

RESEARCH ARTICLE

Contrasting response of native and non-native plants to disturbance and herbivory in mountain environments

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Abstract

Aim: Climate warming and increasing human disturbance are expected to promote non-native plant invasions in mountain ecosystems. Although biological invasions are also expected to be modulated by biotic interactions, it is still not clear how invertebrate herbivores can affect plant invasion dynamics. Using a large manipulative experiment, we aimed at testing: (1) the effect of soil disturbance and elevation on native and non-native plant communities, and (2) the effect of plant-herbivore interactions, nitrogen deposition, and elevation in driving plant establishment after soil disturbance.

Location: European Alps, NE Italy.

Taxon: Vascular plants.

Methods: We selected remote, uninvaded dry semi-natural grasslands along the core elevational range of non-native plants in the European Alps (c. 100–1300 m) and manipulated soil disturbance, nitrogen deposition, and invertebrate herbivory. Then, we followed the natural establishment under real field conditions of both native and non-native plants over one growing season. We used generalized mixed-effects models to test the effects of the experimental treatments.

Results: Native and non-native species showed contrasting responses to soil disturbance and elevation. Low elevations and disturbance promoted non-native success, while affecting native species diversity negatively. Two-thirds of the experimental sites acquired novel non-natives after disturbance. Most of the observed non-natives were not present in the surrounding vegetation as mature plants, indicating that propagules were able to reach even remote natural areas. While current N deposition levels did not affect plant establishment, we found that after disturbance invertebrate herbivory might play an important role in facilitating non-native invasions by reducing native cover.

Main conclusions: Our findings show that highly resistant ecosystems such as continuous grasslands can be easily invaded once the resident vegetation has been removed, and that natural herbivory pressure from invertebrates might amplify the negative effects of disturbance on resident native species irrespective of elevation. Together, these results indicate increasing risks of future plant invasions on mountains under global change.

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KEYWORDS

alien invasions, altitude, exotic plants, herbivory, nitrogen addition

1 | INTRODUCTION

Native plants inhabiting temperate mountains are currently under threat by multiple global change stressors (Alexander et al., 2018; Dirnböck et al., 2003; Engler et al., 2011). First, climate-induced extinction risks appear to be large, even under moderate scenarios of temperature warming (Thuiller et al., 2005). Second, increasing human disturbance associated with habitat loss and intensive land-use is expected to further reduce plant diversity (Gerstner et al., 2014). By contrast, the same drivers are expected to promote non-native plant establishment and spread (He et al., 2011; Liu et al., 2017), resulting in increasing invasions across mountains worldwide (Pauchard et al., 2009). Species' responses to these drivers should be modulated by biotic interactions (Alexander et al., 2015), but it is still not clear how biotic interactions across trophic levels affect plant invasion. As these invasions pose additional potential threats to resident plant diversity and ecosystem functioning (Alexander, Lembrechts, et al., 2016; Simberloff et al., 2013), it is crucial to understand how abiotic and biotic drivers might interact and favour non-native plants over natives (Sorte et al., 2013).

In the last decades, soil disturbance related to the construction of roads, ski-slopes and other infrastructures has become more frequent across temperate mountain ecosystems (Wipf et al., 2005). Disturbance (through the removal of existing vegetation) decreases competition for light and increases the chances of seed germination and establishment of ruderal plants and species present only in the seed-bank (Corcos et al., 2020; Haeuser et al., 2017; Lembrechts et al., 2017; McDougall et al., 2018). Besides the direct effects on plants, disturbance also affects key soil properties such as nutrient and water content. In particular, soil disturbance is often coupled with nutrient leaching and high nitrogen (N) deposition (Davis et al., 2000). Soil eutrophication usually reduces plant diversity, enabling fast-growing plants to outcompete slow-growing, stress-tolerant species (Stevens et al., 2010). Since most non-natives are fast-growing plants, high N levels coupled with soil disturbance are usually predicted to facilitate invasive plants compared to local natives in and out of mountain regions (He et al., 2011; Lembrechts et al., 2016).

Plant invasions lead to novel interactions across trophic levels, and are themselves likely driven by ecological interactions (Alexander et al., 2018; Grassein et al., 2014; Morriën et al., 2010; Richman et al., 2020; Waller et al., 2016). For instance, the enemy release hypothesis links non-native success in the newly invaded territories to the lack of specialised, co-evolved herbivores (Dostál et al., 2013; Maron & Vila, 2001; Meijer et al., 2016; Schultheis et al., 2015). Previous studies indicate that invasive seedlings seem to be more tolerant to herbivory than natives (Rogers & Siemann, 2002), and that this differential damage can alter community composition in the long-term (Barton & Hanley, 2013; Relva et al., 2010). Native vertebrate herbivores have been demonstrated to promote non-native plant invasions (Averill

et al., 2018; Christianen et al., 2019; Stokely et al., 2020), but also invertebrates can influence plant dynamics through both direct consumption and many indirect effects that are often difficult to disentangle (Denyer et al., 2010; Maron & Crone, 2006; Tamburini et al., 2018). However, the interaction between invertebrate herbivory and other drivers of plant invasion has been poorly investigated so far (Dostál et al., 2013; Simberloff et al., 2013). Given the likely emergence of complex interactions between biotic and abiotic drivers under global change, there has been a call to develop experimental approaches under realistic field conditions, to advance our understanding of plant invasion dynamics (Alexander, Diez, et al., 2016). However, most of the few previous experimental studies on non-native establishment manipulated propagule pressures through seeding (Lembrechts et al., 2016), while studies evaluating natural succession are rare (but see Corcos et al., 2020).

