliceous crystalline rocks alternating with predominantly calcareous units.

All three protected areas permit various forms of land use within their boundaries such as agriculture, hunting and forestry. A rough estimate suggests that about one third of their total area consists of agriculturally used land, with a relatively high infrastructure density and a widespread network of gravel roads providing vehicle access.

Sampling design

Site Layout: The underlying method was based on the road survey protocol of the Mountain Invasion Research Network (MIREN) (Haider et al. 2022). At each site three plots were established, all sized 50 m x 2 m and arranged in a T-shape (Fig. 2). The first plot (road margin plot) was placed parallel to the road directly next to the unvegetated edge of the road margin. The second plot (intermediate plot) was positioned at a 90° angle adjacent to the centre of the road margin plot. The third plot (interior plot) abutted the second plot and ended 100m from the road margin plot.

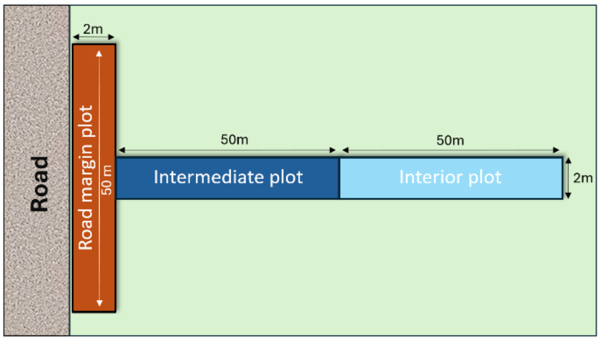

Figure 2: Schematic overview of the site layout with a T-shaped arrangement of the 3 plots along a road.

Site selection: Sites were selected using a random stratified sampling approach in ArcGIS Pro 3.4.0 (ESRI 2024). The areas of interest were chosen from parcels of pastures and meadows, which includes meadows with occasional grazing (INVECOS 2024 data and internal data of park administrations) within a 20 m buffer around all transport corridors wider than 2m (Intermodales Verkehrsreferenzsystem Österreich, GIP.at). Due to the cartography sometimes showing pastoral land parcels within densely forested areas in the Karwendel study area, the forest cover layer provided by the state Tyrol was subtracted from pastoral land before proceeding. With the spatial statistics tool 'multivariate clustering' using the k-means method (MacQueen 1967) with optimized seed locations, the selected polygons were stratified into four clusters. The optimal number of clusters was determined using the pseudo F-statistic, and clustering was based on each polygon's z-transformed mean elevation, growing season length, number of summer days per year (daily maximum temperature ≥25°C), total summer precipitation (April - September), annual maximum dry-period length (all Geosphere Austria 2024), aspect (national 10 m DEM), geochemical properties (National geological map, KM500 and Table A2), and agricultural use (pasture versus meadow with and without occasional grazing) (INVEKOS 2024). More detailed information about climate and geochemical data can be found in the section 'Data collection'. A summary of the clusters and the variables distribution within them can be found in Figure A1 and A2.

With the data management tool 'create random points' a roughly even number of points were placed into the different clusters. Due to the considerably smaller area of meadows and grasslands with combined use of mowing and grazing, the cluster representing this type of grassland (Cluster 1) received fewer sites leading to a final distribution of surveyed sites as follows: 40, 92, 51 and 77 sites, respectively (as seen in Figure 1). In case of obstacles or difficult terrain in the field the sites were moved from one roadside to another or along the road as long as site conditions remained similar. In 40 cases the terrain did not permit the sampling of the interior plot. These plots were consequently omitted from statistical analysis.

Data collection

Field data: At each study site, we recorded information on the current agricultural use (pasture, meadow or abandoned). This was inferred by the presence or absence of livestock excrement and shrub encroachment. We also noted the livestock species observed at the time of the assessments or according to the visible excrements. For each of the three plots within a site, we visually estimated the total vegetation top cover (100% - % of visible soil) (Peratoner and Pötsch 2019). We identified five plant species characteristic for the prevailing vegetation type (Tasser et al. 2019) recorded at species level using identification keys (Dietl and Kessler 1999) and smartphone apps (Flora Incognita) and assigned their frequencies inside the plot in four categories (single, several, common, very common). At a later stage this information was used to determine the plant syntaxonomy at association level according to Mucina & Grabherr et al. (1993) and Tasser et al. (2010), as well as a broad vegetation type (see Table A1). Plant taxonomy and nomenclature followed Fischer et al. (2008). Additionally, we recorded the presence of invasive alien plant species and visually estimated their total percent cover over all vegetation layers in the plot. 18 potentially occurring IAPS (Table 1) were predetermined based on a selection made by Kueffer et al. in European Environment Agency (2010) and local expert knowledge (Pagitz, pers. comm.). The definition of terms regarding alien plants follows the suggestion made by Pyŝek et al. (2004). Thus, IAPS in the context of this work are naturalized plant species which have the potential to spread over a large area but aren't necessarily transforming or degrading the invaded ecosystem. As a proxy for grazing intensity livestock excrements were counted within the whole plot and their density was expressed as their number ha^{-1}. The proportion of open soil resulting from livestock trampling was visually estimated as a percentage of the plot area. For monitoring purposes, the surveyors also recorded IAPS observations outside of the study sites. Here, observation refers to coherent populations of the same species with the number of individuals ranging from one to several hundreds. A summary of these non-systematic observations is reported in Table 1.

