



Variation in the effectiveness of nonnative plant removal along elevation gradients in Switzerland

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Received: 10 May 2025 / Accepted: 1 September 2025 / Published online: 13 October 2025
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Abstract

Limiting the spread and impact of nonnative species in mountain ecosystems is a key management objective. While current management strategies may be tailored to species traits and life histories, understanding how management effectiveness varies along elevation gradients could help optimize control measures and ultimately support native plant communities. We hypothesized that management efficiency would increase with elevation due to smaller population sizes and more limiting environmental conditions affecting population performance near range edges. To test our hypothesis, we conducted a removal experiment with two perennial (*Solidago canadensis* and *Lupinus polyphyllus*) and one annual (*Erigeron annuus*) invasive species in the eastern Swiss Alps. Control effectiveness (recovery of plant cover after 1 year) depended on plant life history, with a strong reduction in cover for the perennial species. However, elevation did not significantly affect short-term management outcomes, suggesting consistent efficiency of control measures across the gradient. A germination experiment using soil samples from field sites revealed higher seedling numbers for the annual species and a decline in emergence with elevation for both focal species analyzed, suggesting that seed bank size may influence management outcomes. Based on our findings, we recommend long-term strategies that include the sowing of native seed mixtures to support recovery. Additionally, lower germination at higher elevations suggests that removal success may eventually be greater at species' upper range limits. Overall, our study shows that considering elevation-related variation can help refine nonnative plant management strategies in mountains.

Keywords Biological invasion · Management effectiveness · Elevation gradient · Seed bank · Germination

Introduction

Compared to lowlands, mountain ecosystems have until now experienced relatively low levels of invasion by nonnative species (McDougall et al. 2011). However, an increasing number of invasive plant species are spreading to higher elevations in mountain ranges across the globe (Pauchard et al. 2009; Iseli et al. 2023). Although this is raising concerns about possible detrimental impacts on the unique biodiversity of high elevation ecosystems (Alexander et al. 2016), the relatively limited documented impacts of invasive species

at high elevation so far provides an opportunity to develop and enact effective management strategies (McDougall et al. 2011). Since funding of nature conservation is limited, it is crucial to optimize control strategies and tailor them to a mountain context to achieve the greatest cost-efficiency (Epanchin-Niell 2017).

If possible, invasive plant species should be eradicated in the first phase of an invasion, through rapid detection and using “brute-force” methods such as mechanical removal (Simberloff 2003). However, if plant populations are already established, knowledge about the population biology of the species becomes increasingly important (Simberloff 2003). Perennial nonnative species are most likely best targeted by reducing their survival, while annual species' performance can be greatly impacted by reductions in growth and fecundity (Ramula et al. 2008). In the case of species with large soil seed banks, long term control programs with multiple management cycles may be required (Kettenring and Adams 2011). Finally, control measures should ideally target the

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most sensitive demes within spreading metapopulations, which, depending on the species, might be nascent foci at the invasion front, high-density plots in the core of distributions, or both (Moody and Mack 1988; Pachepsky and Levine 2011). Accounting for this context might be especially fruitful in mountains, where the steep environmental gradients exert a strong influence on plant performance and where spread typically occurs from low to high elevation (Alexander et al. 2016), clearly delineating core and range-front populations.

Plant traits and performance can vary substantially along elevation gradients (Rosbakh et al. 2015; Halbritter et al. 2018) associated with changing environmental conditions such as decreasing temperature and variation in precipitation (Körner 2007). Clinal variation has been observed in some nonnative plant species, with generally lower growth and lower reproductive output reported with increasing elevation (Baret et al. 2004; Bustamante et al. 2017; Alexander et al. 2009). In mountainous regions such as the European Alps, the distribution of nonnative plants can span a relatively wide range in elevation. Therefore, the variation in growth conditions they experience can be expected to have consequences on vital rates within populations. For example, well established populations in central and lower elevations are expected to have higher propagule pressure and a larger soil seed bank because of the generally higher population density and greater age of populations (Seipel et al. 2016). This may lead to greater difficulties in management efforts. In contrast, populations at the range edge have generally fewer individuals and lower propagule pressure (Seipel et al. 2016) and, theoretically, reduced population growth rates near the niche edge (Chase and Leibold 2009; Sexton et al. 2009). These characteristics may make them more vulnerable to local eradication. Understanding whether the effectiveness of management varies with elevation may help when prioritizing the use of limited management resources in mountainous regions.

In this study, we tested the short-term effectiveness (i.e., after 1 year) of targeted removal of three common invasive plant species with contrasting life-histories (*Erigeron annuus*, *Solidago canadensis* and *Lupinus polyphyllus*) along an elevation gradient in the eastern Swiss Alps. We also quantified the contribution of the soil seed bank to the potential regeneration of the populations of the focal species from different elevations. Our aim was to provide management relevant knowledge to help refine existing guidelines of nonnative species management along elevation gradients. Specifically, we ask:

1. Does the effectiveness of mechanical removal of nonnative plants vary with elevation and differ among species with contrasting life histories?

2. Does the soil seed bank size of different nonnative species vary along the elevation gradient?

Since perennial plants invest more resources in below-ground structures such as roots and rhizomes (Klimes 2007; Klimešová et al. 2018) and therefore rely on regeneration from bud banks (Ott et al. 2019), we hypothesized that mechanical removal would be more effective in reducing the recovery of perennial species. In contrast, because annuals tend to invest in rapid growth and in large and long-lasting seed banks, control measures might be less effective at reducing abundance (Rejmanek and Richardson 1996). We expected recovery to be greater at lower elevation due to a higher propagule pressure for recolonization and more favorable growing conditions, such as warmer temperature and longer growing seasons, which can enhance growth, flowering, and seed production (Seipel et al. 2016). We also hypothesized that the annual *Erigeron annuus* would have a larger soil seed bank than the perennial species because of its life history strategy and prolific seed production (Baskin and Baskin 2000). Moreover, we expected the size of the soil seed bank to be negatively related with elevation and positively correlated with the cover of the focal species within our study sites. Hence, we expected high density locations in the range core to have higher potential for regeneration from seeds than populations towards the range edges, which experience an increasingly harsh climate as well as a greater isolation of populations (Seipel et al. 2016).

