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Rock climbing affects cliff-plant communities by reducing species diversity and altering species coexistence patterns

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Abstract

Cliffs are unique ecosystems with an outstanding but relatively unknown plant diversity, harboring rare, endemic and threatened species, but also rock-specialist or generalist species that can become locally common and dominant on cliffs. The rising popularity of climbing represents an increasing threat to cliff biota, affecting community composition and potentially diminishing diversity and species associations. We used a novel sampling design of closely-paired climbed versus unclimbed points along the cliff-face. We sampled along climbing routes of different climbing intensities in El Potrero Chico (Nuevo León, Mexico), identifying plant species and analyzing species associations and community composition in climbed and unclimbed plots. Diversity on the sampled cliffs was high, even greater than in other regional ecosystems. We found reduced abundance, cover, and diversity in climbed plots, irrespective of climbing intensity. Dominant species on the sampled cliffs were the most negatively affected by rock climbing in terms of abundance, and some locally rare species, including endemics and endangered species, were entirely absent from climbed plots. Co-occurrence analysis showed that the number of associations between pairs of dominant and common species were greatly reduced in climbed plots, and that positive associations between locally rare species existed in unclimbed plots but not in climbed plots, which may contribute to the disappearance of endemic and threatened species. Finally, NMDS analysis revealed that the community composition changed significantly due to climbing. Our results indicate that conservation science should convince stakeholders of the need for a holistic conservation of cliff ecosystems and not focus solely on emblematic or rare species, since plant community dynamics and preservation depend on interactions between plant species.

Keywords Cliff plant community composition · Dominant and rare species · Human disturbance · Spatial associations · Species co-occurrence and interactions · Sport ecology

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Introduction

Cliffs are extreme ecosystems that harbor unique plant species diversity. Due to the heterogeneous cliff micro-topography and the accompanying variation in abiotic conditions, diverse vascular plant species can colonize cliff crevices, despite the cliffs' harsh abiotic conditions (García-Callejas et al. 2021). Cliffs can include endemic and highly specialized species, comprising threatened species, which often are the focus of conservation efforts in these environments (deCastro-Arrazola et al. 2021). Certain rock-specialists can be locally rare when their distribution range or local presence is restricted, but other specialists are efficient colonizers in rocky outcrops, growing abundantly (Larson et al. 2000). Generalist species can also become common on cliffs and may even be the dominant species in these environments (Escudero 1996; March-Salas et al. 2018). The degree of dominance of cliff species may be key to understand the dynamics of cliff plant communities.

The spatial coexistence of functionally different species is one of the outstanding characteristics of cliff ecosystems (Farris 1995; Larson et al. 2000). Coexistence patterns and positive associations may arise from beneficial biotic interactions (e.g. mutualistic interactions with floral visitors, shared fungal and bacterial communities; Krah and March-Salas 2022), or from facilitation processes such as nutrients supply from plant litter decay (García-Callejas et al. 2021). Nevertheless, this coexistence, and underlying species associations, cannot be understood as a competitive factor in cliffs. Competition and negative associations lie in the colonization of the available micro-niches, since spatial heterogeneity offers microniches with near plant-by-plant independence in space, and in nutrient and water resources (Cooper 1997; do Carmo et al. 2016). Rising climatic and anthropogenic pressures such as rock climbing could then hinder species coexistence and consequently affect existing ecological associations on cliffs.

The great increase in climbing popularity and intensity is altering cliff plant communities and other cliff organisms including mosses, lichens, birds, and some invertebrates (Adams and Zaniewski 2012; Baur et al. 2017; Lorite et al. 2017; Schmera et al. 2018; Covy et al. 2019). Nevertheless, effects of rock climbing on species coexistence and associations and their consequences for the cliff community configuration remain unknown. Cliff plant communities are usually composed of dominant, common and rare species, each providing different functions due to their different relative densities, life-history and functional traits (Avolio et al. 2019; Gray et al. 2021). Rock climbing may alter each of these ecologically different groups, their associations, and ultimately, the cliff ecosystem itself. Dominant plants (i.e. species important to the structure of an ecosystem due to their high relative density and abundance) can be diminished, while locally rare species (i.e. low-abundance and locally uncommon species that might not be consistently rare throughout their geographical range; Murray and Lepschi 2004) could even disappear if the rock climbing pressure is high. The disturbance of beneficial associations among dominant and among locally rare species could impact the ecological stability of different ecosystems (Calatayud et al. 2020; Gray et al. 2021), but the answer to this question is unknown in cliff ecosystems. For instance, rock climbing could directly trigger an increase in the intra- and inter-species distance, alter the abundance of dominant species, and eliminate both dominant and rare species (Larson et al. 2000). Rock climbing may also decrease the presence of mosses and lichens that help colonization of and nutrient acquisition by cliff plants (Harrison et al. 2022), or obstruct plant accessibility to natural seed dispersers such as ants, birds or lizards. In turn, these effects of rock climbing indirectly affect plant community composition, its viability, and related biotic interactions (Farris 1995; Larson et al. 2000).