Climate conditions at the study sites were characterized using annual climate index grids from the SPARTACUS v2.1 dataset at 1 km resolution provided by GeoSphere Austria (Hiebl and Frei 2016). From this data, the growing season length (GSL) (first sequence of at least 6 days with mean temperature above 5 °C until the first sequence of at least 6 days with mean temperature below 5 °C after 1 July) and sum of precipitation during the summer half-year (April - September) were extracted from NetCDF files as raster from the years 2012-2022 and averaged using cell statistics in ArcGIS Pro.

As **topographic** site variables we used elevation, slope, northness and eastness derived from the Austrian 10 m digital terrain model (Digitales Geländemodell Österreich). From this elevation model, aspect was calculated and transformed into a continuous "northness" and "eastness" index in ArcGIS Pro to represent variation in potential irradiation among sites. Longitude and latitude of the study sites were extracted from ArcGIS Pro.

Geochemical substrate conditions were inferred from the 1:500,000 national geological map of Austria (KM500). For each site, lithology was classified as 'siliceous', 'calcareous' or 'mixed bedrock' using the Geo-Lithological Map by Donnini et al. (2019) (see Table A2).

Level of invasion metrics

In order to understand the current status of IAPS presence in the mountain protected areas of Austria, we use the three descriptive metrics a) IAPS richness b) level of invasion (as the percentage of invaded plots) (Hierro et al. 2004) and c) IAPS cover (considering overlapping plant parts; Peratoner and Pötsch 2019) across invaded sites. To highlight differences in geographical location and anthropogenic disturbance levels, we compared these metrics across the three study areas (Karwendel n=231; Tyrol n=256; Salzburg n=253), four elevational belts (900-1200 m n=165; 1200-1500 m n=172; 1500-1800 m n=255; 1800-2100m n=148), three plot types (road margin n=260; intermediate n=260,interior n=220), and three main grassland types (intensive n=71; intermediate n=346; extensive n=216). Plots within forest communities (n=63), alpine shrubland (n=16), nutrient-rich alpine resting sites (n=16) and wet grasslands (n=12) had no records of IAPS.

Data analysis

To test our three hypotheses regarding to the effects of road proximity, agricultural management, and abiotic gradients we use logistic regression with the binary dependent variable "neophyte presence" (0/1) and all variables describing the site characteristics as fixed effects.

To assess the collinearity of metrically scaled predictors, covariates were first screened by Pearson correlation (Table A3). Terms with correlation ≥ 0.8 were considered redundant and not used for the analysis. This was the case between the 2 temperature (growing season length, number of summer days; Pearson's r = 0.874, p = <.001) and precipitation (summer precipitation, maximum dry period; Pearson's r = -0.802, p = <.001) related climate variables. Due to better fit for the model, we kept growing season length and summer precipitation. Additionally, the predictor elevation was highly correlated with growing season length (Pearson's r = -0.924, p = <.001) and latitude with summer precipitation (Pearson's r = 0.805, p = <.001). Therefore, elevation and latitude were dropped from the model due to the climate variables playing a more direct role in the research question and hypotheses.

Logistic regression was carried out using a generalized linear mixed model in the gamlss framework (version 5.5-0) (Rigby and Stasinopoulos 2005) in R (version 4.5.2) (R Core Team 2025) with a binomial (BI) distribution family and logit link function. To reduce zero-inflation in our response variable and improve model fit, we restricted analyses to the three main grassland vegetation types (intensive, intermediate, and extensive; hereafter referred to as grassland types) and excluded meadows without apparent signs of grazing, as IAPS were absent from all other vegetation types and pure meadows. This leads to a distribution of IAPS absence of n = 552 and presence of n = 57 in our dataset. The site identifier was added as a random term to account for spatial autocorrelation between the plots at the same site. The interior plot, extensive grasslands and mixed bedrock were set as the reference level for the factorial predictors. All covariates were standardized. The model converged after 3 iterations using the Rigby and Stasinopoulos (RS) fitting method (Rigby and Stasinopoulos 2005). Adequacy of the model fit was evaluated qualitatively by visual inspection of diagnostic graphics, including worm plots (van Buuren and Fredriks 2001) and normalized quantile residual plots.

Declaration of AI usage

This study made use of an AI language model (perplexity.ai Pro) to support coding of the statistical analysis and writing. The AI model was used to get suggestions for text structure, terminology and improve phrasing and readability as well as to draft or refine R code for prespecified statistical analyses and to help translate complex phrases from German into English. All conceptual decisions, data analysis, interpretation of results and final wording were carried out and critically checked by the authors.