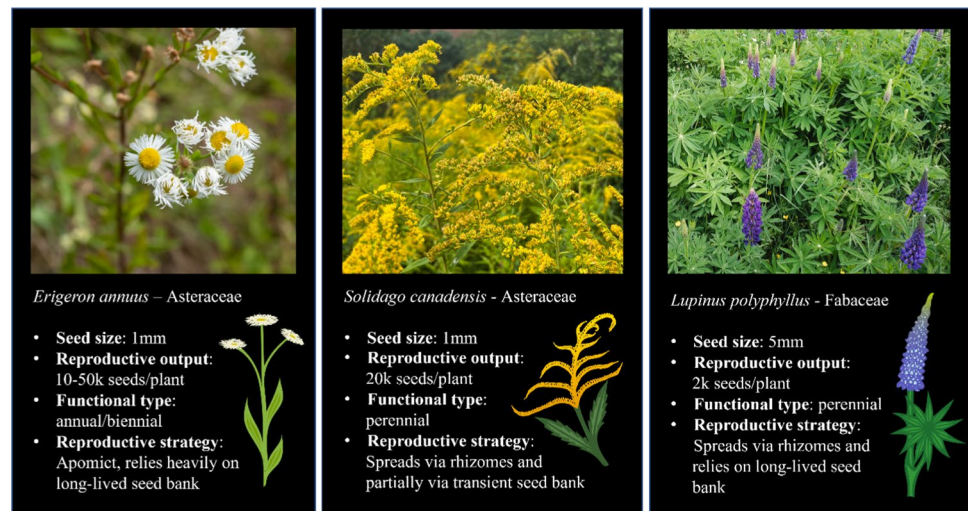
Materials and methods

Study species

We selected three ecologically contrasting invasive plant species of management concern in Switzerland (Fig. 1). All focal species are found across a relatively broad elevation range in the eastern Swiss Alps and are present on the Swiss list of invasive neophytes (InfoFlora 2024), which features species with high spreading potential.

All focal species are forbs originating from North America and were introduced to Europe as ornamental plants. *Erigeron annuus* L. (hereafter *Erigeron*) is generally considered an annual and has a monocarpic life-cycle. *Solidago canadensis* L. and *Lupinus polyphyllus* Lindl. (hereafter *Solidago* and *Lupinus*) are perennials and commonly live longer than 2 years. They have perennial rhizomes, allowing them to accumulate resources and survive unfavorable climatic conditions in winter. In contrast, the roots of *Erigeron* are short and less well anchored in the soil. To spread, *Erigeron* relies on a large number of windborne seeds, which can travel over long distances (Pacanoski and Saliji 2015)

Fig. 1 Pictures (© Sascha Gregori) show the habits of the three focal species as well as a short summary of key characteristics (InfoFlora 2019, 2020, 2025a)



and accumulate in the soil to form a long-lived seed bank (Gregori et al. 2024). Although *Solidago* plants also produce large amounts of seeds, which are mainly spread by wind, the germinability of the latter is generally low (Poll 2007). *Lupinus* has the lowest seed production, yet their germinability is the highest, making their seed bank the longest lasting among our study species (Sapra et al. 2003). Both perennials can also spread vegetatively through perennial rhizomes. This increases long-term management challenges, because regeneration of individuals can begin from rhizome fragments of managed individuals persisting in the soil (Weber 2011). Finally, a common characteristic of our focal species is the production of allelopathic substances, which allow them to suppress co-occurring species and to achieve greater dominance within invaded sites (Oh et al. 2002; Kato-Noguchi and Kato 2022; Kalske et al. 2022).

While the distributions of *Erigeron* and *Solidago* generally overlap and the core of their distributions lie at low to mid elevation, large populations of *Lupinus* have been reported at higher elevation in the European Alps (Seipel et al. 2016; InfoFlora occurrence dataset 2025b). Thus, the latter is one of the few invasive species that is able to tolerate a cold climate and to spread in habitats of the subalpine and the lower alpine zone in Switzerland. In their nonnative range, all focal species mainly invade disturbed habitats such as ruderal sites. Although being categorized as a pioneer species, in the past decades *Erigeron* has increasingly been invading undisturbed semi-natural habitats such as species-rich dry meadows (Tunaitienè et al. 2017). In addition to ruderal sites, *Solidago* has been recorded in protected wetlands as well as in economically important habitats such as tree nurseries. *Lupinus* is mainly found in tall forb communities, but thanks to its symbiosis with nitrogen fixing bacteria it is increasingly found in previously nutrient poor meadows, pastures, and riverbanks (Eckstein et al. 2023),

where it can enrich the soil with nutrients and thus cause localized eutrophication.

Removal experiment

We conducted targeted mechanical biomass removal of the three study species in eastern Switzerland. To identify our study sites, we divided the elevation range of the focal species into bins of 100 m. The objective was to have 20–35 sites per focal species within the considered elevation gradient and to survey 2–4 sites within each elevation bin. Most sites were located along roadsides for ease of access and because these are among the main sites of invasion, especially at higher elevation (McDougall et al. 2018).

At each site, we placed a transect through the longest axis, which was defined as the longest section where plants of the focal species were present (Fig. 2a). Each transect of maximum 25 m was divided into sections of 5 m. Within each section, one paired plot of 1 × 1 m was set up, yielding a maximum of five paired plots per site, each plot containing at least one individual of the focal species and with a minimum distance between plots of 1 m. Within each pair, we set up a removal plot (where plants of the focal species were removed) and a control plot. The edges of each plot were marked with metal nails and washers and its position along the transect was noted to aid its relocation with a metal detector during revisitation in the following year. In the case of low-density sites, especially at high elevation, plots were sometimes more distant from each other (e.g., in a transect of 25 m there might be just 2–4 paired plots). In addition, if sites were very small (i.e., to allow only for a single plot), only one removal plot was set up. The latter situation was found mainly at isolated, high elevation sites at the range edges of the study species (5 sites in total: 1 for *Erigeron*, 2 for *Solidago* and 2 for *Lupinus*).