Conservation research mostly focuses on biodiversity, on the one hand, and rare species, on the other hand (Gaston 2010; Gray et al. 2021), while dominant and common species are frequently overlooked, even though they drive the community structure, facilitate other species colonization, and make up a larger share of biomass in the ecosystem (Gaston 2010; Avolio et al. 2019). Differences in spatial dominance are striking in cliff ecosystems, since cliff plants are not homogeneously distributed along the cliff-face (Graham and Knight 2004). Thus, rock climbing can cause differential effects on species depending on their relative abundance and spatial distribution, as has been shown for generalist versus rock-specialist species (Müller et al. 2004; March-Salas et al. 2018). For instance, dominant species may be able to buffer rock climbing impacts better than rare species, as shown under other environmental stressors and ecosystems (Sasaki and Lauenroth 2011; Qi et al. 2018), while some rare species could disappear. However, the number of individuals in dominant species could be greatly reduced if the climbing intensity increases, following observed trends of plant diversity as a whole (Clark and Hessl 2015; Lorite et al. 2017). As in other ecosystems, a reduction of dominant or common species may affect the community configuration and functionality of cliff plants (Avolio et al. 2019), and the loss of rare species could have dramatic consequences in terms of local or overall biodiversity. Thus, species with dominant and common occurrence on cliffs likewise deserve conservation efforts.

Furthermore, while most previous studies on the impact of rock climbing on cliff vascular plants have focused on the effects on plant cover and species richness, cliff species diversity (usually quantified by diversity indices) has been little assessed. Species diversity is more complex than species richness, since species diversity includes the abundance of each species to evaluate the number of species in a community. The quantification of plant diversity using diversity indices (e.g. Shannon-Wiener Index, H'; Simpson Index, D) can then be useful to better understand cliff species assemblies and their conservation value. These measures are broadly assessed for most ecosystems and habitat types, but remain poorly known for cliffs (but *see* Boggess et al. 2017; Harrison et al. 2022; Reding et al. 2022). Thus, studies should also focus on cliff diversity assessment in order to incorporate this as criterion for decision-making concerning conservation management.

This work presents the first study on cliff vascular plant communities in Latin America. It is conducted in El Potrero Chico, one of the most popular climbing destinations in the world. El Potrero Chico is a famous limestone valley and recreational park with high conservation value located within the "Sierra el Fraile y San Miguel" Natural Protected Area in Nuevo León, Mexico. To test rock climbing impact on cliff plant abundance, cover, diversity, species associations and community composition, we used a closely paired design of climbed *versus* unclimbed plots by establishing a sampling quadrat along the cliff-face (Boggess et al. 2021). In order to assess the role of increasing rock climbing pressures on cliff-plant species, we selected climbing routes with differing climbing intensities. The species were categorized as locally rare, common, and dominant species, in order to assess coexistence and associations in cliff ecosystems and whether rock climbing affects community composition.

Considering previous findings (e.g. Lorite et al. 2017; March-Salas et al. 2018), we predict that (1) rock climbing negatively affects species cover, abundance, and diversity of cliff plants and (2) that these negative effects of rock climbing increase with increasing climbing-use intensity. We explore how rock climbing affects the coexistence of dominant and rare species, and whether it may promote changes in species associations and community composition, as climbing routes can increase intra- and inter-species distance. For this we hypothesize that (3) the loss of individuals due to rock climbing is greater for dominant than for rare species but some locally rare species disappear in climbing areas; (4) that the number of positive species associations are lower in climbed versus unclimbed plots; and (5) that rock climbing alters cliff plant community composition. Testing these hypotheses is relevant for the development of effective conservation strategies for cliff ecosystems.

Materials and methods

Study site

El Potrero Chico (Nuevo León, Mexico) is located on the northern edge of the 'Sierra el Fraile y San Miguel' Natural Protected Area, which has an area of 23,506 ha between 800 and 2,360 m a.s.l. This area is part of the Sierra Madre Oriental mountain range. Rock types include sedimentary rocks of marine origin dating back Mesozoic era, shale, and limestone cliffs (INECC 2017). Limestone supports abundant and diverse cliff vegetation, and favoured the evolution of plant specialization (Farris 1995; Larson et al. 2000; Lichter-Marck and Baldwin 2023). El Potrero Chico has a semi-arid climate with hot summers (average monthly maximum temperatures over 35 °C between June and August) and moderate cold temperatures during winter (average monthly minimum temperatures between 7 and 16 °C). The highest precipitation is reached in September and October with averages ranging from 70 to 130 mm while the rest of the year monthly precipitation is below 50 mm.

El Potrero Chico is one of the world's prime climbing destinations with over 600 climbing routes grouped into 24 climbing sectors. The first recorded climbing in El Potrero Chico was in 1960 but climbing experienced rapid development in this area from the late 1980s. Winter and early spring (between November and May) are the seasons when most climbers visit the area due to the moderate temperatures and lower precipitation. The number of climbers is lower from June to October due to the hot or rainy weather.

