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“MANAGEMENT OF NATURAL RESOURCES ON THE CLIFFS OF EL POTRERO CHICO, NUEVO LEÓN, MÉXICO”

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A mi hijo Leún
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RESUMEN

Los ecosistemas de acantilados son importantes reservorios de biodiversidad, albergando especies únicas y endémicas adaptadas a condiciones extremas. Sin embargo, enfrentan amenazas significativas debido a actividades humanas, como la escalada recreativa, han crecido enormemente en popularidad, con más de 50 millones de escaladores en todo el mundo. Algunos estudios previos han denotado que la escalada afecta a la riqueza de especies y a la abundancia de flora rupícola, pero se desconoce el grado de afección sobre la diversidad vegetal y cómo es efecto en las asociaciones entre especies. Es relevante también el desconocimiento sobre el origen del impacto de la escalada, lo que ayudaría a elaborar medidas de gestión más adecuadas. Estos vacíos de conocimiento los abordamos en mi tesis doctoral.

Mi Tesis está enmarcada en el área natural con gran actividad recreativa de El Potrero Chico (Nuevo León, México). En el **Capítulo 1**, aplicando una metodología innovadora, descubrimos que la escalada deportiva altera la composición de las comunidades rupícolas, reduce la diversidad de especies y debilita las asociaciones ecológicas. Las especies dominantes son las más afectadas, mientras que las raras, endémicas y amenazadas suelen desaparecer en áreas escaladas, desestabilizando las comunidades.

En el **Capítulo 2**, descubrimos que el mayor impacto ocurre durante la apertura de nuevas rutas de escalada, reduciendo la riqueza de especies hasta en un 38%. Las ascensiones posteriores generan disminuciones adicionales en la abundancia de plantas y la cobertura de líquenes, con pérdidas de 60.6% y 42.3% dentro y cerca de las rutas. Estas alteraciones son más severas en áreas con mayor vegetación inicial, destacando la necesidad de regular cuidadosamente estas actividades. Además, recientemente se ha determinado que la tecnología de drones ofrece.

En el **Capítulo 3** hacemos un análisis comparativo entre el método de muestreo tradicional en campo con el del uso de drones y nuestros resultados muestran que, si bien los drones superan a los métodos tradicionales en cobertura y eficiencia, las técnicas in situ siguen siendo esenciales para analizar interacciones a escala fina, Juntos, estos enfoques proporcionan un marco integral para la conservación, permitiendo regular la escalada y proteger a largo plazo los ecosistemas de acantilados y su biodiversidad.

ABSTRACT

Cliff ecosystems are critical reservoirs of biodiversity, hosting unique and endemic species adapted to extreme conditions. However, they face significant threats due to human activities, particularly recreational climbing, which has grown exponentially in popularity, with over 50 million climbers worldwide. Previous studies have indicated that climbing affects species richness and the abundance of rupicolous flora. However, the extent of its impact on plant diversity and the interspecies associations remains unknown.

Additionally, the origin of climbing-related impacts is poorly understood, hindering the development of effective management measures. My doctoral thesis addresses these knowledge gaps. My research is situated in the natural area of El Potrero Chico (Nuevo León, Mexico), which experiences high levels of recreational activity.

In Chapter 1, using an innovative methodology, we discovered that sport climbing alters the composition of rupicolous communities, reduces species diversity, and weakens ecological associations. Dominant species are most affected, while rare, endemic, and threatened species tend to disappear in climbed areas, destabilizing communities.

In Chapter 2, we found that the greatest impact occurs during the opening of new climbing routes, reducing species richness by up to 38%. Subsequent ascents lead to further decreases in plant abundance and lichen cover, with losses of 60.6% and 42.3% within and near the routes, respectively. These alterations are more severe in areas with higher initial vegetation, underscoring the need for careful regulation of these activities. Furthermore, recent findings highlight the potential of drone technology for monitoring and analysis.

In Chapter 3, we conducted a comparative analysis between traditional field-based sampling methods and drone-based approaches. Our results

demonstrate that while drones outperform traditional methods in terms of coverage and efficiency, in situ techniques remain essential for analyzing fine-scale interactions. Together, these approaches provide a comprehensive framework for conservation, enabling the regulation of climbing activities and the long-term protection of cliff ecosystems and their biodiversity.

1. GENERAL INTRODUCTION

Cliffs are extraordinary ecosystems characterized by their steep terrain, inaccessibility, and unique microhabitats. These habitats support a rich diversity of life, including specialized and endemic species, and serve as refuges for biodiversity under extreme environmental conditions. However, cliffs are increasingly threatened by anthropogenic activities such as recreational climbing, route development, and broader environmental pressures like habitat destruction and climate change (deCastro-Arrazola et al., 2021; Harrison et al., 2022; Morales-Armijo, et al., 2024). The ecological significance of cliffs necessitates a deeper understanding of their biodiversity, the mechanisms underlying species coexistence, and the extent of the growing impact of human activities on these fragile ecosystems.