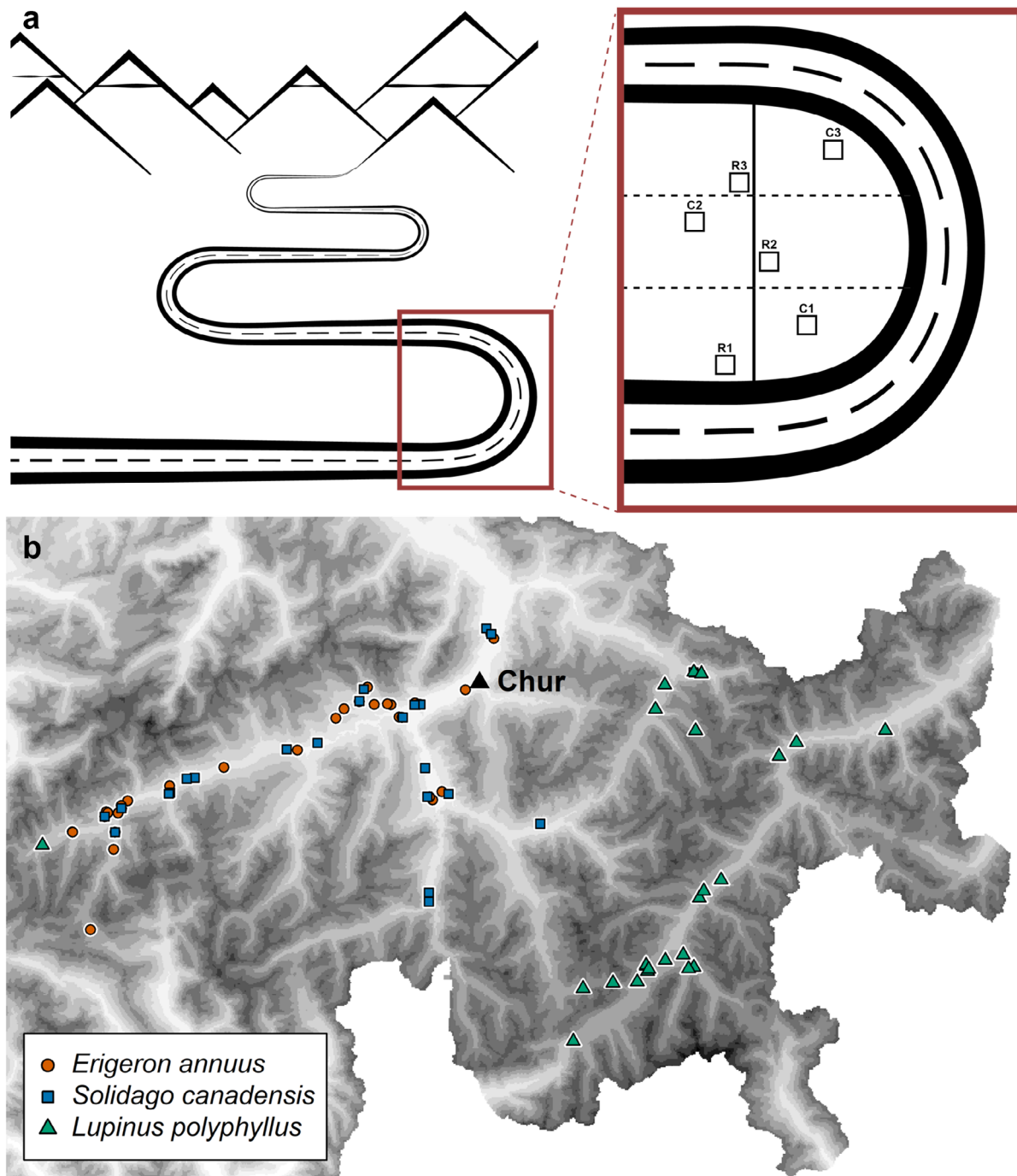


Fig. 2 Overview of the study design of the removal experiment (a). The scheme shows a hypothetical study site with a 15 m long transect, which was subdivided into three bins of 5 m. Within each bin, a removal and a control plot were established, with a minimum distance

of 1 m between them. Map (b) showing the area of the eastern Swiss Alps with the locations of all study sites. The gray scale in the background depicts the elevation range divided into nine bins of equal size, with darker shades indicating higher elevations.

In each plot, we estimated the percentage cover of all nonnative species combined, all native species combined, the focal species, functional groups (native legumes, native graminoids, native forbs) and bare ground, using nine cover classes (0, 0–0.1, 0.1–1, 1–5, 5–10, 10–25,

25–50, 50–75, 75–100, Haider et al. 2022). We estimated plant cover because it considers the size of plants and thus is related to biomass (Axmanová et al. 2012; Jiang et al. 2017), which in turn is a proxy for fitness (Younginger et al. 2017). Hence, estimating cover changes gives insights into

fitness consequences of targeted control measures applied to nonnative plant species. In addition to cover estimates, we counted the number of ramets (for *Solidago*) and stems (for *Erigeron*) within each plot. We carried out these measurements before seed set and before focal plant removal in summer 2021 (07.06.21–30.07.21) and repeated it during revisitation in 2022 (24.05.22–14.07.22).

Removal of target species was carried out mechanically (i.e., in the same way as local managers usually control nonnative plant species in Switzerland) with commonly used tools such as a pickaxe (for perennials) and by hand-pulling (for *Erigeron*). We paid particular attention to removing the entire plant, including the whole rootstock, to avoid leaving root fragments in the soil that could promote rapid regeneration of the perennial focal species. Simultaneously, we avoided creating excessive additional disturbance and left the native vegetation as intact as possible, although disturbance was often substantial in the case of dense populations. If more than one nonnative species was present at a given study site (including other focal species), we removed only the target plant species. Next, we properly disposed of the removed plant material in sealed plastic bags which we brought to the closest incineration plant, to avoid further spreading of propagules through our experiment. Since the management of invasive species in Switzerland involves several different actors (local authorities, NGOs, etc.), we noted whether or not the sites/plots had been recently managed based on a visual assessment.