Sampling design

To examine differences between unclimbed and climbed routes, we designed a closelyadjacent case-control sampling design with a 3 m wide \times 3 m high quadrat placed along the climbing route (Fig. S1). The quadrat was composed by a central Climbed (C) plot of 1 m wide and 3 m high, two immediately adjacent plots of 0.5 m wide and 3 m high, which were not surveyed (i.e. no data were obtained from these plots), and two Unclimbed (U) plots of 0.5 m wide and 3 m high on the left and right side of the 3 m \times 3 m quadrat that were used as controls, since they represent areas not reached by climbers (Fig. S1). The use of a closely adjacent paired design is essential to adequately test the impact of rock climbing on cliff vegetation (Boggess et al. 2021), since this precludes the possibility that variations in biotic or abiotic factors such as aspect, micro-topography and insolation that could act as drivers of differences between climbed and unclimbed plots (Holzschuh 2016; Boggess et al. 2021). Closely-paired transects have the added benefit of avoiding an observer's interference in the undisturbed areas, since unclimbed transects can be surveyed from the same anchor with the help of directional gear placements (Boggess et al. 2021).

To define the position of the climbed plots (and thus, of the sampling quadrat), the bolts installed in the cliff-face were considered as the central point (i.e. 0.5 m to the right and 0.5 m to the left of the bolt), since the bolt represents with high precision the typical middle point that climbers use when ascending. However, to avoid interference with adjacent climbing routes, the selected routes for sampling were at least 5 m distant from the next climbing route. The unsurveyed plots are adapted from March-Salas et al. (2018) and guarantee separation between the unclimbed and climbed plots, since not all climbers follow exactly the same path along a climbing route. This prevents biased data acquisition from casual climber's ascent deviations, as unsurveyed areas cannot be considered completely undisturbed (Boggess et al. 2021). Moreover, in order to characterize the spatial distribution of plants within each plot, both climbed and unclimbed plots were divided in 0.5 m × 0.5 m subplots (i.e. 12 subplots in each climbed plot and 12 subplots in each unclimbed plot; *see* Fig. S2). Pictures were taken from each subplot (*see* below in 'Data collection').

To examine the maximum spatial distribution of cliff-face plants, we established the sampling quadrats at three heights along the climbing route, positioned at the Top, Middle and Bottom (Fig. S1). In order to fit the three quadrats without any overlap, we selected climbing routes of between 15 and 35 m height. The distance from the Middle to the Top and Bottom plot was roughly equidistant.

Data collection

Field surveys were conducted from November 2019 to December 2020. We sampled 12 climbing routes of El Potrero Chico (Table S1), adding up 36 climbed plots with a sampled area of 108 m² and 36 unclimbed plots with a sampled area of 108 m². The sampled routes were placed in contrasted aspects: North (n=5), South (3), East (1) and West (3). We noted the height of each climbing route as well as the climbing difficulty using the Yosemite Decimal System (YDS), grouped in three classes in our sampling sites: beginner (5.6–5.9), intermediate (510a–5.11d), advanced (5.12a–5.13d). To account for physical characteristics of the rock (i.e. micro-topography), we measured the slope of the center of each quadrat in the field, and the proportion of cracks (i.e. crevices) in each 0.5 m × 0.5 m subplot using *ImageJ*, and the estimated both measures at the plot level. These measurements are crucial to eliminate potential bias when testing the climbing effect, since the establishment and survival of plants is more restricted under steeper and negative slopes, and with a lower abundance of cracks (Larson et al. 2000; Holzschuh 2016).

To determine the climbing intensity of each route, we used the Climbing-Use Intensity (CUI) index developed by Clark and Hessl (2015), as a function of the walking time required to reach the cliff base and the popularity of the climbing route inferred by the number of stars (0–4) assigned in a reference and updated climbing guidebook of the area (Madden 2019). In order to use a standardized and categorized measure, we grouped the CUI values by quartiles (Clark and Hessl 2015), resulting in low (Q1), moderate (Q2), high (Q3) or very high (Q4) climbing intensity.

We noted all the species of vacular plants to calculate the species richness in the climbed and unclimbed plots of each route and quadrat, as well as the number of individuals per species (i.e. abundance). Unidentified species in the field were later identified through image determination by local botanical experts but 18 of the 63 species could only be determined at the genus level. Species were further classified as endemic (species restricted to the Sierra Madre Oriental, Mexico), native (non-endemic but present in Mexico), and alien species (Velazco et al. 2011; Salinas-Rodriguez et al. 2017), and according to their rock association as rock-specialists (i.e. restricted to rocky habitats), species with non-strict but close association to rocky habitats (i.e. frequently inhabiting rocky environments but also found in other ecosystems) and generalist species (see Table S2). Shannon-Wiener (H') and Simpson (D) diversity indices were calculated per cliff as well as for climbed and unclimbed plots within each route using the *diversity* function from the *vegan R* package (Oksanen et al. 2020). Based on photos, plant cover was determined by the area (i.e. plant orthogonal projection) using ImageJ (in cm²). We then calculated the percentage of a plant's cover relative to the size of the climbed or unclimbed plot. Additionally, the relative cover (CR_i), the relative abundance (AR_i) and the relative frequency (FR_i) of each species in the sampled plots were calculated (Alanís et al. 2020). We also classified species into dominant (DO), common (CO) and locally rare (RA) by using the Importance Value Index (IVI) of species together with the species distribution range and local presence (Curtis and McIntosh 1951; Velazco et al. 2011). IVI was calculated using the *importance value* function from the *Biodiversity* R package (Kindt and Coe 2005). IVI considers the sum of the relative frequency (number of plots where a species is observed divided by the total number of surveyed plots), the relative abundance (in terms of number of individuals of a species, also referred to as relative density) and the relative spatial dominance (in terms of percentage of rock area cover by a given species) of species. These calculations determine the ecological value in terms of abundance and biomass and thus the dominance of the species in the plant's community (Curtis and McIntosh 1951). Species with the 15% highest IVI were considered dominant species (DO), species with the 15% lowest IVI were considered locally rare species (RA), and species with in-between IVI values were considered common species (CO, Table S2).