Rock climbing, in particular, has emerged as a pervasive activity that poses complex challenges to cliff biodiversity. Its effects extend beyond the physical damage caused by plant removal, cover plant damage and erosion to include disruptions in ecological interactions, nutrient cycling (Langevin et al., 2024), and species associations (Lorite et al., 2017; Harrison et al., 2022; Gray et al., 2021). Recent studies highlight the differential vulnerability of cliff-dwelling organisms, where locally rare species face heightened risks of extinction, while even dominant species may experience significant declines under intense climbing pressures (March-Salas et al., 2018; Calatayud et al., 2020; Gray et al., 2021). Despite this, the ecological dynamics of climbing impacts remain insufficiently understood, especially regarding the effects on community composition, species diversity, and the interdependence of biotic associations within cliff ecosystems.

Traditional methods for studying cliffs have provided critical insights into species richness and abundance but are hindered by logistical and safety challenges (Schwilk et al., 2021; Bollinger & Rousselle, 2022). Advances in technology, such as the use of drones, offer innovative solutions by enabling large-scale, non-invasive surveys that capture high-resolution imagery of cliff faces (Nyberg et al., 2024). These methods hold promise for overcoming the limitations of in situ sampling, allowing researchers to assess vegetation structure, species distribution, and ecological processes with unprecedented efficiency and reduced environmental impact (Nyberg, 2019; McKinley et al., 2020; Bishop et al., 2022).

In my PhD Thesis, I aimed to explore in three chapters the multifaceted challenges facing cliff ecosystems, focusing on understanding the interplay between human activities, biodiversity conservation, and methodological innovation. (1) The first chapter examines the impact of rock climbing on species coexistence and associations, particularly the coexistence between dominant and rare species, proposing hypotheses about the negative effects of climbing and its intensity on plant community composition and stability. (2) The second chapter investigates whether climbing route development or subsequent climbing ascents generate the strong impact on cliff flora and lichens, highlighting the differential impacts on densely versus sparsely vegetated cliffs; moreover, considering the urgent need for effective conservation, we propose a management protocol to address current challenges. (3) The third chapter evaluates advantages and disadvantages of traditional in situ sampling methods against drone-based surveys, assessing the potential of drones to improve spatial resolution, coverage, and efficiency in studying and conserving cliff ecosystems while minimizing ecological disturbance. Collectively, these three chapters aim to inform conservation strategies tailored to the unique dynamics and challenges of cliff habitats.

2. CHAPTER 1

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ORIGINAL RESEARCH

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 spe- cies 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 sampledalong 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 associationsbetween 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 threat- ened species. Finally, NMDS analysis revealed that the community composition changed significantly due to climbing. Our results indicate that conservation science should con- vince stakeholders of the need for a holistic conservation of cliff ecosystems and not focussolely 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 locallyrare when their distribution range or local presence is restricted, but other specialists are efficient colonizers in rocky outcrops, growing abundantly (Larson et al. 2000). Generalistspecies 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-Calle-jas et al. 2021). Nevertheless, this coexistence, and underlying species associations, cannot be understood as a competitive factor in cliffs. Competition and negative associations liein the colonization of the available micro-niches, since spatial heterogeneity offers micro- niches 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 eco- logical associations on cliffs.