In total, we surveyed 32 sites (195 plots) for *Erigeron*, 23 (108 plots) for *Solidago* and 24 (140 plots) for *Lupinus* (Fig. 2b). Our study sites were located in different valleys of southeastern Switzerland, mainly in the Canton of Grisons. The elevation range sampled was 539–1824 m a.s.l. for *Erigeron*, 538–1349 m a.s.l. for *Solidago* and 1265–2158 m a.s.l. for *Lupinus*. During revisitation in 2022, four study sites of *Erigeron* and two of *Solidago* were lost because of roadworks which had completely modified or buried all surveyed plots at these locations. In total, due to various types of anthropogenic modifications to surveyed sites, we lost 33 plots of *Erigeron*, 16 of *Solidago* and three of *Lupinus*.

Germination experiment

We collected soil samples at each location during revisitation of the study sites in the second growing season (2022). Since most seeds are usually present in the topsoil layer (Tóth et al. 2022), four soil samples up to 2–3 cm deep (5 cm diameter cores) were collected outside of the edges of control plots (at max. 1 m distance from the borders of the plots). Each soil core collected corresponded to an approximate soil volume of 50 cm³. At each site, we recorded the number of soil cores collected to account for sampling effort, which

was later used as a covariate in models. The soil samples were pooled to form a single aggregate sample for each site. In three (two for *Solidago* and one for *Erigeron*) sites where only one plot was set up, we collected four soil samples outside of the single removal plots. Collections were not performed for *Lupinus* because a preliminary study indicated that too few seeds were retrieved by our methodology (i.e. zero for more than a third of all samples collected).

The approach used for this experiment was adapted from the emergence method outlined in Ter Heerdt et al. (1996), which maximizes the proportion of seedlings germinating from soil samples. Initially, we air-dried all soil samples and sieved them with a relatively large mesh size (6 mm) to remove large particles such as roots, leaves, and stones. Next, since our two Asteraceae focal species have small seeds of about 1 mm length, we used sieves with small mesh size (2 mm). After these preparatory steps, we set up the germination experiment at a greenhouse facility at ETH Zurich. The pooled soil samples of each site were distributed in separate trays in 2 cm thick layers on top of an irrigation mat made of recycled fibers covered by a permeable polyethylene foil, which reduces evaporation and algae growth. Next, we placed the trays on tables with constant water supply. The fabric on the bottom of trays, which is designed to efficiently hold water, ensured constant moisture. In addition, the abundant light and constantly warm temperature (25 °C) allowed for optimal germination conditions. Trays were checked and watered regularly (every 3–4 days). In addition to the 49 soil samples (*Erigeron*: $n=28$; *Solidago*: $n=21$) collected in the field, we set up seven negative controls to check for seeds which might disperse into the greenhouse and could thus influence our results. In these control trays, we paid particular attention to seedlings of the focal species emerging, especially of *Erigeron*, which was present outside the greenhouse. To set up these control trays, we used sterile commercial compost. Only a single seedling of *Erigeron* was found in one control tray, which suggests that wind dispersed seeds had a negligible effect on the outcome of this experiment.

The emerging seedlings were counted and divided into functional groups as in the field survey, but only the two focal invasive species were identified to species level (Fig. S1, Hanf 1970; Muller 1978). In addition, we counted the total number of seedlings which germinated for each study site. Seedlings were discarded immediately after recognition, to avoid excessive shading and root proliferation and thus to maximize germination within soil samples. If a positive identification was not possible, especially in early stages (e.g., when only the cotyledons were visible), single seedlings were transplanted into separate pots to grow until they had developed sufficiently to identify, which was especially important in the case of the focal species. The

experiment was set up in two different rounds of approximately 36 days (01.07.22–08.08.22/18.08.22–23.09.22). Between these two cycles, all samples were allowed to dry out completely for 10 days. Next, the samples were mixed thoroughly within their trays to promote the germination of buried seeds.

Statistical analysis

All analyses were performed in R (R Core team 2022; version 4.4.2). Model assumptions were investigated by simulating residuals with a uniform distribution using the *simulateResiduals* function of the *DHARMa* package (Hartig 2016, version 0.4.6).

Removal experiment

We fitted generalized linear mixed effect models (GLMM) using the *GlmmTMB* function from the *GlmmTMB* package (Brooks et al. 2017; version 1.1.8) to account for our nested data structure. We fitted separate models for each species, where the cover of the focal species in a plot was the response variable, based on the mid-points of our cover classes and specified as beta distributed to account for the bounded nature of the data (i.e., values lie between 0 and 1). Plots nested within sites were fitted as random effects. The fixed effects were elevation (first and second order polynomial using the “poly” function), treatment (control or removal), year (2021 or 2022) and all two- and three-way interactions. In these models, the main effect of treatment represents the average difference in cover between removal and control plots across both years, and the main effect of year represents the average difference in cover between 2021 and 2022 across treatments. When a treatment x year interaction is present, these main effects should not be interpreted in isolation, as the interaction term captures the change in treatment effect over time, which is the primary focus of our analysis. A significant three-way interaction would indicate that the effectiveness of our experimental removal depends on elevation. We tested the significance of the polynomial elevation term using a likelihood ratio test for each species, removing the polynomial when it was not supported. Prior to modeling, we normalized elevation between 0 and 1 to aid effect size comparison and to promote model convergence. Finally, we added background management (which was recorded as a factor, “yes” or “no”) as a covariate to account for additional control measures that may have influenced cover scores. To avoid overfitting, we sequentially dropped non-significant terms from the final models, but also present the full models in Table S1 for comparison.

In addition to these focal species models, we analyzed the change in cover of all other functional groups for which

cover was estimated, to pinpoint additional changes in vegetation within study sites. We fitted one model for each cover group (cover of forbs, graminoids, legumes and bare ground) and for each study species, resulting in 12 models in total. Fixed and random effects were the same as in the focal species models, except that background management was excluded. Polynomial effects of elevation were tested as outlined above.

Germination experiment

We fitted negative binomial regression models (NBRM) to account for the left-skewed distribution of our response variable (the total number of seedlings of the focal species). For each species, we fitted a single model considering elevation (testing and then dropping the second order polynomial in the case of *Erigeron* only, since a polynomial model did not converge for *Solidago*) and mean cover of the focal species in each site as predictors. In each of these models, we added the number of soil cores as a covariate to control for variation in sampling effort (i.e., the total sampled soil volume). To obtain the best possible cover estimate for each study site, we calculated mean cover of all plots in 2021 and control plots in 2022 (which were unaffected by the removal treatment). In the model for *Erigeron*, we eliminated one influential outlier which was characterized by low average cover, high elevation and by far the highest germination rate (152 seedlings emerging in total), based on the high studentized residual (> 3) and Cook’s distance (> 1.5) obtained in the NBRM.