Results

In total, the five different invasive alien plant species (IAPS), *Juncus tenuis, Matricaria discoidea, Erigeron annuus, Solidago canadensis* and *Galinsoga quadriradiata* were recorded across all study sites (Table 1). The Naturpark Karwendel had the highest IAPS richness with all five of them being present there in the study plots, while only two (*Juncus tenuis* and *Matricaria discoidea*) were recorded in the Hohe Tauern National Park Salzburg. The only recorded IAPS inside study sites in the Hohe Tauern National Park Tyrol was *Matricaria discoidea*.

Table 1: List of potentially occurring invasive alien plant species (IAPS) in the three study areas. The table shows the number of invaded plots from a total of 740 surveyed plots, their mean and median cover and the elevational ranges of the observations. Additionally, the number of non-systematic observations of IAPS done on the way to or from study sites up to 1km outside of protected area boundaries are shown.

Species name	**Number of plots**			**Mean / median cover (%)**	**Elevational range (m)**	**Non-systematic observation**		
	Karwendel	NPHT Salzburg	NPHT Tirol			Karwendel	NPHT Salzburg	NPHT Tirol
Artemisia verlotiorum								
Buddleja davidii					990	1		
Erigeron canadensis								
Erigeron annuus	4			3.0 / 1.5	990 - 1200	3	6	
Galinsoga quadriradiata	1			0.1 / 0.1	900 - 1300	3		
Heracleum mantegazzianum								
Impatiens glandulifera					890 - 1610	2	4	
Impatiens parviflora					970 - 1530	3	1	
Juncus tenuis subsp. tenuis	5	30		1.2 / 0.8	1010 - 1730		16	
Lupinus polyphyllus					1670			1
Matricaria discoidea	4	4	6	1.1 / 1.0	1060 -1920	2	8	7
Reynoutria japonica s.str.					970	1		
Reynoutria sachalinensis								
Reynoutria x bohemica								
Robinia pseudoacacia								
Senecio inaequidens								
Solidago canadensis	3			1.0 / 1.0	920 - 1490	8	1	
Solidago gigantea					1070		1	