Here, to disentangle the role of soil disturbance, invertebrate herbivory, N deposition and their potential interactions in explaining plant establishment dynamics of both native and non-native plants, we set up an experiment along the elevation extent of non-native invasion in the Alps (c. 100–1300 m). In mountainous areas, both abiotic and biotic drivers (e.g. temperature, human disturbance, and herbivory pressure) are expected to vary with elevation and to potentially interact in determining non-native success. First, we tested the hypothesis that conditions at low elevations should favour non-native plant establishment compared to high elevations. At low elevations, we expected warmer temperatures coupled with soil disturbance to be beneficial for non-native establishment over natives, as non-native plants are generally ruderal, warm-adapted species introduced in the lowlands (Marini et al., 2013). Second, we tested whether the combined effect of warmer temperatures, N addition and herbivory pressures on native plants (Zuo et al., 2012) promotes non-native establishment and success after soil disturbance.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The study area was located in the Julian Prealps in the province of Udine (Friuli Venezia Giulia region, NE Italy). The area is mainly covered in mountains and climate depends primarily on elevation. During the field season (from May to August 2019), mean temperature at the minimum elevation in the study area (100 m a.s.l.) was 20.7°C, and 11.3°C at the maximum elevation in the study area (1630 m a.s.l.). The mean annual precipitation is c. 1500–2300 mm. We selected 15 dry semi-natural grasslands regularly mowed once per year along the elevational extent of non-native invasion in the study area (c. 100–1300 m a.s.l.) (Figure 1a). Selected grasslands

presented were found on shallow, well-drained soils rich in bases and were dominated by *Brachypodium rupestre*, *Bromopsis erecta* and *Festuca* spp. Selected sites were located in remote areas (cover of urban areas in a 500 m buffer: mean = 6.4%, SD = 13.7%), they were little invaded by non-natives and presented a continuous vegetation cover (Table S1). For each site, we also quantified the distance to the nearest paved road as a proxy for non-native propagule pressures (Dainese et al., 2017). Dry semi-natural grasslands are considered very resistant to non-native plant invasions due to the high competition of resident native species (Boscutti et al., 2018). At each site, we identified a block of 12 × 3 m, where we performed a mechanical soil disturbance by removing completely the existing vegetation and tilling the soil up to 20 cm (Figure 1b; Figure S1). Even if mixing together soils might affect differentially soil microbiota (Reinhart & Rinella, 2016), the scale of our experimental treatment was comparable to the scale of real disturbance events (e.g. road construction). We excluded vertebrates from the block by fencing the disturbed block with a nylon net (mesh: 4 × 4 cm). In the disturbed block, we performed two treatments: N addition and herbivory exclusion. Herbivory exclusion was nested within N addition, nested within the disturbed block. Each block included 4 plots (2 × 2 m) separated by 1 m and divided in 4 subplots (1 × 1 m) (N = 15 × 4 × 4 = 240 subplots). First, we fertilized half of the plots adding N in the form of urea CH₄N₂O pellets, spreading them evenly and leaving them to be dissolved by rain. The amount of added N corresponded to 20 kg/ha (4 g/m², urea 46%). In the Alps, N total deposition rate ranges from 10 to 23 kg ha⁻¹ year⁻¹. Second, we excluded invertebrate herbivory in half of the subplots by setting up nylon cages (1 × 1 m) (Figure 1c; Figure S1). The cages were made of a light tulle with mesh size of 0.2 × 0.4 mm. We performed a pilot study to measure for a month the potential micro-climatic effects of the tulle and did not find any difference between inner and outer temperature ($t = 1.142$,

$df = 5481$, $p = 0.254$). In the study area, natural seed release mostly occurs in late summer-autumn. Hence, the exclusion cages -installed in spring- did not prevent the seed rain to reach the soil. In each site, we further identified two undisturbed control subplots (1 × 1 m) where no treatment was performed (Figure 1c). We did not cross all treatments for the controls since the focus of the experiment was on the vegetation dynamics after disturbance. In addition, to measure local temperature, we installed five data-loggers at 1.5 m from the ground in five sites along the elevational gradient at 110, 429, 650, 850 and 1330 m a.s.l. Temperature and elevation were strongly correlated in the study area (Pearson correlation $r = -0.95$; $p < 0.001$), while distance to the nearest road and elevation were not correlated (Pearson correlation $r = -0.07$, $p = 0.229$).

Moreover to study which invertebrate herbivores were excluded using our treatments, we sampled in each site for the whole duration of the experiment herbivore communities using pitfall traps and sweep-netting (Appendix S1). Herbivore abundance did not vary with elevation, although there was a trend for a negative effect of temperature on several groups (Appendix S1).