Data analysis

We conducted all statistical analysis with *R version 4.0.3* (R Development Core Team 2020). We used Linear Mixed-effects Models (LMMs) implemented in the *lme4* package and the *lmer* function (Bates et al. 2015) to test the effect of rock climbing (referred to as climbing) on plant abundance, cover, and species richness, and whether this effect differed among different climbing intensity levels. Plant abundance, cover, and species richness were included as response variables in three separate models. Cliff section (three levels: Bottom, Middle, Top), climbing difficulty (three levels: beginner, intermediate, advanced), climbing effect (two levels: climbed vs. unclimbed), climbing intensity (four levels: low, moderate, high, very high) and the two-way interaction between climbing sector (i.e. a climbing area with multiple routes) was included as random factor, and the slope and the percentage of cracks as covariates. Additionally, in two separate models, we used LMMs including climbing effect as fixed factor and route nested in sector as random factor to test whether Shannon-Wiener and Simpson diversity indices calculated per study site (i.e. route) differed between climbed and unclimbed plots.

To detect patterns of co-occurrence among cliff species and whether this co-occurrence varies among the species-dominance levels (i.e. rare, common, dominant species), we used the *cooccur* function from the *cooccur* R package (Griffith et al. 2016). This species cooccurrence analysis was conducted for species occuring in the same route, same cliff section and same climbing effect, as interaction would occur at this spatial level. In this way, the presence/absence co-occurrence matrix of all species (Fig. S3) and the co-occurrence within climbed and unclimbed plots were analyzed and mapped in different figures, highlighting the positive, negative (both considered as non-random associations) or random associations. If the presence of one species favours the presence of another in a non-random way, the association is considered positive; the association would be negative if the presence of one species systematically hinders the presence of another. Random associations are those that do not deviate from their expected co-occurrences by more than 0.1 considering the number of plots generated (Griffith et al. 2016). Only co-occurring species are shown in the matrix, so the analysis represents an approach of the number of species co-occurring, and thus coexisting and potentially interacting in each condition (i.e. by climbing effect and route section). Subsequently, we calculated the number of co-occurrences between pairs of groups of species dominance level (as explained above, classified according to the Importance Value Index – IVI – of the sampled species; Curtis and McIntosh 1951; Velazco et al. 2011). We also used LMMs to test how climbing affected the abundance and cover of each of the three dominance groups. These models included the group of species dominance level (three levels: rare, common, dominant), climbing effect and their two-way interaction as fixed factors, and route nested in sector as a random factor.

Finally, we tested for changes in community composition between sites that can be attributed to climbing. To this aim, we first used permutational multivariate analysis of variance using distance matrices with the *adonis* function from the *vegan R* package (Oksanen et al. 2020) in order to assess the extent that factors influence the species composition while controlling permutations by routes (i.e. sites). Second, we implemented non-metric multidimensional scaling (NMDS) analysis to visualize and interpret the species configuration according to climbing. We also conducted NMDS analysis for testing for variation in species composition among and within communities (i.e. among routes, and among the bottommiddle-top sections within each route). Here, we used the *MetaMDS* function of the *vegan R* package (Oksanen et al. 2020) that calculates Bray-Curtis distances for the communityby-site matrix.

In all LMMs, we tested the assumptions of normality and homogeneity of variance of the residuals using the Shapiro-Wilk test and the Bartlett test, respectively, and also checking visually. If the residuals were not normally distributed, we transformed the response variable. In the case of heteroscedasticity, we applied a weighted least square regression (Strutz 2016) by including weights (1/variance) into the model, using the extract model *weights* command. Whenever there were significant main effects containing more than two levels or significant interactions, we applied post-hoc contrasts using the *lsmeans* package (Lenth 2016) with the Tukey's test.

Results

A total of 578 individuals from 63 species were recorded, corresponding to 52 genera and 30 families (*see* Table S2). Although the total surveyed climbed and unclimbed area was the same, we found 170 individuals of 37 species in climbed plots and 408 individuals of

52 species in unclimbed plots. The most frequent species (i.e. number of plots where the species is present) were *Agave lechuguilla* (n=21 plots), *Chrysactinia pinnata* (19), *Stenaria nigricans* (17), *Cheilanthes standleyi* (15), and *Linum lewisii* (15). The least frequent species were *Echeveria elegans* (1), *Echinocereus enneacanthus* (1), *Pinguicula gracilis* (1) and *Sedum palmeri* (1), among others (Table S2). The most abundant species (i.e. number of individuals per species) were *Chrysactinia pinnata* (n=51 individuals), *Cheilanthes standleyi* (49), *Agave lechuguilla* (46), *Stenaria nigricans* (41) and *Euphorbia prostrata* (25) (Table S2).