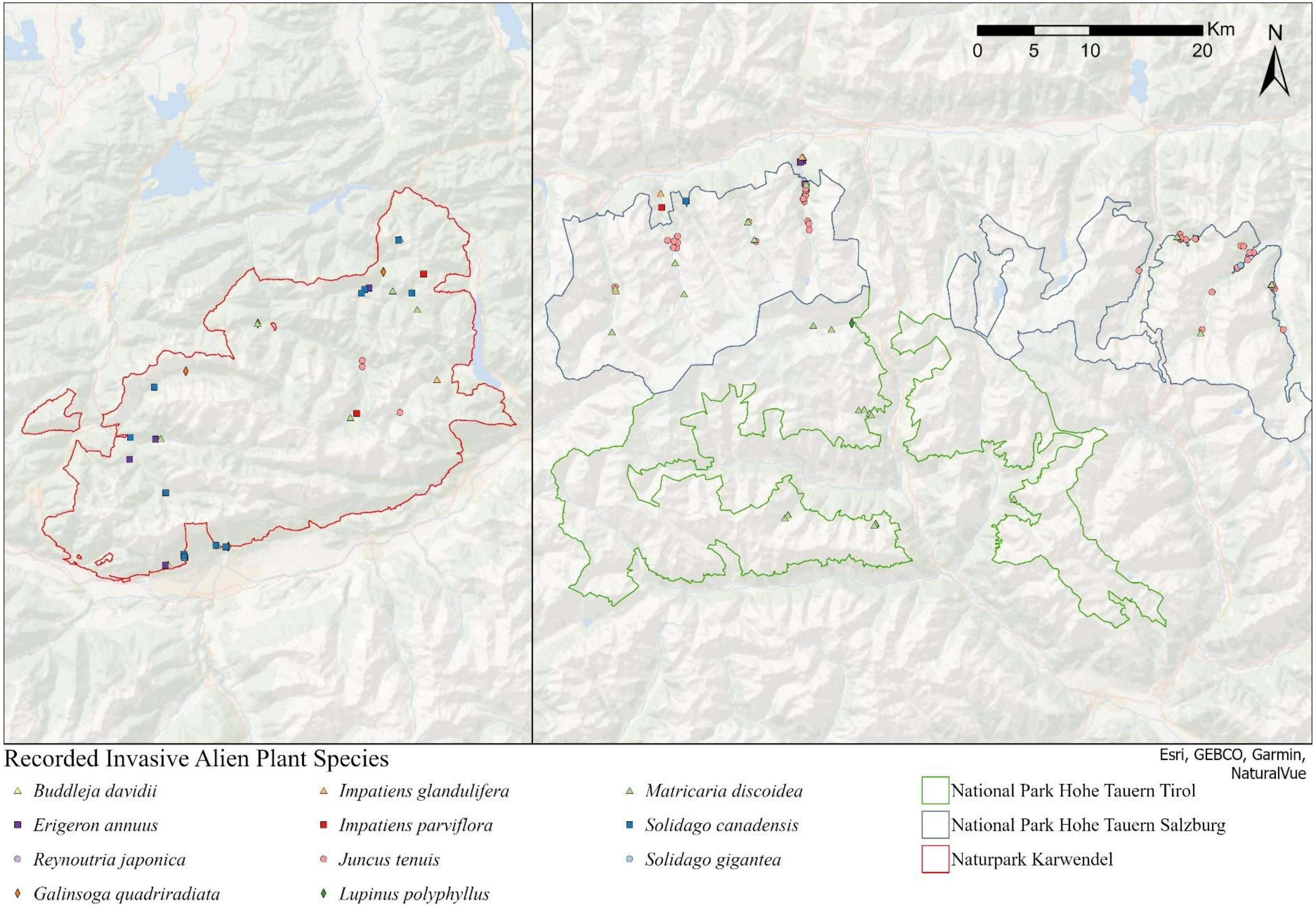

Figure 3: Distribution of invasive alien plant species (IAPS) observations in and around of the three study areas. This map also includes the non-systematic records done on the way to or from study sites up to 1 km outside of protected area boundaries.

Juncus tenuis was the most common IAPS found in the study plots (n = 35). It occurred particularly often in the National Park Hohe Tauern Salzburg (n = 30). The second most common IAPS was *Matricaria discoidea* (n = 14), which was recorded with similar frequencies across plots of all three study areas. With only few occurrences the remaining three species *Erigeron annuus* (n = 4), *Solidago canadensis* (n = 3) and *Galinsoga quadriradiata* (n = 1) were exclusively found on plots in the Naturpark Karwendel. Outside of surveyed sites, the study areas accommodate several additional IAPS species and locations, which were recorded unsystematically and can also be seen in Table 1 and Figure 3. The species recorded at the highest elevation was *Matricaria discoidea* at 1,920 m a.s.l. in the Hohe Tauern National Park Tyrol. But also, several other IAPS have reached elevations up to or above 1,500 m a.s.l. (see Table 1). The cover remained relatively low across invaded sites with an average of 1.25 % (±

