

## Research

### Disturbance and indirect effects of climate warming support a plant invader in mountains

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#### Oikos

2022: e08783

doi: 10.1111/oik.08783

Subject Editor: Anna Traveset

Editor-in-Chief:

Gerlinde B. De Deyn

Accepted 4 January 2022



Climate warming and increased disturbance (resulting from intensified land use) are expected to enhance the invasibility of plant communities and the performance of exotic species also at high elevations, and thus pose additional threats to mountain ecosystems. The invasion success of introduced genotypes will also depend on their degree of pre-adaptation to high elevation climatic conditions, which may vary intraspecifically across source populations. For populations currently spreading in the lowlands, climate warming might reduce the climatic distance to high-elevation sites and thus remove a barrier to upwards spread.

Here, we investigated the various facets of mountain invasions in a single, integrative experimental study. We applied a community transplant approach between high- and low-elevation sites in the European Alps to address effects of climate warming and disturbance through land use on community invasibility and the performance of the exotic species *Senecio inaequidens*, a potential future plant invader in the Alps. Additionally, the transplant sites served as common gardens to test the influence of climatic pre-adaptation to current (high site) and future (low site) climatic conditions on the performance of *S. inaequidens* in the transplanted communities. The 16 invasive central and western European *S. inaequidens* source population locations covered a wide geographic range, and thus a wide amplitude of climatic distances and presumed pre-adaptation to our gardens.

Our results attest to a strong effect of disturbance, which increased community invasibility, and promoted the performance of the exotic species. Contrary to our expectation, experimentally induced climate warming did not increase community invasibility. However, the performance of the *S. inaequidens* populations was positively related to their pre-adaptation to the climatic conditions of our common gardens. Climate warming might thus promote the invasion of exotic species by reducing the climatic distance between mountain ranges and locations of potential source populations.



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Keywords: climate warming, common garden experiment, mountain ecosystems, plant invasions, *Senecio inaequidens*, small-scale disturbance

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## Introduction

Biodiversity in montane regions is threatened worldwide by two components of global change: increasing land-use conversions and climate warming (Petitpierre et al. 2016). Moreover, there is mounting evidence of exotic species invading montane regions (Becker et al. 2005, Marini et al. 2009). The number of exotic species in alpine areas is still relatively low compared to other ecosystems (McDougall et al. 2011, Zefferman et al. 2015), but like in lowlands, plant invasions at high elevation will be favored by increasing human landscape use and the resulting disturbance (Marini et al. 2009, Haider et al. 2018), and by higher temperatures (Sorte et al. 2013, Petitpierre et al. 2016). Both global change drivers have the potential to increase the invasibility of native communities and thus the invasion of exotic species.

Increased human land use in montane areas (tourism, expanding infrastructure, construction of buildings, ski pistes) results in the destruction of biomass, usually creating patches of open habitat (i.e. disturbance). Consequently, disturbance leads to reduced competition and has been shown to promote plant invasions also in montane regions (Petryna et al. 2002), because exotic species often possess traits ideally suited to disturbed sites, including rapid growth rates and high seed production (van Kleunen et al. 2015). The benefits for exotic species through disturbance are expected to be particularly strong in highly productive and competitive plant communities (Alpert et al. 2000, Moles et al. 2012).

Climate warming, which is particularly pronounced at high elevation (Pepin et al. 2015), might further enhance the invasibility of native montane communities (Petitpierre et al. 2016). Here, weakened biotic resistance to exotic invaders or native range expanders moving up from lowlands might result from reduced competitive performance of the dominant resident species (Alexander et al. 2015), and the disruption of established biotic interactions (Alexander et al. 2018). Furthermore, climate is one of the most important filters in species invasions (Rouget et al. 2004, Richardson and Pyšek 2012), and rising minimum temperatures and extended growing seasons might reduce the climatic barrier which currently restricts many abundant exotic species to lower elevation (Alexander et al. 2011, Petitpierre et al. 2016). Given that invasive species are typically capable of rapid spread, it is likely that they will respond quicker than most native species to the upward shift of climatic barriers. Thus, climate warming is likely to promote growth, competitive ability and reproduction of exotic species currently spreading in the lowlands by decreasing the distance between current lowland climate and future highland climate (Compagnoni and Adler 2014).

The establishment success of exotic populations colonizing montane areas will also be governed by their degree of climatic pre-adaptation. The steep climatic gradient associated

with elevation can present an effective barrier to upward migration of any species (Alpert et al. 2000). However, widespread exotic species might have already locally adapted to diverse climatic conditions across their introduced ranges (Oduor et al. 2016). Such intra-specific differentiation in concert with the increasing transportation of seed material by humans (Barros and Pickering 2014) enhances the probability that climatically pre-adapted genotypes get introduced either to valleys in montane areas from which they might migrate upwards (Kalwij et al. 2015) or directly to high elevation (McDougall et al. 2005).