Four of the species found are listed in the IUCN Red List of Threatened Species: *Echeveria elegans* is listed as Endangered (EN) and was only found in unclimbed plots (Solís et al. 2013). *Agave bracteosa, Brahea dulcis* and *Dasylirion berlandieri* are listed as Least Concern (LC). *Echeveria elegans* and *B. dulcis* are endemics considered as rock-specialist and rock-associated species, respectively, while *A. bracteosa* and *D. berlandieri* are both endemic and generalist species.

Climbing effect on cliff-species abundance, cover, and diversity

Plant abundance, cover and species richness were significantly lower in climbed plots than in unclimbed plots $(\chi_1^2 \ge 14.89; p < 0.001; see Table 1)$. Plant cover was affected by a significant two-way interaction between climbing effect and climbing intensity; however, this interaction was neither significant for species richness nor for abundance (Table 1). Plant cover was lower in climbed plots in all climbing-intensity levels but the greatest differences between climbed and unclimbed plots were found in low (post-hoc test: t=4.397; p=0.001) or very high (post-hoc test: t=4.265; p=0.002) climbing intensity (Fig. 1). A significant effect of climbing intensity was found in species richness and a marginal effect was found in abundance (Table 1). Post-hoc tests did not reveal significant differences in species richness and abundance between pairs of intensity levels ($t \le 2.446$; $p \ge 0.095$). Species richness (r=0.84), abundance (r=0.85) and plant cover (r=0.68) were significantly and positively affected by the percentage of cracks, and the abundance was significantly and negatively affected by cliff slope (Table 1). Moreover, neither climbing difficulty nor cliff section had a significant effect on plant richness, abundance or cover (Table 1). Additionally, climbing difficulty and its interaction with climbing effect were not significant in any of the variables $(\chi_2^2 \le 3.299; p \ge 0.192).$

The overall mean Shannon-Wiener (*H'*) and Simpson (*D*) diversity indices were 3.54 and 0.96, respectively. Shannon-Wiener diversity in climbed plots (overall $H'_C = 3.09$) was lower than that in unclimbed plots ($H'_U = 3.58$), and the mean Shannon-Wiener diversity index among sites was significantly lower in climbed plots than in unclimbed plots ($\chi_1^2 = 23.51$; p < 0.001; Fig. 2). Simpson diversity was lower ($D_U = 0.96$; $D_C = 0.93$) but not significantly different in climbed plots compared to unclimbed plots ($\chi_1^2 = 0.93$; p = 0.334). This is probably because the Simpson diversity index gives more weight to common or dominant species and underestimate rare species with only a few representatives, which is the case for cliffs.

effect (Climbed vs. Unclimbed), clipped vs. Unclimbed), clippe were included in the LMMs: slope were included in the LMMs: plants or their coverage vary with c ** 0.01 > $p \ge 0.001$; *** $p < 0.001$, a	s richness, abundance and plant cover. To she limbing intensity and their two-way interaction as these abiotic factors may affect the climbin cliff height. Transformations applied to the res and \cdot reflects marginal effects (0.1 $p \ge 0.05$)	ow whether the climbing effect varie n in the Linear Mixed-effect Models ng impact. Cliff section (Bottom, Mi sponse variable are indicated after the	es among climbing (LMMs). The perce (ddle, Top) was inclu e variable name. Sig	intensity levels, we inc ntage of cracks (Perc. c aded to assess whether mificance is shown as *	luded climbing racks) and cliff the presence of $0.05 > p \ge 0.01$;
Response variable	Parameter	Chi-Square	df	p-value	
Species richness					
	Percentage of cracks	58.834	1	< 0.001	* **
	Slope	0.201	1	0.654	
	Cliff-section	0.052	2	0.975	
	Climbing difficulty	1.497	2	0.473	
	Climbing effect	15.324	1	< 0.001	* **
	Climbing intensity	19.299	3	< 0.001	* **
	Climbing effect × intensity	1.508	3	0.680	
Abundance $^{\diamond}$ 0.6					
	Percentage of cracks	55.547	1	< 0.001	* * *
	Slope	4.423	1	0.035	*
	Cliff-section	1.266	2	0.531	
	Climbing difficulty	3.177	2	0.204	
	Climbing effect	25.358	1	< 0.001	* **
	Climbing intensity	7.201	3	0.066	
	Climbing effect \times intensity	1.561	3	0.668	
Plant cover $^{\diamond}$ 0.3					
	Percentage of cracks	20.320	1	< 0.001	* **
	Slope	2.324	-	0.127	
	Cliff-section	0.237	2	0.888	
	Climbing difficulty	0.007	2	0.997	
	Climbing effect	28.911	-	< 0.001	* **
	Climbing intensity	1.715	ŝ	0.634	
	Climbing effect × intensity	11.513	3	0.009	**