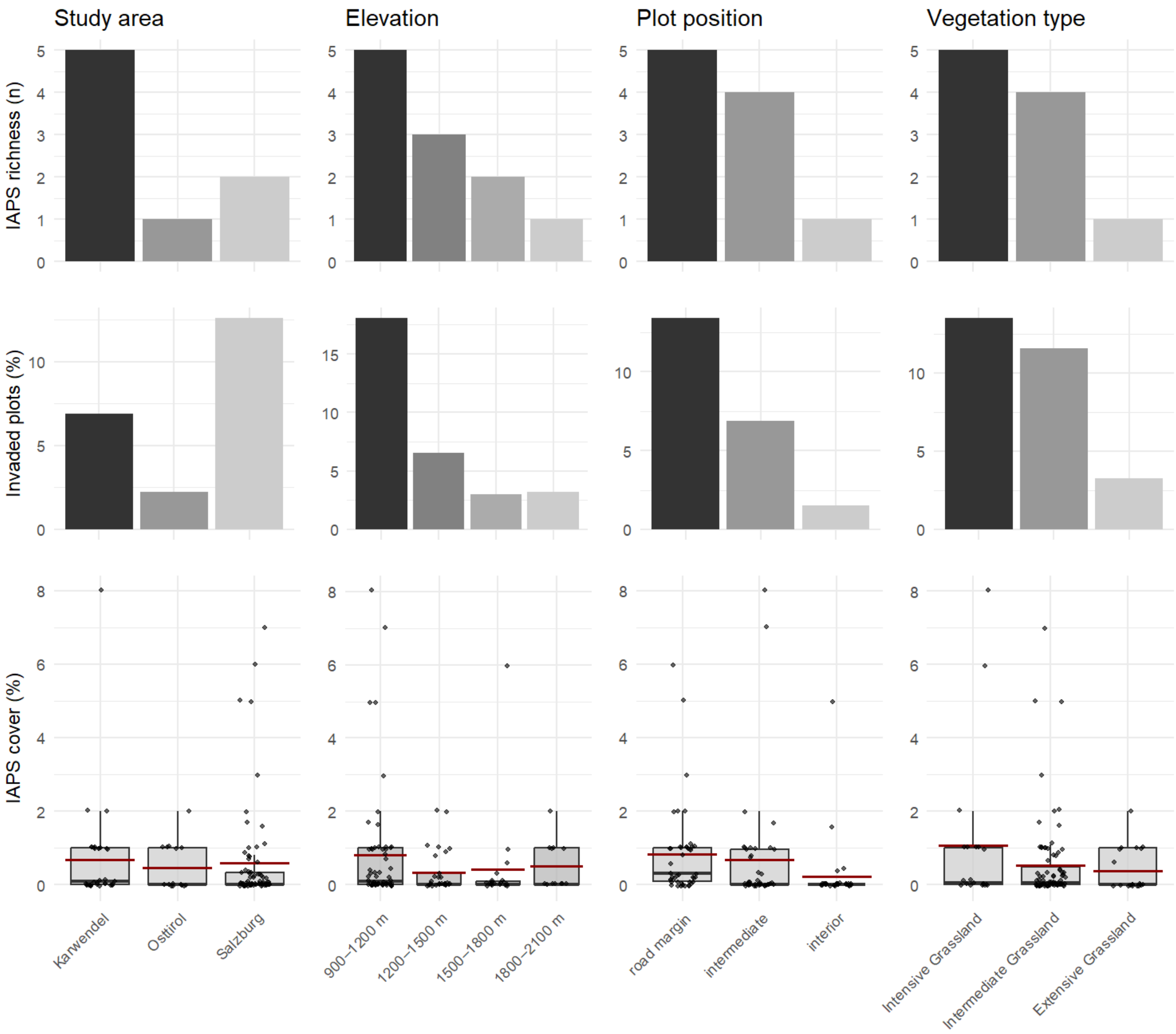

Figure 4: Descriptive metrics for the level of invasion. The graphic shows differences between study area, elevational belt, plot position and vegetation type for 1) IAPS richness, 2) percentage of plots with and without IAPS presence and 3) IAPS cover across all sites with at least one invaded plot with the red line indicating the mean cover.

2.89 %, with a strong right skewness of 2.59) An *Erigeron annuus* occurrence in the Naturpark Karwendel had the highest estimated cover with 8%.

Across all study sites the proportion of invaded plots is 7.7 %. However, between the study areas are notable differences, with the Hohe Tauern Salzburg having the highest proportion of 13.4 %. Naturpark Karwendel has 7.2 % invaded plots and Hohe Tauern Tirol 2.3 %. (see Figure 4). Elevation shows a clear trend for IAPS richness and proportion of invaded plots, while mean cover values remain steady after the lowest elevational belt. The road margin plots show higher levels of invasion for all descriptive metrics compared to intermediate and interior ones, although plots away from the road still exhibit invasion, but at considerably lower levels. A very similar trend can be seen for vegetation type, where intensive grasslands show the highest level of invasion between all vegetation types followed by intermediate and then extensive grasslands. For reference, Figure A3 shows the elevation distribution, the closest proxy for propagule pressure, for plots of these vegetation types.

Drivers of invasion risk

The logistic regression detected several predictors having significant ($\alpha \leq 0.05$) effects on the likelihood of IAPS occurrence across 609 observations (Figure 5). The final model yielded a global deviance of 99.42 and generalized (pseudo) R^2 of 0.367 with 120.1 degrees of freedom for the fit. A likelihood ratio test comparing the null model (random intercept for SiteID only) to our full fitted model showed a highly significant improvement (χ^2 (2.8) = 61.0, $p < 0.001$).

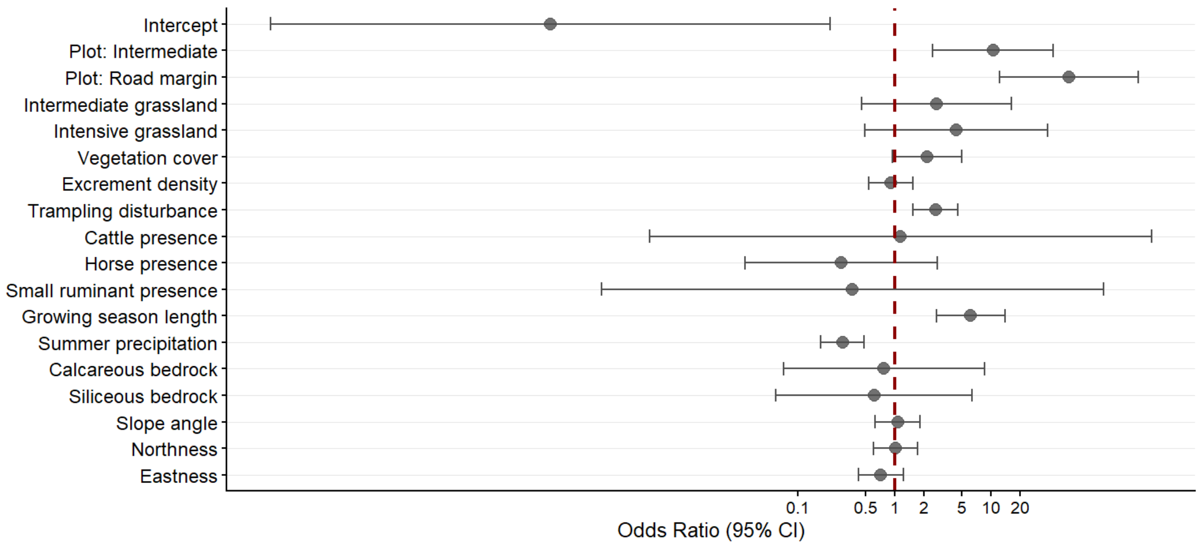

Figure 5: Forest plot from the generalized linear mixed model with the odds ratio of road proximity (plot type), management factors (vegetation type, vegetation cover, excrement density, trampling disturbance and livestock presence) and abiotic conditions (growing season length, summer precipitation, bedrock properties, slope angle, northness and eastness) regarding the occurrence of invasive alien plant species in alpine summer pastures.