Here, we report on a common garden experiment that jointly investigated whether disturbance, reduced biotic resistance of the resident community through climate warming and climatic pre-adaptation increase the establishment success and performance of an exotic species in an alpine region. We expect that these three factors affect both the invasibility of the resident communities and the performance of potentially pre-adapted genotypes of the exotic species. We established a common garden site at both high and low elevation in the European Alps. We reciprocally transplanted disturbed and undisturbed turfs of the resident grassland communities between these sites. In these turfs we planted seedlings from 16 invasive European source populations of South-African ragwort *Senecio inaequidens* that varied in their climatic similarity to the common garden sites and thus in their potential degree of climatic pre-adaptation. We hypothesized that the establishment success and performance of *S. inaequidens* are promoted through 1) disturbance, particularly in productive, low elevation communities, 2) reduced biotic resistance of high-elevation turfs through climate warming simulated through their transplantation to the low-elevation common garden and 3) climatic similarity between the location of *S. inaequidens* source populations and the common gardens.

## Material and methods

### Study species

To test our hypotheses, we chose the perennial herb *Senecio inaequidens* (Asteraceae), which is one of the plant invaders in Europe with the highest range expansion rates. The species was introduced at the end of the 19th and the beginning of the 20th century from South Africa and Lesotho where it occurs at altitudes up to 3100 m a.s.l. (Lachmuth et al. 2010). To date, populations have established in large parts of central and western Europe, covering a wide climatic gradient (Fig. 1). Experimental studies further demonstrated genetically based clinal variation in vegetative growth along elevational gradients in Europe (Monty and Mahy 2009). Moreover, *S. inaequidens* is likely still expanding its range

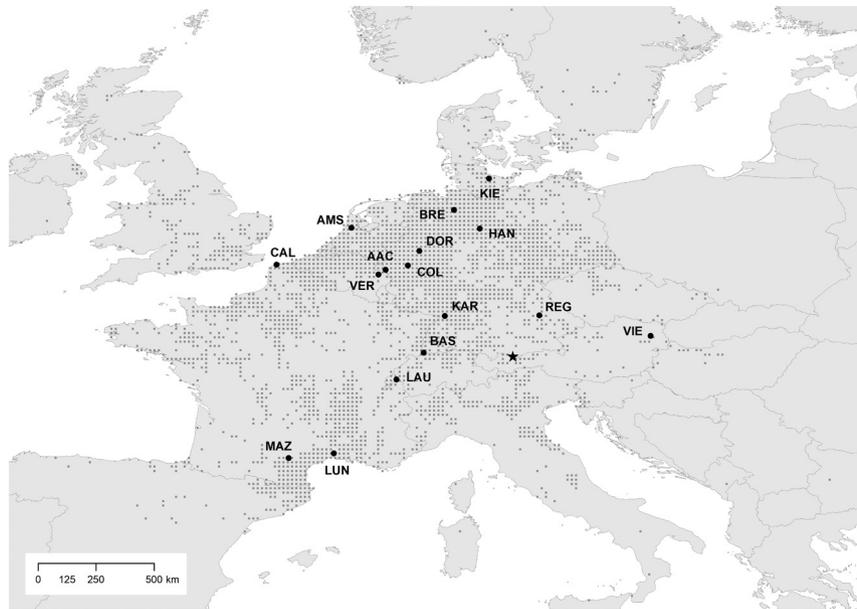


Figure 1. Geographic range of *Senecio inaequidens* in central and western Europe (grey dots; after Meusel and Jäger (1992), refined and updated 2016 by Erik Welk). Black dots indicate the source populations, while the black star denotes the location of the common garden sites in the German Alps. Abbreviations are given in the Supporting information.

and the lack of high elevation populations may be caused by a dispersal lag rather than physiological limits of the invasive genotypes (Vacchiano et al. 2013).

We sampled 16 populations of *S. inaequidens* distributed across central and western Europe (Fig. 1, Supporting information). For each population, we obtained the year of first observation in the respective area (25 km radius) from floristic literature and databases (Lachmuth et al. 2010, Supporting information). Populations selected for the experiment had been established for at least 16 years (up to 111 years, median 24 years) by the time of seed collection as this time period is sufficient for local adaptation (Carroll et al. 2007, Lachmuth et al. 2011). Based on AFLP markers (Lachmuth et al. 2010, 2015) that were polymorphic for our 16 populations, we calculated mean pair-wise co-ancestry coefficients of individuals among and within invasive populations in Europe using the admixture F model approach implemented in the R-package RAFM (Karhunen and Ovaskainen 2012). Just as individual-level relatedness coefficients are useful in gene mapping, since they estimate how much two individuals are expected to resemble each other, population-level co-ancestry coefficients quantify the average expected similarity between local populations as well as between individuals within populations (diagonal of the co-ancestry-matrix; de Villemereuil et al. 2020). Together with phenotypic data the coefficients can thus separate signals of selection in quantitative traits from those of random drift (Karhunen and Ovaskainen 2012). Since the original R-package has been developed for co-dominant markers, we used a new version adapted for dominant markers (Karhunen and de Villemereuil 2016) in R ver. 3.4.3 (<www.r-project.org>). To obtain the posterior mean co-ancestry matrix we ran the *AFM* function with 50 000 iteration steps, discarded

the first 20 000 samples as burn-in and thinned the remaining samples by storing every 10th iteration step.

For our experiment, we used pre-grown seedlings instead of a seeding approach to avoid uncontrolled establishment of *S. inaequidens*. The species is not present (yet) at any of the two common garden sites, and from a nature conservation point of view it would be unethical to risk establishing this problematic species by planting potentially dormant seeds. However, we thus miss information about the first stage of the species' life cycle and will interpret our results with caution.