Climbing effect on cliff-species associations and community composition

The species co-occurrence analysis revealed 18 non-random and 648 random associations in climbed plots (Fig. 3A), and 78 non-random and 1575 random associations between species in unclimbed plots (Fig. 3B). All 18 non-random associations in climbed plots were positive (Fig. 3), while 75 positive and 3 negative non-random associations existed in unclimbed plots. In unclimbed plots, negative associations were found between Cheilanthes standleyi (Dominant) and Polygala sp. (Dominant), and in Chrysactinia pinnata (Dominant) with Tradescantia sp. (Common) and Bouvardia ternifolia (Common). The taxa with the highest number of positive associations in climbed plots were *Helenium sp.* and *Croton* fruticulosus, both common species with four co-occurrences each. The taxa with the highest number of positive associations in unclimbed plots were Notholaena sp. (Common; N=10 positive associations), Stenaria nigricans (Dominant; 8), Neoplinglea sp. (Common; 8), and Carlowrightia texana (Common; 7). The analysis also showed that in unclimbed plots, four positive associations existed between pairs of rare species (i.e. V. coahuilensis -S. suffrutescens; Gochnatia sp. – C. cortesianus; P. oleracea – O. engelmannii; Linum sp. – N. intergrifolia) but there were no relationships between pairs of rare species in climbed plots (Fig. 3). Moreover, in both, climbed and unclimbed plots, rare species were positively associated with common species but not with dominant species (Fig. 3).

The total number of co-occurrences detected between each possible pairs of species groups according to the dominance type (e.g. Dominant-Dominant, Dominant-Common, Dominant-Rare, etc.) was always lower in climbed compared to unclimbed plots (Fig. 4; *see* raw data in Table S3). In addition, the number of individuals in dominant, common and rare species was lower in climbed plots compared to unclimbed plots (Fig. S4). However, while mean abundance in dominant or common species per route was significantly lower in climbed plots (Dominant: t=4.419; p=0.001; common: t=4.078; p=0.003), mean abundance in rare species was lower but not significantly in climbed plots than in unclimbed plots, probably due to the relatively low number of individuals in rare species (Fig. S4).

Moreover, we tested for variation in species composition inter- and intra-routes (i.e. changes among and within communities) by implementing NMDS among and within routes, respectively. Species composition significantly varied between routes ($F_{11,21} = 2.546$; p=0.001) but not within routes (i.e. no differences in species composition existed among bottom, middle and top sections within the routes; $F_{2,34} = 0.762$; p=0.776). Finally, NMDS analysis with 2,047 permutations showed that the composition of species significantly differed between climbed and unclimbed plots when controlled by site and section ($F_{1,21} = 1.116$; p=0.007; Fig. 5), so species composition differed due to climbing.

Discussion

Our study in El Potrero Chico (Mexico) found that rock climbing decreased species diversity as well as the number and type of associations between pairs of species, leading to a strongly altered cliff-plant community. Positive species associations that were significant in unclimbed plots disappeared in climbed plots, highlighting that climbing causes a lower number of positive associations between pairs of dominant species and the absence of ben-



Fig. 1 Effect of climbing on mean species richness (A), abundance (B) and plant cover (in %) (C) per climbing-intensity level. Bar-plots (Means \pm SE) of the two-way interaction between climbing effect and climbing intensity are shown for each variable (*see* Table 1)



Fig. 2 Effect of climbing on the Shannon-Wiener diversity index at the study sites. (A) Mean Shannon-Wiener diversity index±SE by sampled sites is shown in the bar plot for climbed and unclimbed plots. (B) Shannon-Wiener diversity present in each site (i.e. sampled route 'r'). Grey and white colors represent climbed and unclimbed plots, respectively

eficial coexistence between pairs of locally rare species. Losing rare species and their interactions due to climbing could trigger a local decline of endemic and threatened species. In our study, this was the case with *Echeveria elegans* (EN), which occurred in unclimbed plots but not in climbed plots. The negative effect of climbing observed for the association between pairs of different dominant species is also worrying, since dominant species drive community dynamics and facilitate interactions of other species even under the distinctive harsh conditions of cliffs (Qi et al. 2018). The reduced species diversity and abundance observed in climbed versus unclimbed plots also reflects decreased species coexistence. In this sense, our results strongly support that climbing and not intra-population variability drives cliff community composition in El Potrero Chico.



Fig. 3 Presence/absence co-occurrence matrix of species growing in climbed (**A**) and unclimbed (**B**) plots. Pairwise co-occurrences were restricted to species found in the same site and cliff-section and separated between those co-occurring in each climbed (A) or unclimbed (B) plot. Positive associations are colored in blue, negative associations in yellow and significant random associations in grey. The species pair combinations without any observed or expected co-occurrence according to the analysis were removed by default, and therefore are not shown in the matrix. The level of dominance is highlighted in bold for each of the species. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species



Fig. 4 Number of co-occurrences (log transformed) between paired dominance groups of species calculated for unclimbed plots (in white) and for climbed plots (in grey) growing in the same site and cliff section. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species. Raw data are shown in Table S3

Climbing impact on the presence and diversity of species

Supporting our hypothesis, climbing negatively impacted plant abundance, cover, species richness, and species diversity in the cliff populations sampled in El Potrero Chico (Figs. 1 and 2). Negative effects of climbing on plant abundance, cover and species richness were already documented in previous studies (e.g. Camp and Knight 1998; Lorite et al. 2017; March-Salas et al. 2018; Schmera et al. 2018). However, this is the first time that responses of plant species diversity to climbing in a cliff ecosystem were estimated, revealing relatively high diversity compared to other nearby regional ecosystems and negative effects from climbing. The Shannon-Wiener diversity in the studied cliffs (H' = 3.54) was comparable and even higher than that of other ecosystems of Nuevo León (Mexico) such as temperate forest (H' = 0.72-1.74), thorny or submontane scrubland (H' = 1.94-3.02) and medium