The great increase in climbing popularity and intensity is altering cliff plant communitiesand 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 etal. 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 provid- ing 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 ecologi-cally 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 den-sity 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 geographicalrange; 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 etal. 2021), but the answer to this question is unknown in cliff ecosystems. For instance, rockclimbing 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 colo-nization 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 spe- cies, on the other hand (Gaston 2010; Gray et al. 2021), while dominant and common spe- cies 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 (Gaston2010; 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 rela-tive abundance and spatial distribution, as has been shown for generalist *versus* rock-spe- cialist species (Müller et al. 2004; March-Salas et al. 2018). For instance, dominant speciesmay be able to buffer rock climbing impacts better than rare species, as shown under otherenvironmental stressors and ecosystems (Sasaki and Lauenroth 2011; Qi et al. 2018), whilesome rare species could disappear. However, the number of individuals in dominant speciescould 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 dra-matic 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 vas- cular 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 diversityis 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 plantdiversity 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 etal. 2021). In order to assess the role of increasing rock climbing pressures on cliff-plant spe-cies, 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 pre- dict that (1) rock climbing negatively affects species cover, abundance, and diversity ofcliff 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 closely-adjacent case-control sampling design with a 3 m wide × 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 × 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 mid- dle 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 guar-antee 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 distributionof plants within each plot, both climbed and unclimbed plots were divided in 0.5 m × 0.5 msubplots (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 sampledarea of 108 m^2 and 36 unclimbed plots with a sampled area of 108 m^2. The sampled routes were placed in contrasted aspects: North (n = 5), South (3), East (1) and West (3). We notedthe 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 characteristicsof 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 Inten-sity (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 climbedand unclimbed plots of each route and quadrat, as well as the number of individuals per spe-cies (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 determinedat the genus level. Species were further classified as endemic (species restricted to the SierraMadre 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 associationas rock-specialists (i.e. restricted to rocky habitats), species with non-strict but close associ-ation 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 cm^2). 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 werecalculated (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; Velazcoet 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 rela- tive 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 differedamong 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 effect and climb-ing intensity were modelled as fixed factors. Climbing route nested in climbing sector (i.e. a climbing area with multiple routes) was included as random factor, and the slope and thepercentage 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 co-occurrence analysis was conducted for species occuring in the same route, same cliff sectionand 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 associa- tions. 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 ofgroups of species dominance level (as explained above, classified according to the Impor- tance 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 eachof 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 attrib-uted to climbing. To this aim, we first used permutational multivariate analysis of varianceusing distance matrices with the *adonis* function from the *vegan R* package (Oksanen etal. 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 multi- dimensional scaling (NMDS) analysis to visualize and interpret the species configuration according to climbing. We also conducted NMDS analysis for testing for variation in spe- cies composition among and within communities (i.e. among routes, and among the bottom-middle-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 community- by-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 vari- able. In the case of heteroscedasticity, we applied a weighted least square regression (Strutz2016) 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 (Lenth2016) 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 frequentspecies 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 thanin unclimbed plots ($\chi^{2}_{1} \geq 14.89$; $p < 0.001$; *see* Table 1). Plant cover was affected by a significant two-way interaction between climbing effect and climbing intensity; however, thisinteraction 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 differencesbetween 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 significanteffect 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 ($t \leq 2.446$; $p \geq 0.095$). 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 hada significant effect on plant richness, abundance or cover (Table 1). Additionally, climbingdifficulty and its interaction with climbing effect were not significant in any of the variables($\chi_2^2 \leq 3.299$; $p \geq 0.192$).

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.

Table 1 Climbing effect on species richness, abundance and plant cover. To show whether the climbing effect varies among climbing intensity levels, we included climbing effect (Climbed vs. Unclimbed), climbing intensity and their two-way interaction in the Linear Mixed-effect Models (LMMs). The percentage of cracks (Perc. cracks) and cliff slope were included in the LMMs as these abiotic factors may affect the climbing impact. Cliff section (Bottom, Middle, Top) was included to assess whether the presence of plants or their coverage vary with cliff height. Transformations applied to the response variable are indicated after the variable name. Significance is shown as * $0.05 > p \ge 0.01$; ** $0.01 > p \ge 0.001$; *** $p < 0.001$, and · reflects marginal effects ($0.1 > p \ge 0.05$)

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 ^ 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 × intensity	1.561	3	0.668	
Plant cover ^ 0.3					
	Percentage of cracks	20.320	1	< 0.001	***
	Slope	2.324	1	0.127	
	Cliff-section	0.237	2	0.888	
	Climbing difficulty	0.007	2	0.997	
	Climbing effect	28.911	1	< 0.001	***
	Climbing intensity	1.715	3	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 inunclimbed plots. In unclimbed plots, negative associations were found between *Cheilanthesstandleyi* (Dominant) and *Polygala sp.* (Dominant), and in *Chrysactinia pinnata* (Domi- nant) with *Tradescantia sp.* (Common) and *Bouvardia ternifolia* (Common). The taxa withthe highest number of positive associations in climbed plots were *Helenium sp.* and *Crotonfruticulosus*, both common species with four co-occurrences each. The taxa with the highestnumber 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. suf-frutescens*; *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 asso-ciated 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 andrare 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 inclimbed plots than in unclimbed 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 signifi- cantly 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 diver- sity 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 significantin unclimbed plots disappeared in climbed plots, highlighting that climbing causes a lowernumber of positive associations between pairs of dominant species and the absence of ben-