2.2 | Plant data collection

To study natural plant establishment dynamics, we carried out a floristic survey both inside and outside the disturbed blocks (Figure 1b). In each of the 15 sites, to characterize the surrounding vegetation, we recorded all plant species and we visually estimated their cover in a 12 × 3 m plot outside the disturbed block. We classified plants as native or non-native according to Poldini (2002). We considered as non-native species that are established in the study area irrespective of their invasiveness. During the entire growing season (from May to August) every 2 weeks, we monitored plant

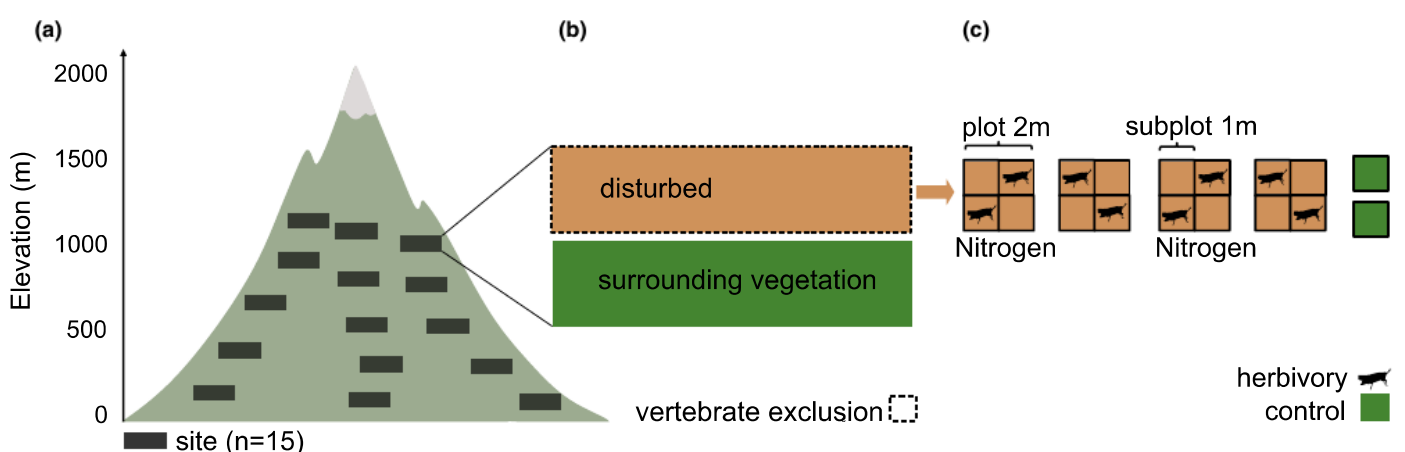


FIGURE 1 (a) Experimental design showing the 15 sites selected along the elevational gradient in Friuli (Northeast Italy). The experimental sites were spread over multiple mountain ranges within an area of c. 140 km²; (b) in each site, we carried out soil disturbance on a block of 12 × 3 m; (c) within the disturbed block, we created 4 plots (2 × 2 m), each plot was divided in 4 subplots (1 × 1 m) for a total of 16 disturbed subplots per site. We installed cages to exclude arthropod herbivores and added N in half of the disturbed subplots. In addition, we defined two control undisturbed subplots per site where no treatment was performed. Plant establishment dynamics has been monitored over one growing season [Colour figure can be viewed at wileyonlinelibrary.com]

establishment inside the disturbed blocks by taking pictures of each 1 m² subplot with a digital camera (DSC-W330 Sony) (Figure S2). To study plant dynamics, we quantified bare ground and species cover at four different times (2, 4, 6 and 14 weeks after disturbance) for each subplot using ImageJ (Schneider et al., 2012). When vegetation biomass peaked, after c. 100 days since the disturbance, we recorded all plant species and cover in each disturbed subplot and in the two control subplots, and we harvested total aboveground plant biomass. We oven-dried and weighed biomass after keeping the samples at 60°C for 72 h. Due to the size of the experiment and the high plant diversity ($n = 265$ species), the species could not be harvested individually. Hence, to compare the native versus non-native response, we used plant cover obtained from the pictures. As the plant cover did not reach 100% at the end of the experiment (mean 69.4 ± 30.8 SD%), species cover can be considered a good proxy per biomass. Total plant biomass and total plant cover per subplot were highly correlated (Pearson correlation $r = 0.75$, $p < 0.01$).

2.3 | Statistical analyses

2.3.1 | Response of natives and non-natives to disturbance under natural conditions

First, we investigated the effects of soil disturbance and elevation on native and non-native species richness under natural conditions, that is, we only considered the disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where the soil was not disturbed (Figure 1c). For native and non-native species separately, we fitted a generalised linear mixed-effects model (GLMM) assuming a Poisson distribution with species richness as response variable and elevation, disturbance and their interaction as fixed effects. Both models included as random structure plot ID nested within site ID.