This confirms that the environmental predictors substantially enhance explanatory power beyond random site effects alone. The residual diagnostics (Figure A4 and A5) did not show major violations of the assumptions. Due to the binomial distribution of the dependent variable all mentioned coefficients β are on the logit scale. A detailed table for all parameter estimates can be seen in Table A4. Figure 5 shows the converted odds ratio for all coefficients. The intercept (β = -8.185, t = -2.41, p = 0.016), which includes interior plot, extensive grassland, livestock absence and mixed bedrock as the reference values, indicates near-zero baseline IAPS probability on undisturbed mountain grasslands. Plot type strongly influenced occurrences (Figure 6 A). The road margin plot (β = 4.15, t = 4.91, p = <.001) and intermediate plot (β = 2.34, t = 3.20, p = 0.001) show roughly 60-fold and 10-fold higher odds of IAPS occurrence, respectively, compared to the interior plot. Regarding management factors, trampling disturbance (β = 0.98, t = 3.59, p = <.001) is the only significant predictor of IAPS occurrence with increasing percent of disturbance leading to higher probability of invasion (Figure 6 B).

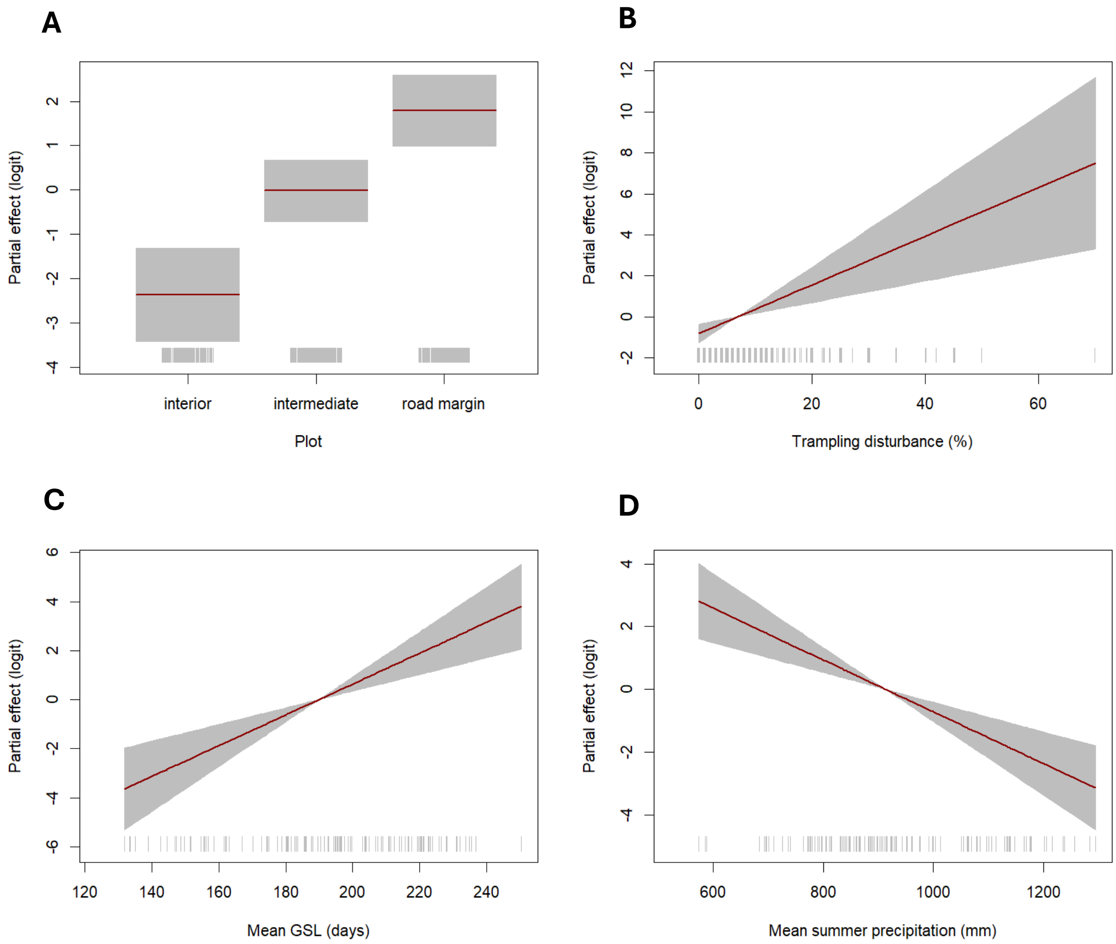

Figure 6: Partial effects of the A) plot type, B) trampling disturbance, C) mean growing season length (GSL) and D) mean summer precipitation on the probability of IAPS occurrence in alpine summer pastures. The red line represents the estimated partial effect with the grey background indicating the standard error. The data distribution of each variable can be seen as a jittered 1-D histogram above the x-axis in grey.