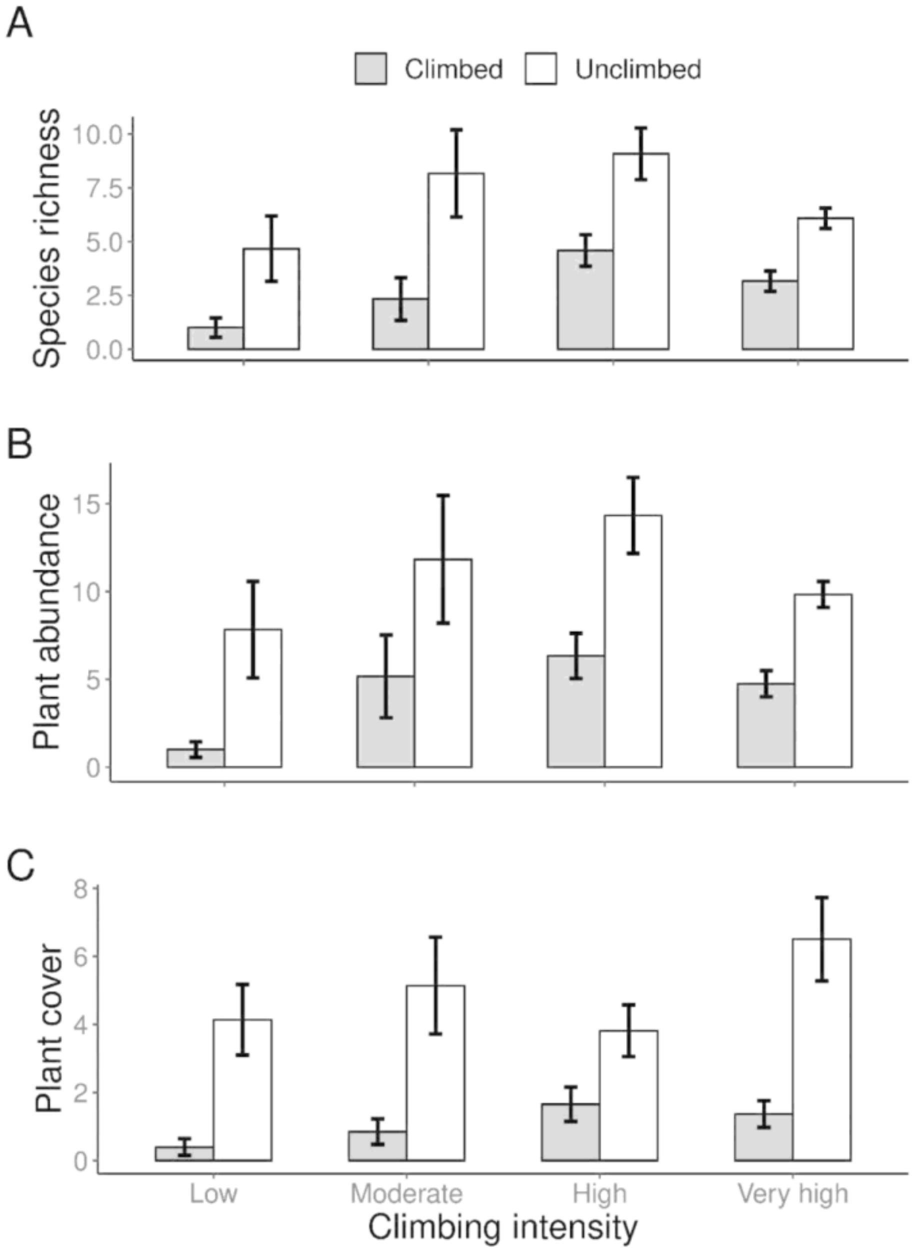

Fig. 1 Effect of climbing on mean species richness (**A**), abundance (**B**) and plant cover (in %) (**C**) per climbing-intensity level. Bar-plots (Means ± SE) of the two-way interaction between climbing effect and climbing intensity are shown for each variable (*see* Table 1)