We collected seeds from five mother plants in 2006 or 2007 in each of the 16 *S. inaequidens* populations. Within populations, we mixed seeds from different mother plants at equal parts and germinated them on a 3:2-mixture of fine compost and sand in the greenhouse. Seed age was not considered problematic, because observed germination rates in the greenhouse were still high, and additionally we corrected for initial seedling size in all statistical models. Temperature was 20°C during the day and 10°C during the night (12 h/12 h), and seedlings were watered every day. After four weeks, they had developed first true leaves and were planted into the common gardens. Since planting at the high-elevation site was one month later than at the low-elevation site, seedlings were raised in two batches. Directly before planting, we measured stretched height of each seedling as a proxy for biomass to later account for differences in size at the beginning of the experiment.

### Transplant experiment

Two common gardens (hereafter 'sites') were established in the German part of the European Alps (Supporting

information). The low-elevation site in the village of Grainau (758 m a.s.l.; 47°28'34.29"N, 11°00'40.45"E) was located in a typical species-rich, montane hay meadow and is usually mown two or three times per year. The high-elevation site at Hochalm (1737 m a.s.l.; 47°26'29.12"N, 11°03'42.26"E) was part of a larger alpine pasture, which is usually grazed by young cattle for one to two weeks per year. The extensive grazing leads to high species richness and makes these ecosystems valuable for nature conservation. During the experiment, both sites were fenced to exclude large animals and mown at the end of the growing season to simulate the previous management regimes.

To investigate the effects of disturbance, climate warming and community origin on community invasibility and invasion success of the different *S. inaequidens* populations we established a community transplant experiment at the two sites. The community transplant approach has become a widely used and accepted standard in ecological climate change research over the past decade (Alexander et al. 2015, Vandvik et al. 2020a). However, a possible limitation of our experiment is that the climate-warming treatment was not replicated and applied along a single elevation gradient. Hence, results need to be carefully interpreted and cannot be easily generalized.

In each garden, 112 turfs with a size of 25 × 25 cm and a depth of 15 cm were cut with a spade and removed from the holes in late September 2013. Aboveground vegetation on the turfs was cut down to 2 cm above the soil surface. Half of the turfs were reciprocally transplanted to the other site, i.e. each site contained 56 turfs from the low-elevation site (hereafter 'lowland origin' or 'lowland community') and 56 turfs from the high-elevation site (hereafter 'highland origin' or 'highland community'). The turfs from the high-elevation site transplanted to the low-elevation site represented climate warming. The transplanted turfs were inserted in the holes created through turf removal whereby half of the turfs from each origin were turned upside down (Welk et al. 2019), mimicking disturbances caused for example by vehicles that tear up the ground such as snow groomers, construction and farm vehicles, quads, mountain bikes or grazing animals. We monitored the effect of our one-time disturbance by regularly estimating vegetation height and cover in each plot (Supporting information). Within gardens, we randomized the positions of the turfs entirely, since our sites had no inclination and seemed environmentally homogenous, thus rendering the establishment of blocks to represent suspected environmental clines arbitrary. In total we had four turf (hereafter 'plot') treatments at each site: 1) lowland origin – undisturbed, 2) lowland origin – disturbed, 3) highland origin – undisturbed and 4) highland origin – disturbed (Supporting information).

The pre-grown seedlings of *S. inaequidens* were planted in April 2014 at the low-elevation site and in May 2014 at the high-elevation site (i.e. seven and eight months after turf transplantation, respectively). In the centre of each plot, we planted four seedlings in a square with a distance of approximately 8 cm between seedlings and 8 cm from the edge of

each turf plot (in total 896 seedlings). For another research question in the same project, but not analyzed here, the four seedlings per plot were planted in 'monocultures', two-population-mixtures and four-population-mixtures according to a 'broken-stick' design (Bell et al. 2009), which is a design commonly used in biodiversity experiments to ensure that all species are equally represented at each diversity level. In our case, this design assured that each population occurred once in each of the three diversity levels and in each of the four plot treatments – again, randomized entirely within sites. Since 'mixture' by itself was not of interest for this paper, it was later included only in the random structure of our statistical models.

To test, if climatic pre-adaptation matters for seedling survival and growth, we calculated climatic distances between each of the source population locations and the two common garden sites. Since the source populations were located in temperate as well as in Mediterranean areas (Fig. 1), we decided to include both temperature and precipitation in the calculation of climatic distance, which acknowledges the different seasonal rainfall patterns. The combined use of temperature and precipitation is a typical approach to describe species niches as well as climatic distances (Broennimann et al. 2012, Sporbert et al. 2020). To approximate the climate that source populations may have adapted to during the time period since the establishment of our youngest populations, we extracted monthly mean temperatures and precipitation sums for the sampling locations spanning the time period from 1989 to 2006 from climateEU (Marchi et al. 2020, for details see the Supporting information). Climatic conditions at the common gardens during the experiment (May 2014–April 2015) were derived from mean monthly temperatures and precipitation measurements at nearby climate stations (for details see the Supporting information). To estimate climatic distances between the source population locations and common garden sites we calculated a Euclidean distance matrix using the monthly temperature means and precipitation sums, centered and scaled to values between 0 and 1 (Oksanen et al. 2017). In view of the fact that the data for different response variables were collected at different points in time (below), we calculated the climatic distances for the analyses of above-ground biomass and flowering probability based on climate data for the months May to August only, whereas for the analysis of survival we used climate data for all months. Because in Europe *S. inaequidens* does not yet exist at locations with climate similar to that of our high-elevation garden site, all climatic distances to this garden were larger than the highest distance to the low-elevation garden. However, this circumstance did not influence our results, as demonstrated in separate analyses for the two common garden sites (Supporting information).