Second, we compared the whole disturbed block with the surrounding vegetation (Figure 1b). Based on presence/absence community data, we calculated Jaccard dissimilarity between disturbed and undisturbed plant communities, separately for native and non-native plants. We used the function "betadiver" of the R-package "vegan" (Oksanen et al., 2019), to calculate beta-diversity using the Jaccard index and its replacement and richness components (Legendre, 2014). These analyses tested whether the vegetation established after disturbance was a subset of the species pool already occurring in the existing vegetation or whether disturbance released species mostly present in the seed-bank from competition (i.e. high species turnover). As there are several methods to partition beta-diversity, we also calculated Sørensen index using the function "betapair" of the R-package "betapart", and partitioned the total beta-diversity in turnover and nestedness components (Baselga, 2010; Baselga & Orme, 2012). As the results of the two methods converged, we presented the Jaccard index in the main text and the Sørensen index in Supporting Information (Table S2).

2.3.2 | Response of natives and non-natives to N addition and herbivory exclusion after disturbance

We analysed the effect of the experimental treatments on plant establishment in the 240 disturbed subplots of the experiment, excluding the control subplots. First, we fitted a LMM with elevation, herbivory exclusion, N addition and their two- and three-way interactions as fixed factors and ln-transformed total biomass as response variable. The random structure of the LMM consisted in plot ID nested within site ID. Second, we fitted a LMM with elevation, herbivory exclusion, N addition, status (native or non-native) and their two- and three-way interactions as fixed factors using ln-transformed species richness as response variable. The random structure of the LMM consisted in subplot ID nested in plot ID nested within site ID. Third, we analysed the effects of the experimental treatments on bare ground cover over time. We considered the first 6 weeks of the experiment and the final measurement before cutting the aboveground biomass (measurements were taken at the second week after disturbance, fourth, sixth and fourteenth week). As fixed factors we fitted elevation, herbivory exclusion, N addition, time (ln-transformed week of the experiment), and their two- and three-way interactions. We used as random structure subplot ID nested within plot ID nested in site ID. Finally, we tested for the effect of the experimental treatments on native and non-native plant cover over time. To improve the linearity and residuals distribution, we used square root transformed plant cover as response variable. We used elevation, herbivory exclusion, N addition, status (native or non-native), time (ln-transformed week of the experiment), and all the two-way and three-way interactions. We included as random structure subplot ID nested in plot ID nested within site ID.

2.3.3 | Model selection procedure

Full models described above included all of the two-way and three-way interactions between the fixed factors and main effects. Starting from the full model, we used a backward deletion procedure, removing one-by-one the interactions if the p-value was higher than 0.05 and re-ran the model to avoid overfitting and to correctly interpret the main effects. All main effects were left even if not significant.

2.3.4 | Multi-model inference

To evaluate model selection uncertainty, we also performed a multi-model inference analysis. With our information-theoretic approach, we compared the fit of all possible candidate models nested within each of the full models presented above. In a set of n models, each model i can be ranked using its difference in AICc with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\text{MIN}}$). A model in a set can be considered plausible if its ΔAICc is below 2. Multi-model inference analyses were performed with the MuMIn package (Barton & Barton, 2015; Burnham et al., 2011). Final models selected according to the backwards stepwise deletion were consistent with the ranking

of the plausible models based on AICc (Tables S3–S7). Hence, we presented the results of the reduced models from the backward deletion procedure in the main text and reported the multi-model inference analyses only in Supporting Information.

2.3.5 | Model diagnostic

In all models, to assess possible collinearity issues between fixed effects, we estimated variance inflation factors (VIFs). VIF values were always close to 1, indicating very little collinearity among predictors (Akinwande et al., 2015). Model assumptions were visually evaluated using diagnostic plots of model residuals. All analyses were run with R 3.5.1 (R Core Team, 2017), using the package “lmer” to fit GLMMs (Bates et al., 2015).

3 | RESULTS

3.1 | Response of natives and non-natives to disturbance under natural conditions

Overall, we recorded 251 native plant species and 14 non-natives (Table S8). Soil disturbance had a negative effect on native richness and a positive effect on non-native richness (Figure 2a,b; Table 1). Moreover, increasing elevation negatively affected non-native richness (Figure 2b; Table 1), while native richness tended to be affected positively by increasing elevation (Table 1).

Both native and non-native communities showed high beta-diversity between disturbed communities and undisturbed surrounding vegetation ($\beta_{\text{Jaccard}} > 0.70$) (Figure 3). For native plants, total beta-diversity was mostly due to species replacement ($\beta_{\text{replacement}} = 0.58 \pm 0.03$; $\beta_{\text{richness}} = 0.17 \pm 0.03$), that is, in disturbed blocks, most of the emerging native seedlings were novel

species (mean = 60%, SD = 11%). For non-native plants, total beta-diversity was mostly related to species richness difference ($\beta_{\text{replacement}} = 0.07 \pm 0.04$; $\beta_{\text{richness}} = 0.73 \pm 0.08$). In 67% of the sites, several non-native species occurring after disturbance were not observed in the close surrounding as adult plants (Tables S1 and S2).

3.2 | Response of natives and non-natives to N addition and herbivory exclusion after disturbance

In each subplot, we recorded an average of 12 species (min = 2, max = 22). The most frequent species were: *Plantago lanceolata* L. (native, $n = 127$), *Erigeron annuus* L. (non-native, $n = 99$), *Peucedanum oreoselinum* (L.) Moench (native, $n = 89$), and *Trifolium pratense* L. (native, $n = 89$).