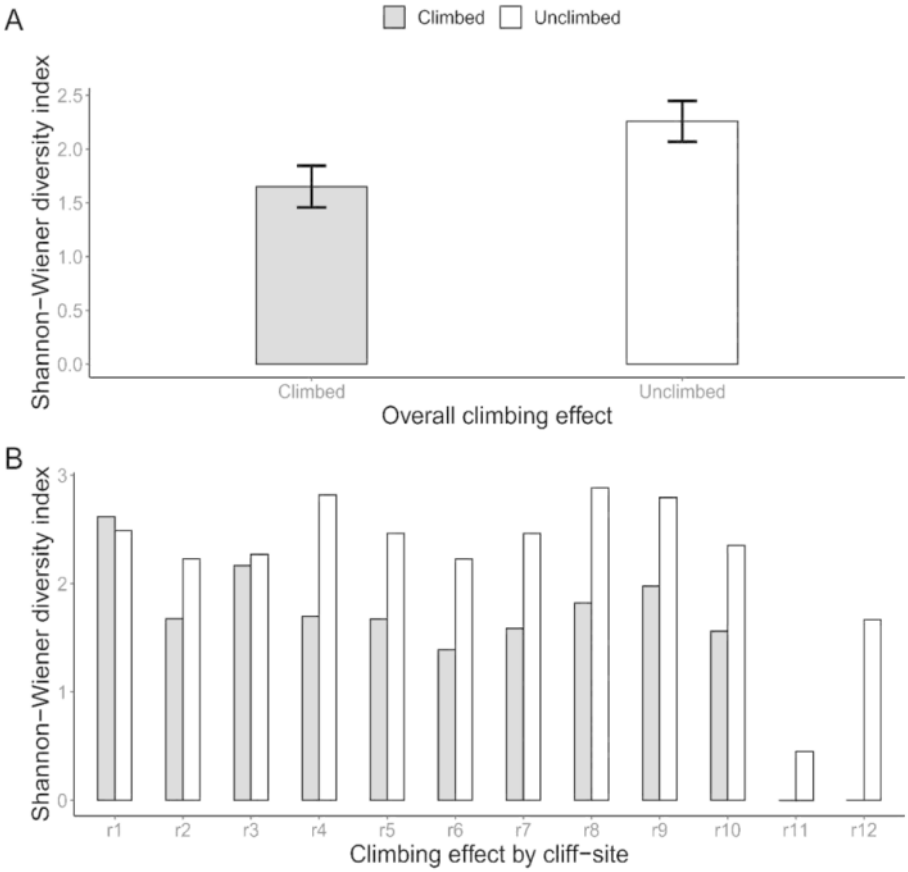

Fig. 2 Effect of climbing on the Shannon-Wiener diversity index at the study sites. **(A)** Mean Shannon- Wiener diversity index ± SE by sampled sites is shown in the bar plot for climbed and unclimbed plots. **(B)** Shannon-Wiener diversity present in each site (i.e. sampled route 'r'). Grey and white colors representclimbed 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 associationbetween 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. Inthis sense, our results strongly support that climbing and not intra-population variability drives cliff community composition in El Potrero Chico.

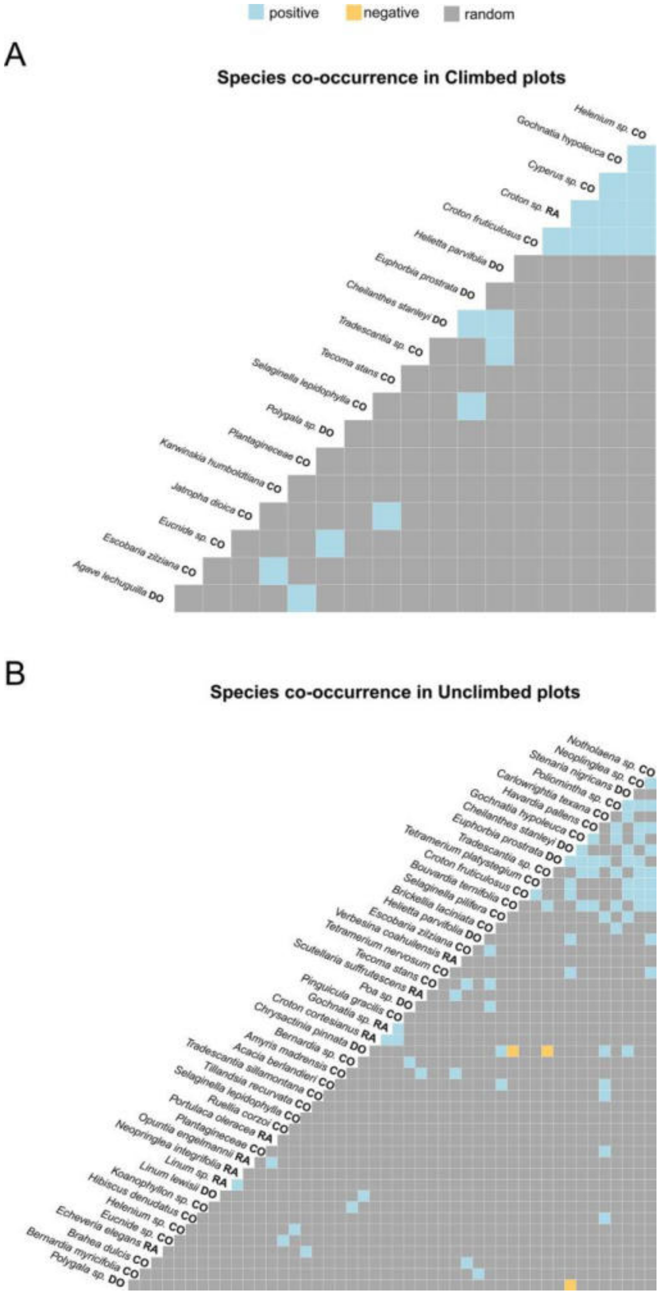

Fig. 3 Presence/absence co-occurrence matrix of species growing in climbed (**A**) and unclimbed (**B**) plots. Pairwise co-occurrences were restricted to species found in the same site and cliff-section and sepa- rated between those co-occurring in each climbed (A) or unclimbed (B) plot. Positive associations are col-ored 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 bydefault, and therefore are not shown in the matrix. The level of dominance is highlighted in bold for eachof the species. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species