We assessed invasion success of *S. inaequidens* at the individual level by quantifying the flowering probability and above-ground biomass by the end of the vegetation period as well as survival from the start of the experiment through the next winter. In September 2014, we assigned a reproductive status of either vegetative or flowering to target plants at

both sites. To prevent naturalization of *S. inaequidens* we cut buds and flowers regularly (i.e. before the onset of seeds). We termed plants flowering if they had developed either buds or flowers throughout the season since we had no reason to assume that budding plants would not have been able to flower. We harvested the target plants by cutting them at 2 cm above the surface. Since *S. inaequidens* is highly tolerant to mowing and re-sprouts from either its woody stem base or main root after both mowing and over-wintering (Heger and Böhmer 2005), regrowth after winter should not be negatively affected by this approach. In the lab, plants were dried in the oven at 80°C for 72 h and dry mass was weighed. Since the target plants were planted one month earlier at the low-elevation site, and thus grew one month longer (five months) than those at the high-elevation site, we estimated their above-ground biomass after four months (i.e. August). To this end, we regressed above-ground biomass at harvest against stretched height at harvest, using a linear mixed effects model (function *lmer* in *lme4* package; Bates et al. 2015) with source population and treatment as crossed random factors (Supporting information). We then calculated the August above-ground biomass based on height measurements from August and the parameter estimates of the mixed model. To evaluate survival of the target plants after a full year (including winter), we revisited the low-elevation site in May 2015 and the high-elevation site in July 2015. After this final census, all target plants (dead or alive) were dug out including the whole root, and were disposed.

## Statistical analyses

For statistical analyses we used (generalized) linear mixed animal models (R package *pedigreemm*; Bates and Vazquez 2014) in R ver. 3.4.3 (<[www.r-project.org](http://www.r-project.org)>). We adapted these models in a way that allowed weighing the population random effect for population co-ancestry (de Villemereuil et al. 2018) to account for non-adaptive differentiation because of genetic drift, which might mask or falsely suggest local adaptation. This way, populations with high co-ancestry are considered less independent repetitions, whereas distantly related populations are considered relatively more independent. The same holds for individuals within populations. By contrast, in a standard mixed model all populations would be considered entirely independent samples. In the hypothetical case of zero among-population and constant within-population co-ancestry, the applied animal models would be identical to the respective standard mixed models. At the between-species level, this type of correction is well established in comparative mixed effects analyses of macro-evolutionary change (Housworth et al. 2004).

Above-ground biomass was analyzed with a linear mixed effects model, whereas for flowering and first-year survival we used generalized linear mixed models with a logit link function and binomial error distribution. Biomass was ln transformed to achieve homogeneity of variance and normal distribution of residuals, as confirmed by model diagnostic plots. As explanatory variables we included as fixed effects the

continuous variable climatic distance, the factors site (high-elevation, low-elevation), community origin (highland, lowland) and disturbance treatment (undisturbed, disturbed) as well as all possible three- and two-way-interactions among those variables. The main assumption of hypothesis 1 (disturbance promotes *S. inaequidens*) would be supported through a significant positive main effect of disturbance. To confirm the sub-ordinate assumptions of hypothesis 1 (stronger disturbance effect in low elevation communities), significant disturbance-by-community origin and disturbance-by-site interactions would indicate a stronger effect of disturbance for lowland turfs and at the low-elevation site, respectively. According to hypothesis 2 (reduced biotic resistance of high-elevation turfs through experimentally induced climate warming, i.e. after transplantation), a significant site-by-community origin interaction would show the best performance of *S. inaequidens* in the highland turfs transplanted to the low-elevation site. Hypothesis 3 expects a significant negative main effect of climatic distance on *S. inaequidens*. In addition to the explanatory variables, all models contained the plant height at the time of planting as a covariate and the crossed random effects of source population (weighted for co-ancestry) and plot, the latter nested within mixture ('monoculture', two-population- or four-population-mixture). The continuous explanatory variables (plant height and climatic distance) were centered by subtracting the mean and scaled by dividing the centered mean by its standard deviation. The full models were fitted with a maximum likelihood approach and simplified in a step-wise backward procedure based on likelihood ratio ( $\chi^2$ ) tests to obtain the minimal adequate models. Thereby, non-significant main effects were never deleted when they were part of a significant interaction.

## Results

Disturbance had a clear positive effect on *Senecio inaequidens* biomass production (Fig. 2). The disturbance treatment promoted a strong increase in biomass at the high-elevation site, but only a slight increase at the low-elevation site (significant interaction of site and disturbance,  $\chi^2=48.759$ ,  $p < 0.001$ ; Fig. 2a, Supporting information). In disturbed plots, above-ground biomass was greater in both lowland and highland community origin, but this effect was stronger for the lowland origin (significant interaction of community origin and disturbance,  $\chi^2=18.072$ ,  $p < 0.001$ ; Fig. 3a, Supporting information). Biomass production decreased with increasing climatic distance from the source population location. However, this effect was only apparent at the low-elevation site (significant interaction of climatic distance and site,  $\chi^2=18.850$ ,  $p < 0.001$ ; Fig. 4a, Supporting information).