Vegetation cover is marginally significant (β = 0.78, t = 1.85, p = 0.065), while grassland type did not prove to be a significant driver of invasion risk, after taking spatial autocorrelation into consideration. The only significant abiotic conditions are the climatic gradients, with a longer growing season (β = 1.81, t = 4.35, p = <0.001) showing a positive relation with invasion likelihood (Figure 6 C). Additionally, decreasing summer precipitation (β = -1.23, t = -4.68, p = <0.001) increases the odds of invasion (Figure 6 D).

In summary, road proximity had the strongest effect on invasion likelihood, with both mean and median IAPS cover decreasing further from infrastructure. This is consistent with our first hypothesis. For the second hypothesis, only trampling disturbance, but not excrement density significantly increased neophyte occurrence. The third hypothesis received partial support with a longer growing season favouring IAPS occurrence, while aspect was not a significant predictor of invasion risk.

Discussion

The methodological strength of our study includes the large sample size across extensive environmental gradients in protected alpine summer pastures. Together with the standardized and field-proven MIREN road survey protocol our study provides robust statistical power and enables comparability with other mountain invasion studies worldwide. However, selective site positioning limited spatial coverage across the extensive study area, potentially missing informative landscape-scale patterns. Surveyor identification errors in plant taxonomy and syntaxonomy cannot be ruled out completely, while management intensity could only be assessed through proxies rather than direct measures. Finally, the 1-km resolution climate data potentially failed to capture aspect-dependent microclimates (Yin et al. 2023) that could influence local invasion dynamics .

The higher level of invasion observed in plots directly located parallel to roadsides, as opposed to plots located further away from structures, strongly highlights their important role for invasive alien plant species (IAPS) spread and establishment in mountain areas (Seipel et al. 2012). In this context, Follak et al. (2018) underlined that roads are important vectors for the spread of alien species in lowland areas of central and northern Europe. We showed now that they also produce similar patterns for the distribution of IAPS at higher elevations and along less trafficked mountain roads crossing protected mountain summer pastures in the Austrian Alps.

The observed differences in the level of invasion from intensively to extensively managed grasslands didn't prove to be significant after accounting for spatial autocorrelation. Although, the results show that concerning grazing intensity, damages to the sward induced by trampling are the main factor increasing the likeliness of IAPS occurrence. These findings are consistent with the well-established role of disturbance as a primary driver of plant invasion (Pauchard et al. 2009, Lembrechts et al. 2016). However, the weaker trends and larger uncertainty for some agricultural management predictors, together with reliance on indirect grazing intensity proxies, suggest additional factors at play in pastoral plant invasions, such as temporal variation in disturbance regimes, herbivory, or herd composition. Nevertheless, our results indicate that reducing grazing-induced sward damage enhances resistance of mountain summer pastures to plant invasions. Notably, sward damage also depends on slope, soil conditions, animal weight and stocking rate among other management factors (Dumont et al. 2007). This underscores that pastoral management cannot be disregarded when assessing invasion risk in alpine grasslands.

Climatic conditions emerged as an important correlate of invasion in our study, but their effects are slightly nuanced. Although we hypothesized that warmer, south-facing slopes would harbour more IAPS, our study did not show clear evidence that aspect made a difference in the likelihood of IAPS occurrence. On the other hand, our model did reveal a clear relationship between the length of growing season as well as summer precipitation and the probability of IAPS occurrence. This indicates that climatic conditions do shape invasion patterns in mountain summer pastures. This is also consistent with the idea that climate acts as an ecological filter for alien plants along elevational gradients (Alexander et al. 2011) , where nonnative species typically arrive at human-disturbed sites in the lowlands and spread upward, but only climatic generalists with wide elevational tolerances persist at higher altitudes due to the progressive elimination of species unable to tolerate changing climate conditions. However, climatic filtering alone cannot fully explain observed distribution pattern. With the change in temperature and precipitation correlating strongly with elevation it's important to consider the argument made by Pauchard et al. (2009), who suggest that the elevational decline in plant invasion is largely a consequence from the scarcity of neophytes pre-adapted to harsh mountain conditions, the low alien propagule pressure, and the reduced human disturbance at higher elevations, rather than climate acting as an insurmountable barrier. Our results thus support a view in which climatic conditions are the necessary abiotic frame but not sufficient drivers of invasion risk in mountain ecosystems. In connection with this, it's important to highlight that ongoing climate change can further amplify the risk of plant invasions by expanding this abiotic frame for broad-niched invasive alien species.