Fig. 5 Biplot showing variation in species composition between climbed and unclimbed plots. Predicted values of the species two-dimensional spatial configuration with regard to NMDS1 and NMDS2 axes are shown. Polygons show differential species composition between climbed and unclimbed plots according to the NMDS analysis. Each point represents a single species, and symbols and colors divide species into dominant, common, and rare

sub-evergreen forests (H' = 3.15), but lower compared to medium sub-deciduous forests (H' = 4.29-5.80) (Alanís et al. 2020). However, climbed routes had a 14% lower diversity at the study site, and climbing may sometimes cause an indirect negative effect on unclimbed areas by hindering inter- and intra-species interactions and cliff-colonization, reducing the total cliff plant species diversity. Maintaining relatively high diversity is essential for cliff communities functioning and ecosystem preservation (Larson et al. 2000).

Contrary to our expectations, climbing had a negative impact irrespective of the climbing intensity. Negative impacts were found at each level of climbing use intensity and this impact did not increase with increasing intensity, reflecting the absence of any linear patterns with climbing intensity (Fig. 1). This result matches relatively well with observations in climbing areas of Jura Mountains (Switzerland) of Schmera et al. (2018) but contradicts previous studies showing that climbing effects strongly depend on climbing intensity (Clark and Hessl 2015; Lorite et al. 2017). The absence of linear patterns with climbing intensity may be explained because the greatest impact of climbing likely occurs during the opening of a new route, since route equippers (i.e. persons establishing the route on the cliff by incorporating metal bolts or anchors) frequently remove plants and mosses to facilitate the climbers' ascent. Also, first ascents could be more impactful for cliff plant communities. Thus, the impact would not increase significantly with increasing frequency of climbers, as indicated by Schweizer et al. (2021) in a study on changes in lichen cover on a boulder during simulated increases in climbing frequency. They found that the effect of climbing is strongest during the first 50 ascents and that subsequent ascents did not cause any further significant damage, meaning that the climbing impact on lichen cover stabilized over time. Thus, an assessment of plant communities over time starting from undisturbed cliffs, followed by the opening of new routes, and the increase of climbing activity is required to confirm this unresolved question.

Changes in cliff species associations and community

Rare species are particularly threatened by anthropogenic threats (Vitousek et al. 1997), but literature on the impact of climbing on rare species is scarce. Eleven of the locally rare species were found in unclimbed plots, but only three locally rare species occurred in climbed plots (Figs. 3 and 4). Five of these rare species present in unclimbed plots are specialized on cliff habitats and all rare species present in climbed plots were generalists. The loss of rare species in an ecosystem is worrisome, since rare species make up a large share of the diversity of ecological assemblages and promote positive interactions (Calatayud et al. 2020). Therefore, the disappearance of locally rare species would not only decrease diversity in cliff ecosystems, but also alter beneficial biotic interactions. Remarkably, *E. elegans*, listed as Endangered species (EN), was only found in unclimbed plots, suggesting that climbing may burden rare and threatened species. The negative climbing effects found on species diversity and on the presence of endemic, rare and threatened species illustrate that diversity indices together with endemic status and conservation value are all essential for framing adequate local conservation strategies.

As might be expected, the greatest total loss of individuals due to climbing occurred in dominant species. Dominant and other common species have at times been undervalued in conservation actions (Gaston 2010), but the loss of individuals of dominant species could significantly impact community structure (Avolio et al. 2019) and affect species establishment (Gilbert et al. 2009). The ecosystem structure on rocky outcropts may also be affected by a reduction in dominant and common species, due to their greater abundance and biomass in the system (Avolio et al. 2019; Gray et al. 2021). In cliff ecosystems, dominance associates with abundance, frequency and cover, and depends on the available ecological micro-niche. The Importance Value Index (IVI) values in our study system ranged from 0.17 to 9.33, being relatively low compared to some ecosystems such as woodlands (e.g. Didita et al. 2010) but higher than in other plant communities such as agroforests and thorny shrublands (e.g. Asigbaase et al. 2019). Due to the patchy structure and heterogeneity of the cliff-face (Kuntz and Larson 2006; do Carmo et al. 2016), direct competition is probably not frequent in cliffs. Cliffs are usuall not totally covered by plants and therefore different cliff species are only seldomly sharing exactly the same abiotic resources (e.g. soil nutrients, water, light), restricting competition to the spatial occupation of available micro-niches (Kelly and Larson 1997; Larson et al. 2000). However, species with increased adaptive capacity and plasticity (for example, great dispersal abilities in cliff habitats, well-adapted root traits, drought tolerance strategy) would be more prominent and dominant on the rock faces (Larson et al. 2000), which may help communities to buffer decreasing environmental predictability (e.g. March-Salas et al. 2021; March-Salas et al. 2022). The spatial organization of individuals and species in cliff ecosystems reflects important assemblage processes. In cliffs, dominant species could attract more pollinators, have reduced distance among individuals, lower rock erosion and provide more substrate to other cracks through litter decay, so positive interactions could appear between distinct groups of species. Thus, dominant species should be also considered when designing cliff protection measures, since they are essential for the maintenance of the ecosystem, especially under environmental or human disturbances such as climbing (Gaston 2010).