Total biomass was not affected by elevation and N deposition, while we observed a significant effect of herbivory exclusion (Table 2a), i.e. when herbivores were present biomass decreased by c. 20% (Figure 4).

For species richness, we found an interaction between status and elevation (Table 2b), i.e. species richness of native plants was higher than species richness of non-native plants and it was affected by elevation positively, while non-native richness decreased with elevation (Figure S3). Herbivory exclusion and N addition did not have any effect on overall species richness (Table 2).

By analysing the temporal dynamics of bare ground cover, we found an interaction between time and herbivores and between time and elevation (Table 3a). First, bare ground declined with time but more strongly when herbivores were excluded (Figure 5a), that is, herbivores kept the vegetation more open. Second, bare ground declined more slowly over time at high elevations than at low elevations (Figure 5b). Bare ground cover did not respond to N addition.

For plant cover, we found an interaction between status and herbivores (Table 3b), that is, plant cover of natives decreased in

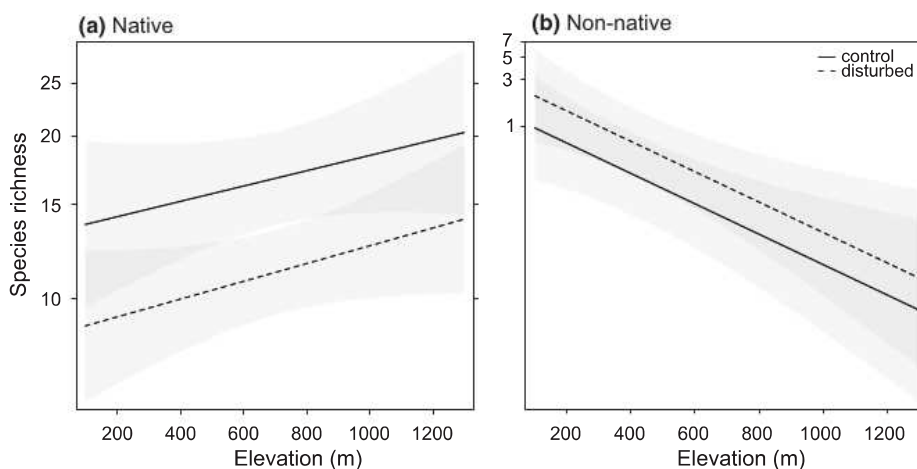


FIGURE 2 Effects of soil disturbance and elevation on (a) native and (b) non-native plant species richness along the elevational gradient in Friuli (Northeast Italy). For native species richness, the effect of elevation was marginal ($p = 0.051$). Models only contained subplots under natural conditions: disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where soil was not disturbed ($n = 60$ disturbed subplots and 30 control subplots)

TABLE 1 Effects of disturbance and elevation on native and non-native species richness. Coefficients are estimated from final generalised linear mixed-effects models assuming a Poisson distribution. Models only contained subplots under natural conditions: disturbed subplots where herbivores were present (no exclusion cages) and with no N addition, and the control subplots where soil was not disturbed ($n = 60$ disturbed subplots and 30 control subplots)

Response variable	Fixed factors	Estimate	SE	df	z	p
(a) Native species richness	Disturbance (yes)	-0.400	0.059	29	-6.63	<0.001
	Elevation	0.145	0.074	13	1.95	0.051
(b) Non-native species richness	Disturbance (yes)	0.742	0.352	29	2.109	0.035
	Elevation	-1.438	0.454	13	-3.168	0.002