Results

Removal experiment

Mechanical biomass removal resulted in a low recovery of cover in the following year for the perennial species *Solidago* and *Lupinus* (significant year $\times$ treatment interaction, Table 1; Fig. 3; see also plots of cover change in Fig. S2), and a less pronounced but still significant decrease in the case of the annual *Erigeron*.

The cover of *Erigeron* decreased with increasing elevation (Table 1), a pattern that was different between years and weaker in 2022 (significant year $\times$ elevation interaction, Table 1). The cover of *Solidago* did not change significantly with elevation (Table 1). In contrast, the cover of *Lupinus* in 2022 increased towards higher elevation, while in 2021 the cover peaked at mid-elevation (significant year $\times$ elevation interaction, Table 1). Moreover, the cover of *Lupinus* was lower in plots that had received background management (Table 1), which in some sites led to substantially lower

Table 1 Analysis of deviance tables of GLMM models used to analyze the effectiveness of mechanical removal on the cover of the three focal nonnative species

<i>Erigeron annuus</i>		
Variable	Chi-square	P
Year	94.4	<0.001***
Removal treatment	0.3	0.601
Elevation	8.3	0.004**
Year × removal treatment	7.0	0.008**
Year × elevation	21.7	<0.001***
<i>Solidago canadensis</i>		
Variable	Chi-square	P
Year	26.1	<0.001***
Removal treatment	8.7	0.003**
Year × removal treatment	33.7	<0.001***
<i>Lupinus polyphyllus</i>		
Variable	Chi-square	P
Year	53.3	<0.001***
Removal treatment	17.8	<0.001***
poly(Elevation, 2)	4.3	0.038*
Background management	7.9	0.005**
Year × removal treatment	80.3	<0.001***
Year × poly(Elevation, 2)	13.3	0.004**

The degrees of freedom (d.f.) for each predictor were always equal to one (d.f.=1), except for the polynomial and its interaction terms in the *Lupinus* model, where in each case d.f.=2. Site ID and Plot ID were included as random effects (not shown). Non-significant interaction terms and non-significant main effects that were not involved in any significant interactions, were removed from the final models. Significant relationships with a significance threshold of $\alpha=0.05$ are indicated in bold

biomass. Contrary to our main hypothesis, biomass removal effectiveness did not increase with elevation for any species,

as indicated by the non-significant three-way interactions that were dropped from the final models (Table 1; Table S1).

Focal plant removal also caused changes in cover of other groups, with effects that differed between focal species. The management of the perennial focal species led to an increase in bare ground within managed plots (*Solidago*: $\chi^2=9.360$, $df=1$, $P<0.05$; *Lupinus*: $\chi^2=32.208$, $df=1$, $P<0.001$, Table S2, Fig. 4). Removal of *Lupinus* also led to a significant increase in the cover of native graminoids ($\chi^2=3.954$, $df=1$, $P<0.05$, Table S2), indicating some degree of recovery of the native plant community. Removal of *Erigeron* did not cause significant changes in the other cover groups (non-significant year × treatment effects, Table S2). The magnitude of changes in cover of functional groups following invasive plant biomass removal did not vary with elevation (non-significant year × treatment × elevation effects, Table S2).

Germination experiment

The emergence rate of *Erigeron* was much higher (4.08 seedlings/soil core) than that of *Solidago* (0.72 seedlings/soil core). Moreover, we observed that *Erigeron* seedlings appeared to dominate the seed bank in sites in which it grew, representing 49.7% of total seedlings emerging on average, while those of *Solidago* generally accounted for a substantially lower proportion of total seedlings (14.9%).

For *Erigeron*, germination was higher at sites with higher average cover of *Erigeron* and for larger samples (more soil cores; Table 1). Although not statistically significant ($P=0.074$, Table 1), elevation had a slightly negative effect

Fig. 3 Scatterplots indicating the relationship between the cover scores of the three focal species and the elevation of sites in the two growing seasons (2021: upper row; 2022: lower row). The regression lines are displayed as fitted values from GLMMs with beta distributed response variables with year, treatment, elevation and their interactions as predictors (interactions not significant; see Table 2). Note the different y-axis scales for *Erigeron*