Our analysis shows for the first time significant species associations in cliff ecosystems (but *see* Cooper 1997), and these mathematical associations may reflect beneficial ecological interactions between species (Holt 2017). The total number of associations between pairs of species was 60% lower in climbed compared to unclimbed plots and positive associations were 73% lower in plots subjected to climbing. These declines may affect the dynamics of cliff populations. In addition, results of unclimbed plots show significant positive associations among various rare species. Paired rare-rare species associations existed in unclimbed plots but disappeared in climbed plots, suggesting the strong fragility of this type of biological interaction to anthropogenic perturbations (Vitousek et al. 1997; Schatz et al. 2014). The existence of positive associations between pairs of rare species in unclimbed plots is remarkable, considering their low abundance.

Our analysis also indicated that dominant and other common species would have positive effects and may facilitate rarer species, as has been found in other ecosystems such as tallgrass prairies or grasslands (Smith and Knapp 2003). In unclimbed plots, the highest number of co-occurrences existed between different dominant species, and positive associations were found between them. In climbed plots, only two positive associations between dominant species existed and positive associations between common species accounted to 45% of all positive co-occurrences. Co-dominance is a common phenomenon that occurs when two or more species are similarly dominant in a biotic community, and studies show that dominant associations may indirectly favor establishment and even population growth of rare species, since it may control the presence of other common species (Avolio et al. 2019), in line with our results in unclimbed plots. Studies also suggest that co-dominance is an important driver of community structure and functioning, promoting long-term community stability (Smith and Knapp 2003; Crutsinger et al. 2008; Gray et al. 2021). Overall, climbing reduced all types of potential species associations. However, three negative associations were found in unclimbed plots, all involving dominant species, suggesting competition for the colonization of available micro-niches, or simply dispersal limits or an effect of general occurrence in the investigated area. Cliffs offer resource-poor patches and show spatial niche partitioning, so co-existence of different species capable of adapting to diverse conditions and positive co-dominance are essential for successful habitat colonization and functioning in these ecosystems (Gray et al. 2021).

Changes in species diversity and species associations in the sampled sites in El Potrero Chico resulted in a significant change in plant community composition due to climbing (Fig. 5). The community composition varied among routes but not within the same route (as found in previous studies; Boggess et al. 2017; Harrison et al. 2022), suggesting that climbing would affect different community assemblages and that climbing is an important factor affecting the composition within cliff plant communities. If the change in species composition persists, it may jeopardize the structure and stability of cliff communities. This is especially true if this change triggers the loss of unique species or relevant biotic interactions, as was found in this study, and under the current climate change context (Ives and Carpenter 2007). However, cliffs are spatially heterogeneous systems so the effect of climbing could vary depending on the number of species and individuals.

Conservation of cliff plant communities in climbing areas

Generally, the consequences of losing rare species at community or even ecosystem level are poorly understood (Jain et al. 2014), even though rare species are often the focus of conservation efforts (Gaston 2010). Our findings suggest that a loss of rare species will lead to a decrease in the number and type of species associations, potentially affecting ecological assemblages and rare species persistence. However, our insights highlight that conservation in cliff ecosystems should also focus on dominant species and their interactions, as well as on species diversity, since they can act as a buffer against disturbances and environmental variability, promote positive associations with common and rare species, and ultimately maintain cliff plant community functioning (Gaston 2010). In this sense, conservation science should convince stakeholders of the need for a holistic conservation of cliff ecosystem and not only focus on emblematic or rare species.

In addition, the shift in the community assemblage and the absence of patterns regarding climbing intensity suggest that conservation efforts should focus on determining priority areas for conservation rather than merely trying to limit the impact on climbing routes itself. This includes controlling the opening of new routes with prior assessments of biodiversity impact, and with specific training for the local personnel that carry out the opening and maintenance of climbing routes. Prior scientific assessments would furthermore serve to identify areas with low conservation value where continuing rock climbing activity has low or no impact on local biodiversity. If these premises are rigorously implemented as management and conservation criteria, this may help to halt the loss of biodiversity and plant individuals in cliff ecosystems.

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Author contribution FMA and MMS designed the study and MMS and JL designed the field-sampling methodology. FMA conducted the field surveys and gathered the data with the help of AS, while EEC helped to identify the cliff-plant species. MMS and JHA analyzed the data. MMS wrote the original draft of the manuscript, with review and editing by JHA, JRA, JL and JFS. All authors accepted the final version of the manuscript. **Funding** This study was funded by CONACYT (National Council of Science and Technology - México). *National Geographic Society* (Grant number EC-50532R-18 – WorldClimb – and NGS-82734R-20 – ReCO-VIDiv –), *American Alpine Club* (AAC), *Asociación Española de Ecología Terrestre* (AEET) and *EcoClimb* project (FEDER-Andalucía 2014–2020 Program - A-RNM-4-UGR20) supported the work that gave rise to the design and conceptual part of this work.

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Data Availability Data will be made available in a public repository upon acceptance for publication.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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