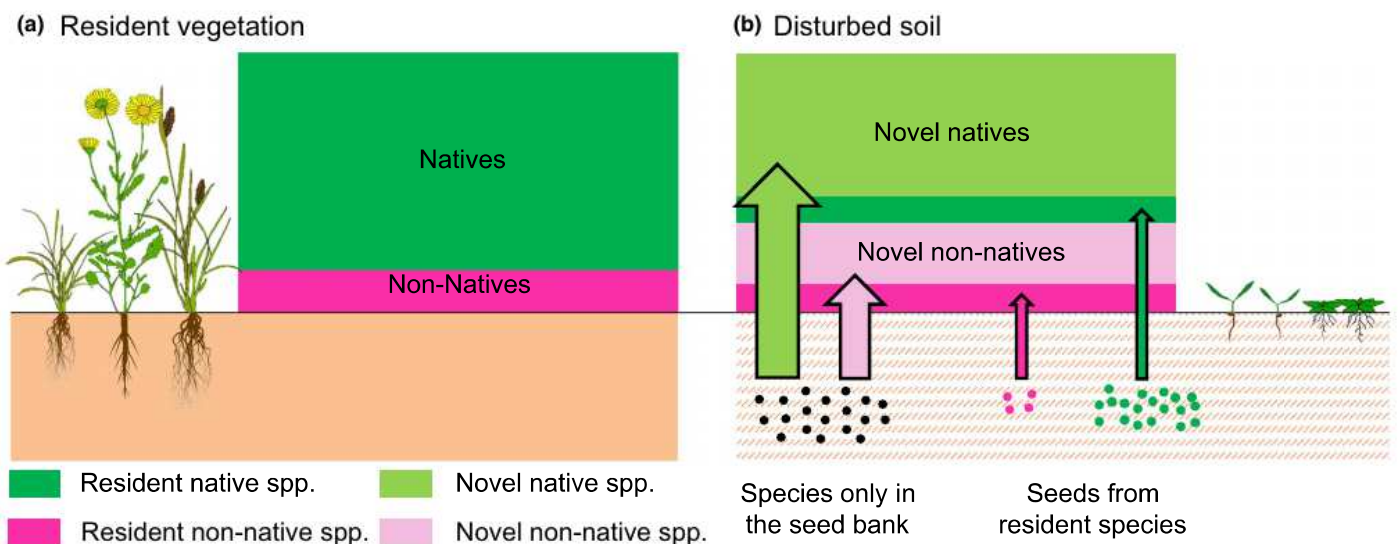


FIGURE 3 (a) In the study area (Northeast Italy), the resident vegetation consisted mainly of native species and only a few non-natives; (b) in disturbed soils, species mainly emerged from the seed-bank resulting in novel species communities. Rectangles represent species pools and their size is proportional to the mean number of plant species per site, while arrow size is proportional to the contribution of the seed bank [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Effects of (a) herbivores, elevation and N addition on ln-transformed biomass, and (b) herbivores, elevation, N addition, status and the interaction between elevation and status on ln-transformed species richness. Coefficients are estimated from final linear mixed-effects models. Besides main effects, we tested two-way and three-way interactions and removed them when $p > 0.05$

Response variable	Fixed factors	Estimate	SE	df	t	p
(a) Biomass	Herbivores (yes)	-0.276	0.051	179	-5.363	<0.001
	Elevation	-0.057	0.182	13	-0.305	0.765
	N (yes)	-0.024	0.071	44	-0.344	0.733
(b) Species richness	Herbivores (yes)	-0.013	0.018	179	-0.733	0.465
	Elevation	0.121	0.044	13	2.734	0.017
	Status (non-native)	-1.296	0.018	238	-73.720	<0.001
	N (yes)	-0.006	0.018	44	-0.329	0.744
	Elevation × status (non-native)	-0.265	0.018	238	-15.054	<0.001

presence of herbivores, while non-native cover did not respond to herbivory exclusion (Figure 6a). We also found a three-way interaction between time, status and elevation (Table 3b), that is, non-native cover increased more over time at lower than at higher elevations (Figure 6b; Table 3b). All plant cover did not respond to N addition.

4 | DISCUSSION

With a large manipulative experiment under realistic field conditions, we investigated the potential interactions between elevation, N deposition, and invertebrate herbivory in driving plant establishment

dynamics after soil disturbance. Native and non-native species showed contrasting responses to these drivers. Irrespective of elevation, soil disturbance increased non-native plant success, while it affected native species diversity negatively. Moreover native species richness increased with elevation while non-native richness decreased at high elevations. Similar to the effects observed for large herbivores (Averill et al., 2018; Relva et al., 2010; Stokely et al.,

2020), we found that invertebrate herbivory might play an important role in plant establishment dynamics by feeding preferentially on native plants. Current levels of N deposition in the Alps seemed to have little effect on both native and non-native species. Altogether our results confirm the high risks of future plant invasions in mountains under warming temperature and increasing human disturbance, and point to the need of incorporating plant-herbivore interactions in future invasion studies.



FIGURE 4 Effect of herbivore presence on total plant biomass of each subplot harvested at the peak vegetative development after soil disturbance. Models contained disturbed subplots ($n = 240$)

4.1 | Response of natives and non-natives to disturbance under natural conditions

Native and non-native plants showed contrasting responses to soil disturbance. As expected, the removal of resident vegetation and the creation of bare ground through soil disturbance promoted non-native establishment (Lembrechts et al., 2016). This confirms that an invading species must have access to resources such as light, nutrients and water, and that it will have greater success in invading a community if it does not encounter intense competition for these resources from resident species (Davis et al., 2000). Most non-natives possess traits associated with faster growth rate and resource acquisition (Van Kleunen et al., 2010). These traits probably enabled them to quickly exploit the resources released by soil disturbance at the expense of resident native species (Lembrechts et al., 2017; McDougall et al., 2018). Consistently, we found a negative effect of disturbance on native species richness, indicating that only a small subset of native species were able to colonize the disturbed soil.