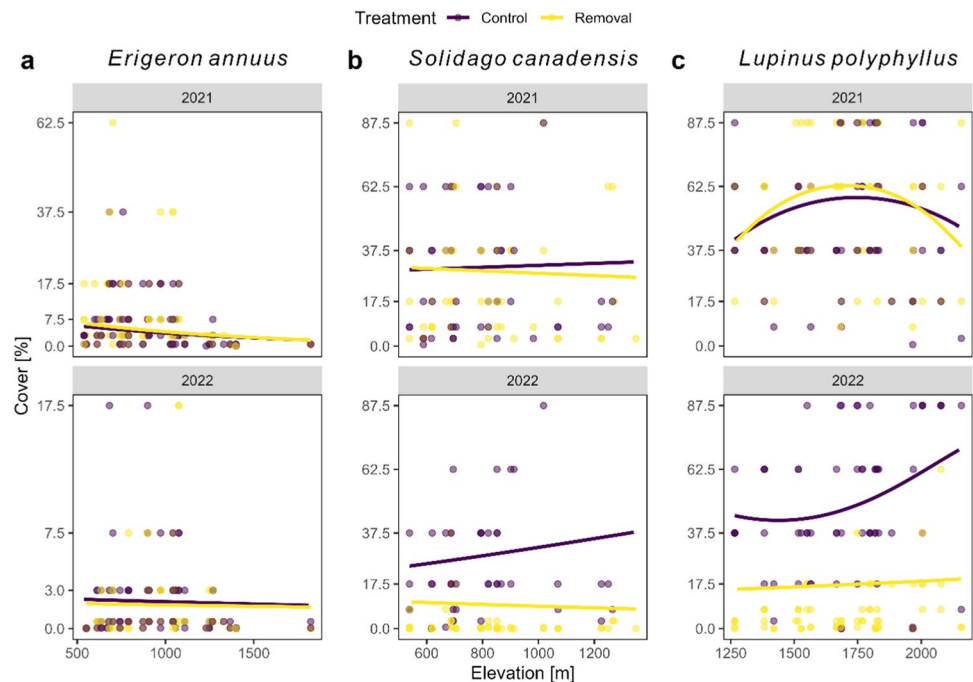
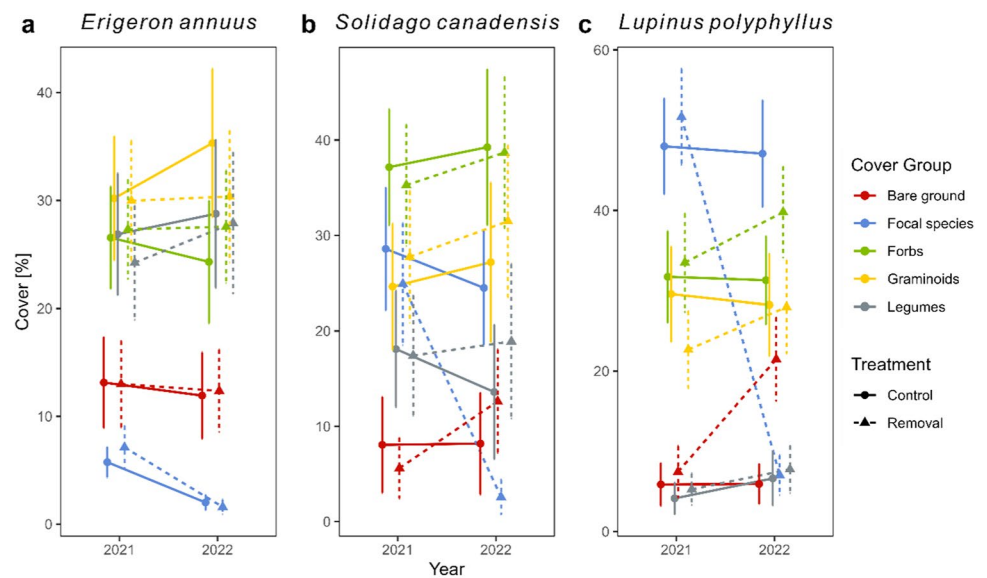


Fig. 4 Average changes ($\pm 95\%$ CI) in percentage cover scores of cover groups recorded over two subsequent growing seasons (2021–2022), illustrating how the managed plots of *Erigeron* (a), *Solidago* (b) and *Lupinus* (c) responded to the removal of biomass compared to unmanaged plots



on the number of germinants of *Erigeron* (Fig. 5a). For *Solidago*, germination decreased significantly with increasing elevation (Table 1; Fig. 5b), while neither average plant cover nor the sampling effort had significant effects on seedling number.

Discussion

Effectiveness of nonnative plant removal

Given the large changes in environmental conditions affecting plant performance and population dynamics across elevation gradients, we hypothesized that the effectiveness of mechanical removal of invasive plants would be greater at higher elevation. However, this was not the case for any of our study species. This may indicate that the variation in environmental conditions affecting invasive species performance along these elevation gradients is not strong enough to slow population recovery, at least in the short-term (one year after management). It is possible that elevation effects on recovery take longer to emerge, for example due to differences in seed bank size or accumulating effects of slower population growth. Nonetheless, we did observe both independent effects of removal and elevation on the cover of populations of all three focal species, pointing to other factors relevant for the management of mountain invasions.

Life history appeared to play a key role in determining the efficiency of management measures. While the cover of our perennial focal species (*Solidago* and *Lupinus*) was strongly reduced by the control measures, the management of *Erigeron* led to a substantially smaller (yet still significant) decrease in cover. These findings are consistent with the elasticity analysis of Ramula et al. (2008), which

showed that population growth of long-lived nonnative species is more sensitive to reductions in survival. In contrast, for annual invasive species such as *Erigeron*, growth and reproduction appear to be more important to promote their spread (Ramula et al. 2008). We observed other differences in cover between years that were likely not related to our removal treatment. In particular, the increasing cover of *Lupinus* at high elevation in 2022 but not 2021 likely reflects prior mowing at some high elevation *Lupinus* sites in 2021 (captured by the background-management covariate). The generally lower cover range of *Erigeron* in 2022 compared to 2021 might also be explained by earlier sampling and/or differences in climatic conditions between years. Both factors can influence plant phenology and aboveground biomass, potentially leading to lower cover estimates in the second year (the covariate 'year' accounts for these sources of variation). Although we observed a strong reduction in abundance of both perennial study species, in most cases some individuals persisted within managed plots, suggesting that a single intervention is not sufficient to eradicate these focal species from invaded sites. The persistence of perennials likely reflects resprouting from protected bud banks that were missed during removal, which enable survival even when aboveground biomass is removed (Klimešová et al. 2018; Ott et al. 2019; Weber 2011).

Mechanical removal of the target species also led to a substantial increase in the area of bare ground. The failure of native vegetation to rapidly re-fill the gaps in managed sites suggests that native species might be affected by recruitment limitation. Indeed, gap creation at managed sites can promote the establishment of other nonnative plant species (Banks et al. 2018), especially through the dispersal of propagules from adjacent populations (Dietz and Edwards 2006). However, in our experiment, co-invasions

Fig. 5 Scatterplots depicting the relationship between (a, c) elevation and (b, d) mean cover of focal plants at a given site and the total number of seedlings of *Erigeron* (a, b) and *Solidago* (c, d) emerging from soil samples. Plots for *Erigeron* were produced by dropping a single, influential outlier (not shown). The regression lines are predictions from Negative Binomial Regression Models (NBRMs) fitted within the range of elevation or mean cover, while all other predictors were kept at their mean values. Red lines depict significant relationships, while black lines indicate non-significant ones