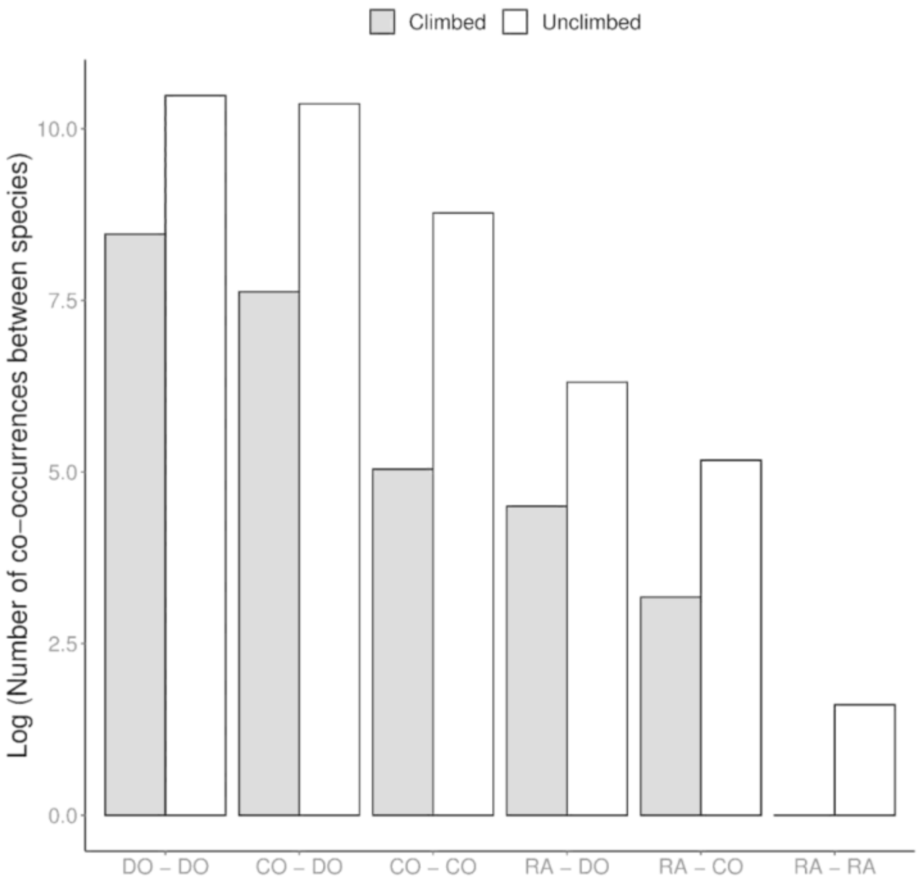

Fig. 4 Number of co-occurrences (log transformed) between paired dominance groups of species cal- culated for unclimbed plots (in white) and for climbed plots (in grey) growing in the same site and cliff section. 'DO' refers to dominant species, 'CO' to common species and 'RA' to locally rare species. 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. 1and 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 responsesof plant species diversity to climbing in a cliff ecosystem were estimated, revealing rela- tively 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 compara-ble and even higher than that of other ecosystems of Nuevo León (Mexico) such as temper-ate forest (*H*' = 0.72–1.74), thorny or submontane scrubland (*H*' = 1.94–3.02) and medium