Our study shows that proximity to roads and sward damage by trampling can facilitate IAPS establishment. Mountain summer pastures additionally experience regular anthropogenic but also natural disturbances, like floods, debris flows or glide avalanches, creating ample opportunities for potential plant invasion. However, Daehler's (2003) meta-analysis reveals that IAPS do not universally prevail over co-occurring natives. Invasive or opportunistic native species can often compete effectively or even outperform non-native species particularly under harsher climatic conditions. Additionally, positive effects of grazing on IAPS suppression (e.g., by reducing successful invader biomass or favouring adapted native species) may potentially have been overlooked in our surveys, as IAPS on heavily grazed pastures could have been trampled or consumed and thus not visible during late-season sampling. Several studies (Frost et al. 2003, Rohal et al. 2024) support the idea that, under carefully managed grazing regimes, livestock can function as biological control agents for certain invasive alien plants or at certain growth stages, but systematic experimental work on IAPS in Europe in this context is still relatively scarce compared with North America. Although, it must also be noted that particularly for severe infestations grazing alone will rarely completely eradicate invasive plants (Tu et al. 2001). Future work could address the above-mentioned gaps by conducting repeated surveys to capture phenological variation and grazing-induced suppression of IAPS. Long-term monitoring that incorporates species-specific traits and propagule pressure, as recommended in the work of Colautti et al. (2006) could help to further disentangle the roles of climate, grazing management, and biotic interactions in driving invasion dynamics as well as expose long term trends of invasion processes in these protected ecosystems.

Practical implications

Our study reveals that IAPS pose a growing, though currently still moderate, threat to alpine pastoral systems within protected mountain areas of the Austrian Alps, driven primarily by proximity to human infrastructure and agricultural practices causing sward damage. While these factors can facilitate establishment and spread, they also underscore that IAPS often have clear introduction pathways, with access being constricted to well-defined corridors like roads and trails making prevention the most effective and feasible strategy in protected mountain ecosystems, (Alexander et al. 2016). Management should therefore focus on early detection, rapid response and biosecurity measures (e.g. mandatory vehicle washing, certified invader-free fodder, seed mixtures and construction material) tailored to key pathways alongside the prevention of new introductions of pre-adapted IAPS directly to higher elevations and between sites (Foxcroft et al. 2013; Glaser et al. 2025). While species-specific pathways matter, broad preventative action and raised general awareness among policy makers and stakeholders including visitors stands as the most important and effective countermeasure to plant invasions.

Naturally, these IAPS vary in the severity of their impacts on the invaded ecosystems, but as a generalization, none of them should be disregarded in a protected area which should have the maintenance of its native biodiversity and natural ecosystem functioning as a top priority for the area's administration (Foxcroft et al 2013). Agriculture, often implicated in invasions through disturbance and material flows, holds equal potential as a protector: with raised awareness and knowledge, farming communities can control the spread of IAPS much like native weeds, safeguarding ecosystems from economic, ecological, and social harm.

Under current global change scenarios, invasive alien propagule pressure is expected to intensify (Glaser et al. 2025). Not only in lowlands but increasingly also in mountain regions as climate warming opens new opportunities for IAPS to expand in new areas previously not suitable for their establishment due to climatic barriers (Petitpierre et al. 2016). In this context, all infrastructure projects in protected mountain areas causing large-scale disturbance, particularly road and trail network expansions, warrant critical evaluation with alien plant invasion risks explicitly considered. Effective responses will require integrated approaches that combine inventory and survey work, prioritization of high-risk sites, regular monitoring, prevention, outreach and stakeholder cooperation. (Foxcroft et al. 2013). Active control techniques need to be selected case-by-case. With prescribed grazing (Frost et al. 2003) constituting a low cost and effort measure compared to manual pulling, particularly for mountain summer pastures, when carefully planned and monitored. Data sharing across jurisdictions, particularly in case of the Hohe Tauern Nation Park, will enhance rapid response efforts, particularly as climate change expands climatic niches and amplifies risks. In the end, whether IAPS range expansions warrant high input mitigation efforts or are seen as inevitable under global change will depend on local land-use needs, perceptions and policies (Alexander et al. 2016). Yet in the Austrian Alps, proactive management can still preserve these invaluable pastoral systems.

Conclusion

This study shows that alpine summer pastures in three large, protected areas of the Austrian Alps are already moderately invaded by invasive alien plant species, but those intrusions are strongly concentrated along access roads. Transport corridors function as the main dispersal corridors and source habitats, while grazing-induced sward damage, longer growing seasons and relatively dry summers increase local invasibility, indicating that climate warming and ongoing land use intensification will likely amplify future invasion risk. Biologically, this means that, while still at an early-stage and spatially restricted, these IAPS populations already threaten biodiversity-rich cultural grasslands and could potentially act as nuclei for further spread if disregarded. Alongside the importance of general awareness among policy makers and stakeholders, our findings suggest that effective protection should focus on prevention and early detection along access roads and agricultural management which minimises strong disturbance without abandoning traditional pastoral use. Future research should extend monitoring across phenological stages and years, experimentally test management options such as targeted grazing and pathway-focused biosecurity, and integrate propagule pressure as well as fine-scale climatic data to better predict invasion hotspots under ongoing climate and land-use change.

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