Overall, 20.6% of the 689 plants that survived the first growing season (i.e. until the time of biomass harvest in August/September 2014) started flowering. Across sites and community origins, flowering probability was significantly higher under disturbed conditions ( $\chi^2=143.758$ ,  $p < 0.001$ ; Fig. 2b, Supporting information). A higher proportion of

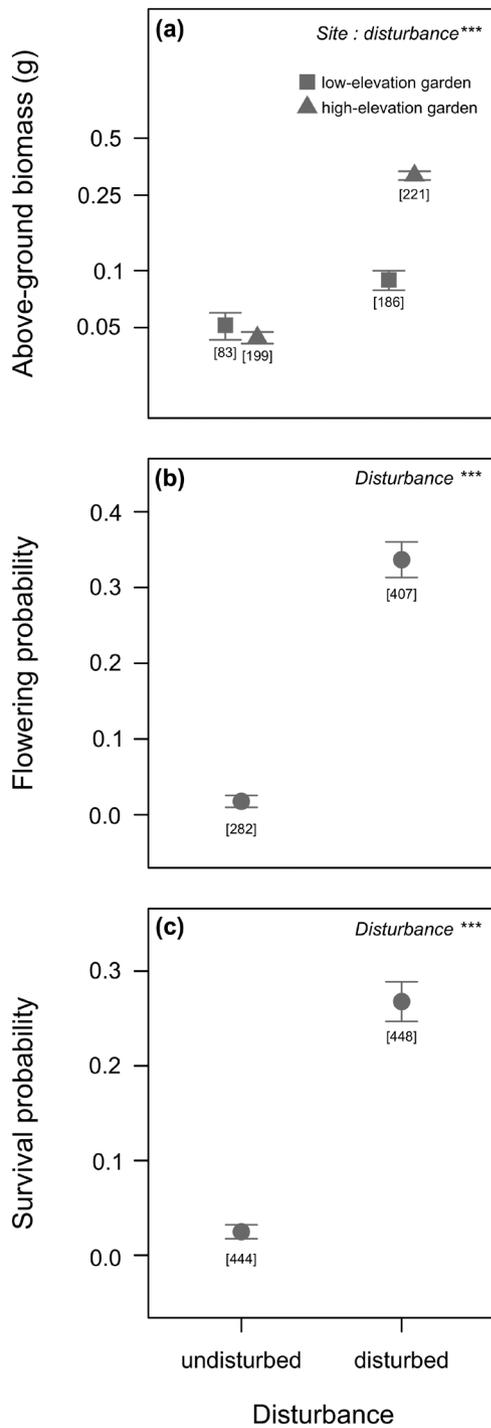


Figure 2. Effects of disturbance treatment on the performance of planted *Senecio inaequidens* individuals. Dots represent raw data means  $\pm$  standard errors. (a) Interactive effects of disturbance treatment and common garden site on oven-dried above-ground biomass; (b) main effect of disturbance treatment on flowering probability; (c) main effect of disturbance treatment on first-year survival probability (spring 2014 to spring 2015). The y-axis of (a) is shown on a log-scale. Sample numbers are given in parentheses and stars indicate levels of significance: \*\*\*  $p < 0.001$ .