Second, elevation affected native and non-native plants, oppositely. Non-native species richness peaked at low elevations where

TABLE 3 Effect of (a) herbivores, time (week), elevation, and N addition on bare ground cover, and b) herbivores, time (week), elevation, N addition and status on root squared-transformed plant cover. Coefficients are estimated from final linear mixed-effects models. Besides main effects, we tested two-way and three-way interactions and removed them when $p > 0.05$

Response variable	Fixed factors	Estimate	SE	df	t	p
(a) Bare ground cover	Herbivores (yes)	-2.555	2.576	792.019	-0.992	0.322
	Time	-38.319	1.125	793.444	-34.065	<0.001
	Elevation	-0.440	3.228	17.528	-0.136	0.893
	N (yes)	-1.983	1.518	45.193	-1.306	0.198
	Herbivores (yes) × time	5.042	1.558	791.875	3.236	0.001
	Elevation × time	2.562	0.803	794.782	3.191	0.001
(b) Plant cover	Herbivores (yes)	-0.379	0.088	1337.245	-4.291	<0.001
	Status (non-native)	-0.232	0.233	1347.897	-0.999	0.318
	Time	3.526	0.064	1337.093	55.133	<0.001
	Elevation	-0.200	0.290	16.665	-0.689	0.501
	N (yes)	0.165	0.118	39.088	1.399	0.170
	Herbivores (yes) × status (non-native)	0.339	0.156	1353.680	2.172	0.030
	Status (non-native) × time	-2.228	0.122	1337.032	-18.276	<0.001
	Status (non-native) × elevation	0.135	0.244	1352.720	0.555	0.579
	Time × elevation	0.147	0.060	1337.191	2.451	0.014
	Status (non-native) × time × elevation	-0.470	0.134	1337.076	-3.507	<0.001

FIGURE 5 Effect of the interaction a) between herbivore presence and time (week of the experiment) and b) between elevation and time (week of the experiment) on bare ground (percent cover) of each subplot. Models contained disturbed subplots ($n = 240$) [Colour figure can be viewed at wileyonlinelibrary.com]

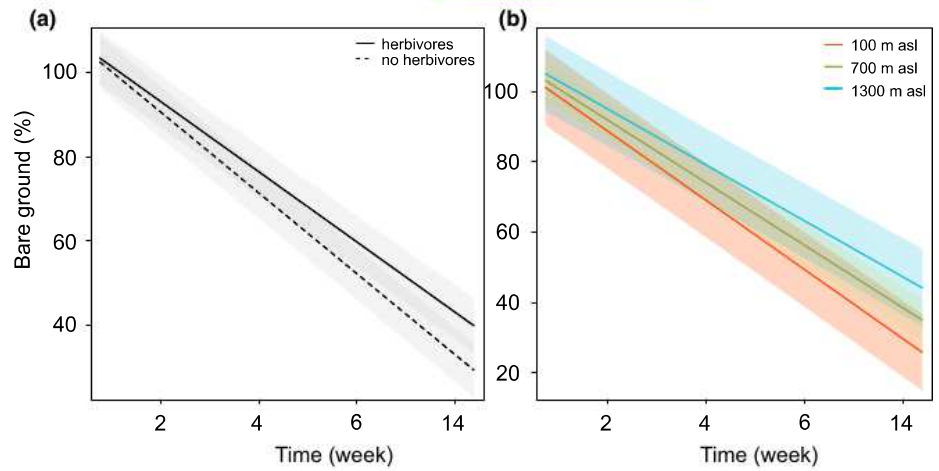
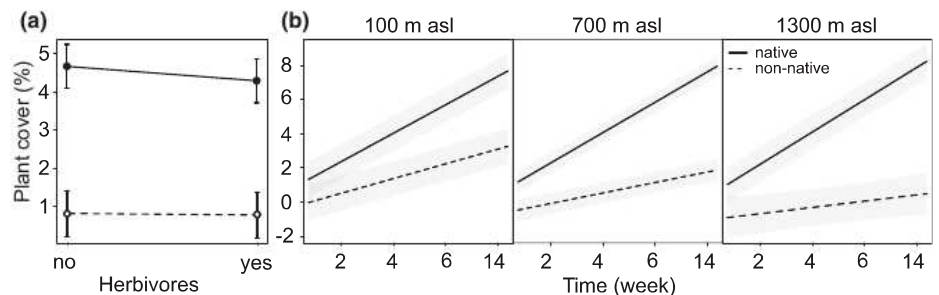


FIGURE 6 Effect of the (a) two-way interaction between herbivore presence and plant species status (native vs. non-native) and (b) three-way interaction between time (week of the experiment), elevation and plant species status (native vs. non-native) on squared root transformed plant cover. Models contained disturbed subplots ($n = 240$)



human activities are more intense and temperatures are warmer (Haider et al., 2018; Marini et al., 2013; Pauchard et al., 2009; Seipel et al., 2016). This confirms that climate can be a fundamental barrier for the establishment of warm-adapted non-native plants (Alexander et al., 2011; Lembrechts et al., 2016; Marini et al., 2013). However, it was not possible to disentangle the effects of temperature and human activities, that is, in addition to warmer conditions, also a higher propagule pressure can contribute to explain non-native success in the lowlands. At low elevations, the probability of introducing species is higher than at high elevations, creating a larger species pool of potential invaders (Alexander et al., 2011; Boscutti et al., 2018; Marini et al., 2013). By contrast, native diversity showed a trend for increasing with elevation. Probably, the truncated elevation gradient of the study (100–1330 m) prevented us to see the hump-shaped pattern that is often reported for native plant diversity (Haider et al., 2018; Marini et al., 2013; Nogués-Bravo et al., 2008).