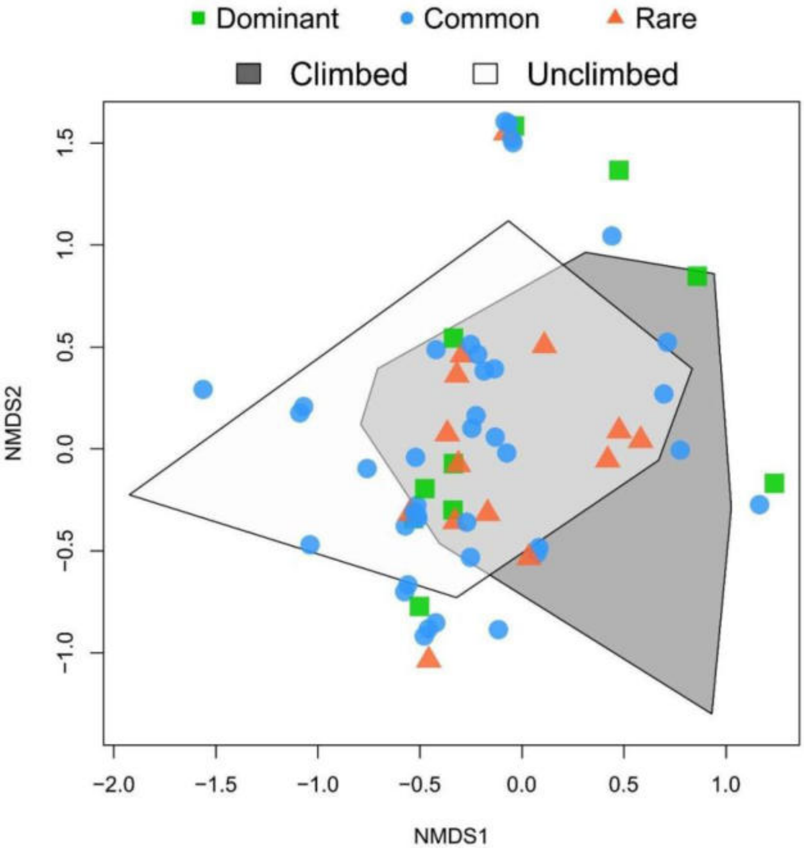

Fig. 5 Biplot showing variation in species composition between climbed and unclimbed plots. Predicted values of the species two-dimensional spatial configuration with regard to NMDS1 and NMDS2 axes are shown. Polygons show differential species composition between climbed and unclimbed plots accordingto 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 unclimbedareas 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 observationsin climbing areas of Jura Mountains (Switzerland) of Schmera et al. (2018) but contradictsprevious 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 open- ing 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 isstrongest 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, fol- lowed 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 spe-cies were found in unclimbed plots, but only three locally rare species occurred in climbedplots (Figs. 3 and 4). Five of these rare species present in unclimbed plots are specialized oncliff habitats and all rare species present in climbed plots were generalists. The loss of rarespecies in an ecosystem is worrisome, since rare species make up a large share of the diver-sity 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*, listedas 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 diversityindices 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 establish- ment (Gilbert et al. 2009). The ecosystem structure on rocky outcropts may also be affectedby a reduction in dominant and common species, due to their greater abundance and bio- mass 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 thornyshrublands (e.g. Asigbaase et al. 2019). Due to the patchy structure and heterogeneity of thecliff-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 nutri- ents, 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 rockfaces (Larson et al. 2000), which may help communities to buffer decreasing environmentalpredictability (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 etal. 2014). The existence of positive associations between pairs of rare species in unclimbedplots 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 growthof 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-dominanceis 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 showspatial niche partitioning, so co-existence of different species capable of adapting to diverseconditions 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 climb-ing would affect different community assemblages and that climbing is an important factoraffecting the composition within cliff plant communities. If the change in species composi-tion persists, it may jeopardize the structure and stability of cliff communities. This is espe-cially true if this change triggers the loss of unique species or relevant biotic interactions, aswas 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 leadto a decrease in the number and type of species associations, potentially affecting ecologicalassemblages and rare species persistence. However, our insights highlight that conservationin 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 sci- ence should convince stakeholders of the need for a holistic conservation of cliff ecosystemand not only focus on emblematic or rare species.

In addition, the shift in the community assemblage and the absence of patterns regardingclimbing 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 lowor no impact on local biodiversity. If these premises are rigorously implemented as man- agement and conservation criteria, this may help to halt the loss of biodiversity and plant individuals in cliff ecosystems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-023-02567-1.

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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 helpedto 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.

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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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2 CHAPTER 2

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RESEARCH ARTICLE

Climbing route development affects cliff vascular plants more than subsequent climbing: A guide to evidence-based conservation management to regulate climbing