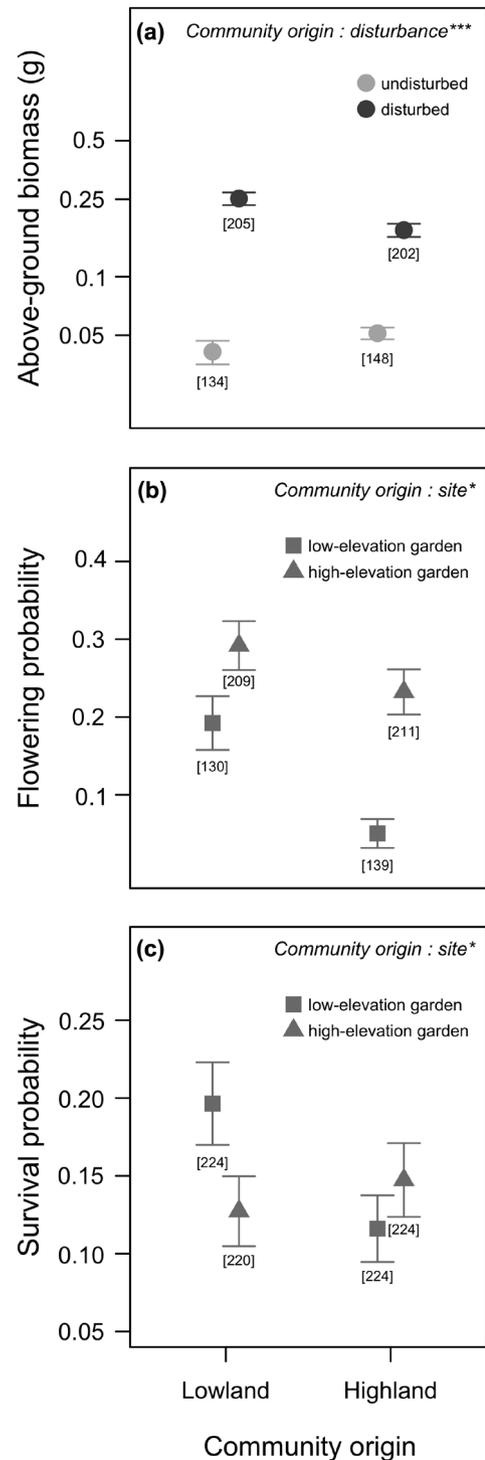


Figure 3. Effects of plant community origin of the transplanted turfs on the performance of planted *Senecio inaequidens* individuals. (a) interactive effects of community origin and disturbance treatment on oven-dried above-ground biomass, (b) interactive effects of community origin and common garden site on flowering probability, (c) interactive effects of community origin and common garden site on first-year survival probability (spring 2014 to spring 2015). Dots represent raw data means  $\pm$  standard errors. The y-axis of (a) is shown on a log-scale. Sample numbers are given in parentheses and stars indicate levels of significance: \*  $p < 0.05$ ; \*\*\*  $p < 0.001$ .

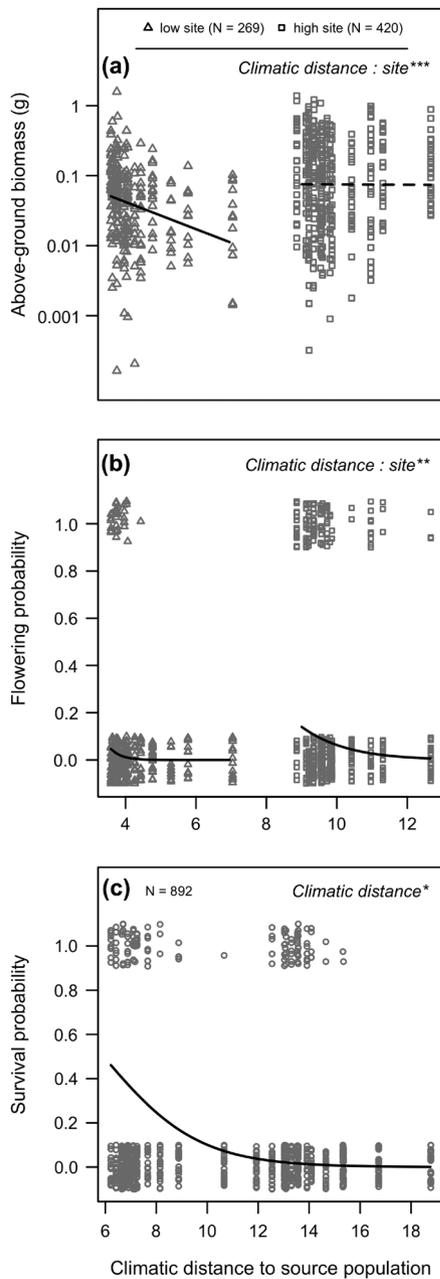


Figure 4. Combined effects of climatic distance to the source population location and common garden site (low/high elevation) on (a) oven-dried above-ground biomass and (b) flowering probability of planted *Senecio inaequidens* individuals harvested in autumn 2014. (c) main effect of climatic distance on survival probability (spring 2014 to spring 2015) of planted *S. inaequidens* individuals. Lines represent model predictions of the minimal adequate pedigree mixed model accounting for population co-ancestry. The dashed line in (a) denotes an insignificant effect of climatic distance on biomass at the high-elevation site (Supporting information). Please note that the climatic distances of (a), (b) and (c) differ, because they are based on different time periods. Symbols denote raw data. Random noise has been added to the binary y-values (0, 1) to enhance readability. The y-axis of (a) is shown on a log-scale. Sample sizes and symbols for panels (a) and (b) are identical. Stars indicate levels of significance: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

plants developed generative parts at the high-elevation site, but this difference was more pronounced in turfs of highland community origin as compared to lowland turfs (significant interaction of community origin and site,  $\chi^2 = 4.146$ ,  $p = 0.042$ ; Fig. 3b, Supporting information). Flowering probability decreased with increasing climatic distance from the source population location. While this decrease was rather abrupt at the low-elevation site, it was more gradual at the high-elevation site (significant interaction of climatic distance and site,  $\chi^2 = 9.234$ ,  $p = 0.002$ ; Fig. 4b, Supporting information).

Of the initial 896 *S. inaequidens* individuals planted, 131 (14.6%) survived the winter of 2014–2015. Across sites and community origins, survival probability was significantly higher under disturbed conditions ( $\chi^2 = 81.896$ ,  $p < 0.001$ ; Fig. 2c), but significantly lower with increasing climatic distance to the source population location ( $\chi^2 = 6.106$ ,  $p = 0.013$ ; Fig. 4c, Supporting information). For both community origins, survival probability was higher at the site of origin (i.e. for highland communities higher at the high-elevation site, and for lowland communities higher at the low-elevation site; Fig. 3c). This difference was more pronounced for turfs of lowland origin (significant interaction of site and community origin,  $\chi^2 = 4.691$ ,  $p = 0.030$ ; Supporting information).

## Discussion

Climate warming, intensification of land use and biological invasions are key components of global change, which might severely threaten high-elevation ecosystems. With a transplant experiment, we showed that disturbance, which is a common consequence of increasing land-use intensity, strongly favored survival, growth and reproduction of an exotic species at high elevation. Disturbance both increased community invasibility, and promoted the performance of *Senecio inaequidens* through the creation of establishment conditions which match the species' typical characteristics (e.g. low competitive ability, fast growth rates, high seed numbers). However, since we did not investigate the effect of our treatments on the germination of *S. inaequidens*, we do not know if disturbance would also favor the first establishment of the species at high elevations. Particularly our survival rates are most likely overestimating the real situation. Still, germination rates of *S. inaequidens* have been reported to be high under a range of conditions, and the numerous seeds survive for several years in the seed bank (Ernst 1998). As such, we do not expect germination success to be more limiting than seedling growth and survival.