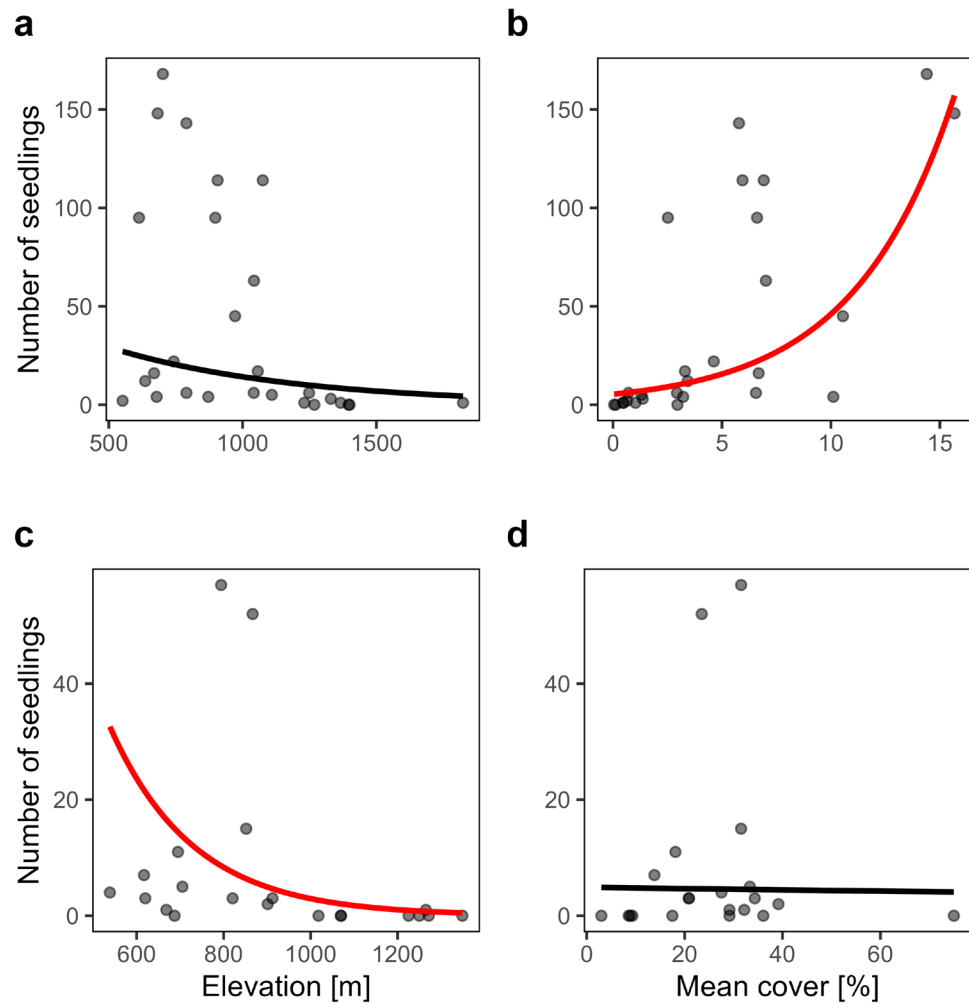


Table 2 Summary of NBRM models analyzing the number of seedlings of focal nonnative species emerging in relation to elevation, mean focal invasive plant cover, and sampling effort (number of soil cores) *Erigeron annuus* – ($N = 26$, $d.f. = 23$)

	Estimate	Std. Error	Z-score	<i>P</i>
Intercept	0.843	1.189	0.709	0.478
Elevation	– 0.001	0.001	– 1.784	0.074
Mean cover	0.216	0.052	4.168	0.000***
Number of soil cores	0.187	0.046	4.035	0.000***

Solidago canadensis – ($N = 21$, $d.f. = 17$)

	Estimate	Std. Error	Z-score	<i>P</i>
Intercept	5.490	2.619	2.619	0.036*
Elevation	– 0.005	0.002	– 2.443	0.015*
Mean cover	– 0.002	0.027	– 0.088	0.930
Number of soil cores	0.094	0.083	1.139	0.255

Significant relationships between the response variable and predictors are indicated in bold. The significance threshold used is $\alpha = 0.05$

were uncommon and we did not observe short-term replacement by other nonnative species, suggesting a negligible influence on short-term post-management dynamics. Low availability of propagules of native species at invaded sites

has been observed in previous studies (Standish et al. 2007; French et al. 2011), so that limitations in the availability of germinable native seeds may slow the recovery of local plant communities.

The cover of two of our focal species was affected by elevation. Multiple correlated climatic and anthropogenic variables covary with elevation in our study region (Fig. S3), such as temperature, precipitation, and human population density, all of which might influence ‘nonnative plant’ population density. While our study was not designed to disentangle these factors, the decline in cover observed for *Erigeron* with increasing elevation is in line with previous findings (Seipel et al. 2016; Becker et al. 2005). This effect might be explained by a combination of an increasing population turnover at higher elevation (i.e., higher mortality combined with lower regeneration) preventing the development of large populations, and declining habitat quality (Seipel et al. 2016). The cover of *Lupinus* was also related to elevation, but tended to be greater at high elevations, although cover peaked at mid elevations in 2021. This

is consistent with the known adaptation of this species to cooler climates (Eckstein et al. 2023). In contrast, no significant effect of elevation was observed on the cover of *Solidago*. Since our sampling included most of the elevation range of this species in Switzerland, this is unlikely to be because we missed important environmental variation. Rather, conditions within the climatic range of this species might allow it to maintain density, even if individual fitness has been shown to decline with elevation (Seipel et al. 2016).

It is important to note that recovery in this experiment is likely somewhat overestimated, because populations were not entirely eradicated and the plot size was relatively small (1 m²), unlike in regular management interventions aiming for complete removal of nonnative individuals. As a result, local seed rain from individuals that remained outside or at the edges of removal plots (especially for *Erigeron*) or rhizome spread (*Solidago*, *Lupinus*), likely contributed to the recolonization of managed plots. This ongoing propagule pressure may have accelerated post-removal recovery, especially in the short term, as observed in other studies on invasive plant management (e.g., Hulme 2006). In reality, recolonization following management will be driven by propagules arriving from other populations (in addition to any missed individuals within the site), which will take longer than in our study, especially if populations are spatially isolated from potential sources. Furthermore, our study reflects a common pattern in the literature where most invasive plant control experiments are conducted at small spatial scales (often ≤ 1 m², Kettenring and Adams 2011), which may limit generalizability but still provides valuable insights into ecological mechanisms. Nevertheless, this limitation does not compromise the conclusion that elevation did not significantly affect removal effectiveness, assuming local seed dispersal or rhizome ingrowth occurred similarly across the elevation gradient.