Besides the effect on species richness, soil disturbance has been identified as a key driver of plant community composition (Corcos et al., 2020; Haider et al., 2018). Beta-diversity between disturbed and resident vegetation was high, indicating that a large proportion of established species did not occur in the surrounding vegetation but only in the seed-bank (Figure 3). Disturbance released from competition several native and non-native species naturally present in the seed-bank, allowing them to germinate and establish. For native plants, this high replacement was due to several annual ruderal species that were able to colonize the soil after disturbance (see also Corcos et al., 2020). For non-natives, very few species occurred in the undisturbed vegetation. After disturbing the soil, in addition to the few non-native species already present in the surrounding vegetation, several others

emerged, showing that propagule pressure in the soil was relatively high. Ten sites out of 15 acquired novel non-native species after disturbance, while the only four sites where no non-native species occurred, were located at mid or high elevations confirming the expected negative effect of increasing elevation on propagule pressure (Alexander et al., 2011).

4.2 | Response of natives and non-natives to N addition and herbivory exclusion after disturbance

Invertebrate herbivores emerged as a potential driver of plant establishment after soil disturbance. They removed overall around 20% of the total biomass and increased bare ground by c. 10% compared to situations where herbivory was excluded. We found herbivores to have a negative effect on native plant cover but a neutral effect on non-natives. Through biomass reduction, increase in bare ground and/or reduction in the rate of resource capture by the resident vegetation (Davis et al., 2000; Meineri et al., 2020), herbivores may release resources, thereby favouring the establishment of fast growing species such as most non-natives (McDougall et al., 2018; Van Kleunen et al., 2010). After soil disturbance, herbivory, and especially seedling herbivory, may become a crucial driver of vegetation dynamics and it can be determinant in facilitating non-native success (Relva et al. 2010). Although our results showed that herbivores hindered native establishment and did not affect non-natives, we could not confirm findings of less herbivore damage on non-native than on native plants (Cappuccino & Carpenter, 2005; Huang et al., 2020; Liu et al., 2007). In addition, we cannot exclude that the lower susceptibility of non-natives might also arise from a ‘sampling effect’ (Loreau,

2000); i.e. the lower number of introduced species compared to resident natives might possess a particular suite of traits associated to higher herbivore resistance (Lemoine et al., 2016). Surprisingly, herbivory effect did not change under N addition nor with elevation. We expected herbivory to increase at elevated N due to a higher nutrient content (Borgström et al., 2017). However, we did not find any direct or indirect effect of N on plant establishment. Similar to other studies (Potter & Bowman, 2020), the lack of N effect can be related to the low amount of N (average deposition rate in the Alps) or to co-limitation of multiple resources (Kaspari & Powers, 2016). At high elevations where temperatures are colder, we expected that invertebrate herbivory decreases in intensity (Bale et al., 2002; Moreira et al., 2016; Zuo et al., 2012). Probably, our elevation gradient (100–1330 m) was too short to capture the expected variation in herbivore pressure (Silvestre et al., 2019; Sohn et al., 2019). Moreover while native cover increased irrespective of elevation over the course of the experiment, non-native cover grew at a much slower rate at high than at low elevations. This might confirm the negative effect of cold temperatures on non-native plants. Finally, more soil remained bare at higher elevations than in the lowlands, creating potential opportunities for invasion. These results point at high risks of future invasion in mountains under warming climate.

5 | CONCLUSIONS

Using a large experiment under realistic field conditions, we showed that the joint effects of warm temperatures and human-induced disturbance favoured non-native plant establishment over natives, suggesting that global change will probably promote the further spread of non-native plants in mountain environments (Pauchard et al., 2009). We also showed for the first time that during the establishment phase, invertebrate herbivory might play a role in shifting competition hierarchies between natives and non-natives. As global change is reshuffling ecological interactions across trophic levels, it is fundamental to incorporate the effects of biotic interactions to fully understand plant redistribution dynamics (Alexander et al., 2018; Alexander, Diez, et al., 2016). Although the magnitude of herbivore effect was expected to increase under warm temperatures (Zuo et al., 2012) and high resource availability (Olff & Ritchie, 1998), we found no interaction between herbivory and abiotic drivers. Our results show that even highly resistant ecosystems such as continuous semi-natural grasslands (Boscutti et al., 2018) can be easily invaded once the resident vegetation is removed. Therefore, besides human-related disturbance, also natural phenomena such as land-slides or small erosion events might be associated with plant invasions due to the existing high propagule pressure observed in most of the seed-banks. Decreasing soil disturbance regime, in particular where propagule pressure is high, appears as a top priority to reduce the probability of invasions of non-native plants across temperate mountains.

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DATA AVAILABILITY STATEMENT

The dataset analysed in this study is available at <https://doi.org/10.5061/dryad.3n5tb2rgc>.

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BIOSKETCH

Costanza Geppert is broadly interested in the effects of global change on biodiversity. This work represents a component of her PhD work at Padova University on the drivers of plant redistribution in mountainous areas under global change. She and the other authors collaborate on questions of biodiversity conservation based at Padova University (<https://biodiversity-lorenzomarinini.weebly.com>).

Author's contributions: CG and LM conceived the study; CG, FB, GLB, VDM, DC, AF carried out the field work; CG and LM analysed the data and interpreted the results; CG and LM led the writing. All authors contributed to and approved the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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