Contrary to our expectation, experimentally induced climate warming (transplantation of turfs from high- to low-elevation) did not increase community invasibility, and thus the performance of *Senecio inaequidens* seedlings was not best in turfs transplanted from high- to low-elevation. However, climate warming is particularly strong at high elevation and thus the reduction of the climatic distance between possibly pre-adapted exotic source populations and colder regions

might promote the performance and the survival of a newly established exotic species.

In our common garden transplant experiment, disturbance had a consistently positive effect on the establishment success of *Senecio inaequidens*, confirming our main expectation for the first hypothesis. In fact, *S. inaequidens* is described as a weak competitor (Lachmuth et al. 2011), which benefits from disturbance and thus release from competition (Scherber et al. 2003, Caño et al. 2007). The positive effect of disturbance is considered to be one of the most important factors supporting invasion success (Alpert et al. 2000, Moles et al. 2012), which holds also true in montane regions (Lembrechts et al. 2016, Geppert et al. 2021). For instance, disturbed habitats near mountain roads are more heavily colonized by exotic species when compared to less disturbed habitats only meters away (Haider et al. 2018). Thus, it is most likely that the number of plant invaders will increase with increasing land-use intensity accompanied by disturbance in montane regions.

We hypothesized that the positive effect of disturbance will be more pronounced in communities with higher productivity and thus stronger competition. Indeed, the disturbance treatment caused a stronger increase in biomass of *S. inaequidens* in lowland turfs compared to highland turfs. However, at the low-elevation site, biomass increase of *S. inaequidens* under disturbed conditions was less pronounced compared to the high-elevation site. Hence, our sub-ordinate expectation of the first hypothesis, that the positive effect of disturbance is particularly strong in productive, low elevation communities, was only partly supported. In our experiment, we applied a one-time disturbance via upside-down transplants (Supporting information), which created beneficial growth conditions for the target species through elimination of the surrounding plant community (see spring panels in the Supporting information). This disturbance effect apparently faded faster at the low-elevation site, where vegetation height and cover had increased drastically in a summer census, as compared to the high-elevation site (Supporting information). Thus, in contrast to our original assumption, the positive effect of disturbance for the exotic species' establishment might eventually be stronger and longer-lasting at high elevation because of slower re-growth and re-establishment rates of the local native species (Moloney and Levin 1996).

Our second hypothesis that the invasive study species *S. inaequidens* performs best in mountain plant communities transplanted to the low-elevation common garden, because of the communities' reduced biotic resistance as a consequence of the experimentally induced climate warming, could not be confirmed. Within the low-elevation common garden, reproduction and survival of *S. inaequidens* was even worse in highland communities compared to lowland communities, suggesting that – at least temporarily – biotic resistance of transplanted turfs even increased. This is likely because vegetation height and cover and thus competition – particularly in spring – was higher for highland communities compared to lowland communities in the low-elevation common garden (Supporting information). A possible explanation for

these unexpected results is that growth in highland plant communities is usually limited by cool temperatures, and transplantation to the low-elevation site resulted in a burst of growth. In addition, temperature warming might have increased soil microbial activity and nitrogen mineralization (Rustad et al. 2001, Wang et al. 2016). Additional nutrient availability might then increase community growth rates and thus inter-specific competition in the whole plant community, particularly in colder ecosystems (Rustad et al. 2001). In contrast, the flowering probability of *S. inaequidens* was highest in lowland plant communities transplanted to the high-elevation common garden, indicating that potentially reduced competition in the plant communities gave an advantage to the exotic species. Overall, the observed, unexpected responses to experimentally induced climate warming highlight that climate change effects are highly complex, since they impact not only the invader, but also the resident community and their interactions. In particular, above-ground biotic interactions seem to play a fundamental role in plant invasions under novel climatic conditions (Hagedorn et al. 2019). Additionally, we need to bear in mind that the observed, unexpected results might be specific to our study sites, which did not include a replication of the climate-warming treatment – an unfortunate shortcoming of many transplant experiments (Alexander et al. 2015, Vandvik et al. 2020b, Nomoto and Alexander 2021).

However, the fact that we did not find an effect of experimentally induced climate warming on the invasibility of mountain communities after more than one year of observation does not rule out long-term effects. Climate warming will likely result in changes in community composition, resulting in shifts of dominant species and biotic interactions, which could weaken biotic resistance to invasion (Alexander et al. 2015). Also, with continued warming, the stock of organic material in shallow high-elevation soils is expected to decrease, particularly in combination with above-ground biomass removal (e.g. through mowing or grazing; Eze et al. 2018), which may reduce biomass productivity and thus inter-specific competition.