Variation in seed bank size

The dominance of *Erigeron* in the soil seed bank that we observed in soil sampled from *Erigeron* populations is consistent with the large number of seeds that this species can produce (InfoFlora 2020). Indeed, the seedling number increased with adult plant density, likely reflecting higher rates of seed production. Allelopathic effects of *Erigeron* are also known to inhibit the germination of other species (Oh et al. 2002), though we have no evidence for this in our study. Annuals rely entirely on regeneration from seeds and hence must invest in seed number and longevity to generate long-lasting seed banks with high germination potential (Ramula et al. 2008). In contrast, many fewer seedlings of *Solidago* were observed, in line with the poor germination

of this species found in previous work (Poll 2007). Low seed regeneration might contribute to the lower recovery found for *Solidago* in the removal experiment, emphasizing its greater reliance on survival (Ramula et al. 2008).

For both *Erigeron* and *Solidago*, we observed significant decreases in the number of seedlings emerging with increasing elevation, possibly due to a combination of smaller population size and greater isolation of populations. Notably, total seedling emergence (i.e., including all focal and non-focal species) did not significantly decline with elevation (Fig. S4), suggesting that the patterns observed in our focal species reflect species-specific dynamics rather than a general reduction in seed bank size along the elevation gradient. While elevation itself is not a causal factor, it integrates multiple climatic and anthropogenic variables (Fig. S3), which could contribute to these patterns. Declining seed bank sizes might help explain observations of higher population turnover rate at higher elevations and the relatively stable upper elevation limits that have been found for both *Erigeron* and *Solidago* in this part of Switzerland (Seipel et al. 2016). Importantly, this result also suggests that if repeated over several years, removing plants before they set seed might in fact be more effective at high elevation, because the soil seed bank will be depleted more quickly. Therefore, to contain the spread of widespread annual invaders like *Erigeron*, an effective strategy might be to target nascent populations at the range edge (Moody and Mack 1988). In so doing, management measures could limit the ability of the invasion to be “pulled” to yet higher elevations by populations at the range front (Pachepsky and Levine 2011), reducing rates of spread and thereby helping to maintain the relatively low levels of invasion seen in high elevation environments (Alexander et al. 2016, McDougall et al. 2011).

Management recommendations

Although the cover of our perennial focal species can be drastically reduced by a single management intervention, focal invasive plants could not be eradicated from most removal plots, indicating the need for long-term control programs to successfully contain these invasive species (Kettenring and Adams 2011). In the case of *Lupinus*, Hansen et al. (2022) showed both the high effectiveness of targeted mechanical removal and the necessity of setting up management programs over multiple years. The latter are typically characterized by a large initial effort, but in following years the workload is greatly reduced since the focus gradually shifts from “brute-force” methods to monitoring and removal of small plants (Mack and Lonsdale 2002). In contrast, for annual invasive species such as *Erigeron*, which can undergo multiple flowering cycles per year, a single removal per year is likely to be ineffective, and a

different strategy may be required. For short-lived species with large reproductive output and broad distributions, we suggest focusing on high-priority sites, such as in protected areas, and applying multiple control cycles per year over multiple years if possible. To properly deal with potentially large seed banks of annual plants, it would be worthwhile to consider topsoil removal. But given the ubiquitous distribution of *Erigeron* in Switzerland, this might be feasible only in small, high-priority sites, and even there it is likely to severely impact native species by locally depleting the native seed bank (Buisson et al. 2006).

One way to promote the restoration of managed sites during long-term control schemes would be to sow native seed mixtures (Kettenring and Adams 2011). This strategy can be implemented through the use of green hay from species-rich donor meadows, which can counteract the invasive species dominance through an increase in interspecific competition while also maintaining the genotypic composition of local grassland communities (Wagner et al. 2021; Valko et al. 2021). In fact, we observed *Solidago* in private gardens at elevations above the elevation limit of wild populations, perhaps because reduced competition in gardens allows it to thrive. In sites invaded by *Lupinus*, previous work has shown that a combination of early mowing, which avoids spread of propagules in meadows (Ramula 2020), and green hay application, which contains viable seeds of native species, can be an effective strategy (Hansen et al. 2022). Unfortunately, Kettenring and Adams (2011) showed that in the majority of nonnative plant control experiments, active revegetation was neglected, hampering restoration efforts at managed sites. If the bare soil surface is left open it may represent an “open-niche”, which can promote reinvasion by the species that were initially removed or invasion by other nonnative species (French et al. 2011; Banks et al. 2018). Therefore, we urge the consideration of seed bank management while designing control programs.

In sum, we found only limited evidence that the short-term efficiency of mechanical removal of invasive species varies with elevation. However, smaller soil seed banks at higher elevation imply that following repeated interventions over multiple years, population control might be more effective at higher elevation in the longer term. Further research into management measures along elevation gradients is needed with more species and in different geographic contexts to assess the generalizability of these patterns.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00035-025-00342-2>.

Acknowledgements We thank Omar Lain Lacosta for assistance with fieldwork and Dieter Ramseier for advice on setting up the germination experiment. This research was funded through the 2019–2020 BiodivERsA joint call for research proposals, under the BiodivClim

ERA-Net COFUND programme (project ‘RangeX’) and with the funding organizations Innovation Fund Denmark, Department of Science and Innovation Republic of South Africa, the Research Council of Norway, the Swiss National Science Foundation, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning and the German Research Foundation. J.M.A. received funding from the Swiss National Science Foundation (grant no. 20BD21_193809).

Author contributions Conceptualization: G.V.F., J.M.A.; Methodology: G.V.F., J.M.A., S.G.; Data collection: G.V.F.; Formal analysis and investigation: G.V.F., J.M.A.; Writing - original draft preparation: G.V.F., J.M.A.; Writing - review and editing: G.V.F., J.M.A., S.G.; Funding acquisition: J.M.A.; Supervision: J.M.A.

Funding Open access funding provided by Swiss Federal Institute of Technology Zurich

Data availability All data and code associated with this article are available, upon reasonable request, on the following GitHub repository: [https://github.com/GeorgF92/RemovalCH_Manuscript].

Declarations

Competing interests The authors declare no competing interests.

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