In accordance with our third hypothesis, survival probability during the first-year and flowering probability increased for our study species with decreasing climatic distance between the location of the source population and the common garden. In the low-elevation common garden, biomass increased with decreasing climatic distance as well. These results point to an adaptation of *S. inaequidens* populations to local climatic conditions during the species' spread across Europe. Similar results were found in Switzerland where growth rate of *Solidago canadensis* declined with climatic distance from the source population location (Moran et al. 2017). Rapid evolution has also been observed for *Ambrosia artemisiifolia*, which allowed the species to expand its climatic niche towards colder sites in the French Alps (Gallien et al. 2016) and which showed latitudinal clines in life history traits in China (Li et al. 2015). Similarly, *Lythrum salicaria* has re-evolved clines of phenology and size across latitude in the invasive, North American range, that match those in

its native European range (Montague et al. 2008). Referring to a common garden experiment by Ramírez-Valiente et al. (2021), adaptation to local temperatures was also observed for tree seedlings *Pinus sylvestris*, indicated by higher seedling survival under conditions similar to the home environment. In contrast, at the species scale, Brendel et al. (2021) did not find that climatic mismatches between the native and the new range of 46 Asteraceae species weakened with residence time.

With increasing climatic distance, biomass production decreased in the low-elevation common garden, while there was no such effect in the high-elevation common garden. At first, this result seems surprising. However, it might be explained by a more than doubling of biomass between low and high elevation sites (mean low biomass: 0.08 ( $\pm$  0.008) g, mean high biomass: 0.19 ( $\pm$  0.011) g). This difference indicates that the low-elevation site posed more adverse conditions for established *S. inaequidens* individuals, possibly because of higher competition intensity, not only in the undisturbed plant communities, but also in the more quickly re-colonized disturbed plots (Supporting information). Differences in micro-climatic conditions such as higher humidity and soil moisture in the dense vegetation and the deeper soils at the low-elevation site may also be disadvantageous for *S. inaequidens* and might have contributed to these effects (Vacchiano et al. 2013). Hence, our results suggest that climatic pre-adaptation might become especially relevant for growth in the context of unfavorable environmental conditions. This interpretation aligns with our findings that in the low-elevation common garden flowering probably abruptly decreased with increasing climatic distance, while the effect was less severe at the high-elevation site. Taken together, these results indicate that a population's adaptation has many abiotic and biotic dimensions that interact with each other. Still, at least parts of our findings support our third hypothesis, that climatic similarity promotes the establishment success and performance of *S. inaequidens*.

As mentioned before, there are some limitations in our study, which had to be considered when interpreting the results. First, it is likely that our experiment, which was limited to juveniles' growth, survival and first reproduction, cannot fully assess the invasion potential of the investigated populations since other life stages (e.g. germination, later life growth) may express different adaptations. However, from our point of view, the gain of additional information about in situ germination performance cannot outweigh the risk of uncontrolled spread of a highly invasive species into natural environments of nature conservation value; especially because germination is not considered as the most crucial phase for the establishment of this species. Another limitation is the inclusion of only two common gardens, mainly attributed to logistic reasons. Conducting replicated experiments in multiple regions is highly desirable, and might provide additional insights into the role of macro-climate or soil conditions as well as potential thresholds of climate warming effects.

Although we did not find an immediate negative effect of experimentally induced climate warming on biotic resistance

of the high-elevation community, we speculate that the above-average warming at high elevations (Pepin et al. 2015) might indirectly favor the establishment of exotic species in mountain communities by reducing the distance between the climatic optimum of the invading species and the conditions at the new high-elevation site. As the elevational range of an invasive species increases in the course of the invasion, there will be an increasing number of pre-adapted high-elevation source populations which will pose an increasing future invasion risk for alpine ecosystems. However, the degree to which an invader can benefit from such reduction in climatic distance might still depend on other dimensions of pre-adaptation of the introduced genotypes as well as concurrent changes in competitive and/or disturbance regimes. Studying long term effects of climate warming and disturbance on the invasibility of high-elevation plant communities is therefore required to gain a better understanding of how these complex interactions might shape mountain invasions in the future.

*Acknowledgements* – We would like to thank K. Bähne, P. Büttner, F. Engel, T. Heinemann, S. Lubosch, F. Pfeuffer and S. Thurner for their help to establish the transplant experiment, and T. Güthoff, P. Haider, E. and M. Lachmuth and Y. Lückert for helping with the monitoring of our target plants. C. Voigt supported us with the raising of seedlings in the greenhouse. Thank you to the Bavarian State Forests and the Grazing Cooperative of Grainau for permitting the establishment of the high-elevation common garden site, and to the Bayerische Zugspitzbahn Bergbahn AG for technical and logistic support at the Hochalm. Thanks also to N. Kern and C. Schunk (TU Munich, Ecoclimatology Group) for providing the climate data for our Hochalm site, and to E. Welk and G. Seidler (MLU Halle-Wittenberg) for providing the distribution data of *Senecio inaequidens* and preparing Fig. 1.

*Funding* – This study did not receive specific funding.

## Author contributions

**Sylvia Haider:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sebastian Palm:** Data curation (equal); Formal analysis (supporting); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Helge Bruelheide:** Conceptualization (supporting); Formal analysis (supporting); Supervision (supporting); Writing – review and editing (supporting). **Pierre de Villemereuil:** Formal analysis (supporting); Writing – review and editing (supporting). **Annette Menzel:** Investigation (supporting); Writing – review and editing (supporting). **Susanne Lachmuth:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (lead).

## Data availability statement

Data are available from the Zenodo: <<https://doi.org/10.5281/zenodo.5783056>>.

## Supporting information

The supporting information associated with this article is available from the online version.

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