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Abstract

1. Cliff ecosystems provide refuge to 35%–66% of the world's endemic plants. However, they face growing threats from sport climbing. Evidence suggests that unclimbed cliffs harbour approximately twice the plant richness compared with climbed cliffs, with increasing impact as climbing intensity increases. Unfortunately, it remains unknown whether the climbing impact on cliff vegetation originates from the development (opening) of climbing routes or from temporal changes resulting from subsequent climbing.
2. We recorded cliff vascular plants and lichens at the protected natural area of El Potrero Chico (Mexico) before and after the development of new climbing routes. Subsequently, we re-recorded the routes at sequential timepoints after 10, 20, and 30 ascents. Additionally, we examined whether the abundance of cliff vegetation influences the extent of climbing impact and whether the surroundings of the routes were also affected.
3. We found that the opening of climbing routes exerted the strongest negative effects on cliff plants, reducing species richness by 38%, while subsequent ascents generated a minimal impact. Worryingly, route opening affected not only species richness in the route itself but also the surroundings of the routes. After 30 ascents, cliff plant abundance decreased by 60.6% within the bolted routes, whereas it decreased by 42.3% in the surroundings. However, this impact depended on the original cliff vegetation abundance. Lichen cover showed a gradual decrease, indicating that cliff-dwelling lichens are affected not only by the opening of the route but also by subsequent ascents.
4. *Synthesis and applications*: Given the almost non-existent regulation of outdoor climbing activities in most countries, we urge the implementation of a conservation management protocol that defines clear strategies to regulate climbing

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Felipe Morales-Armijo and Martí March-Salas equal contribution.

activities and preserve pristine cliffs. On yet unclimbed cliffs with narrow endemic, rare, or threatened species, we propose banning the establishment of new climbing areas. On climbed cliffs lacking protected species, dynamic management actions should be implemented, such as setting a maximum number of routes that can be established and defining limits of acceptable change as climbing intensity increases. The proposed conservation management should help to halt the loss of unique cliff biodiversity and safeguard pristine cliff ecosystems.

KEYWORDS

cliff ecology, climbing regulation, conservation management, endangered species, lichens, limits of acceptable change, monitoring strategy, pristine ecosystems

1 | INTRODUCTION

Cliffs are unique and biodiverse ecosystems that face growing pressures worldwide due to rock climbing and other recreational activities such as rappelling and highline (Chang & Xu, 2020; Larson et al., 2000). They harbour a high diversity of plants and other rock-dwelling organisms, comprising species that are highly specialized in cliff environments, many of them being endemic and endangered species, as well as ecologically more widespread species (Baur et al., 2017; Larson et al., 2000; March-Salas, Lorite, et al., 2023). Given the uniqueness and high conservation value of cliff biodiversity, understanding the threats of rock climbing and developing approaches for an effective conservation management is imperative (deCastro-Arrazola et al., 2021). There is consistent evidence that rock climbing negatively impacts species richness and abundance of vascular plants in cliff habitats, also catalysing a significant decline of rare plants and invertebrates (e.g. Lorite et al., 2017; March-Salas et al., 2018; March-Salas, Morales-Armijo, et al., 2023; Schmera et al., 2018; Tessler & Clark, 2016). These detrimental effects of rock climbing mainly arise from direct trampling, the erosion of cliffs due to repetitive climbers' ascents, or plant removal by trampling, pulling, or uprooting by climbers (Harrison et al., 2022; Holzschuh, 2016). Moreover, as recently shown, the use of climbing chalk (magnesium carbonate) can also affect the germination and survival of rupicolous plants as it triggers changes in soil nutrients and pH (Hepenstrick et al., 2020). Furthermore, the opening of new climbing routes involves removing plants, mosses, and lichens along the planned route transect to ensure safe climbing. However, no studies have investigated which aspect of climbing activity exerts the greatest impact on cliff biodiversity.

Sport climbing is undergoing exponential and unplanned growth, with hundreds of new routes in previously unclimbed areas, leading to a significant decline in pristine cliffs and their biodiversity (Vogler & Reisch, 2011). Notably, nowadays there are more than 640,000 climbing routes in Europe and over 210,000 in North America (The Crag, 2022). Regrettably, the opening of new routes remains unregulated in most countries, with little to no legal restrictions (Hanemann, 2000). Opening a climbing route involves the installation of safety anchors using a drill (i.e. bolting), as well as the removal of unstable rocks that could endanger climbers. Additionally, 'route cleaning' is a common practice during route opening that typically involves removing the individual plants that may obstruct the climber's ascent, soil that accumulates in cliff crevices, and even the use of metal brushes to eliminate mosses and lichens that could be bothersome or slippery for climbers. If the people responsible for establishing and adding the bolts to the climbing routes (hereafter route developers) lack sufficient botanical and biological knowledge, this action may impact endemic, ecologically-relevant, and even endangered cliff-dwelling flora. Besides route opening, the increased climbing intensity may lead to more pronounced impacts on cliff plant communities (Clark & Hessl, 2015; Lorite et al., 2017). However, there are intrinsic variations in the rock-climbing impact, probably related to differences in species composition and site characteristics (Harrison et al., 2022). Thus, the relevance of increased climbing intensity for cliff biodiversity remains inconclusive, as similar impacts have been observed in both low- and high-intensity climbing areas (March-Salas, Morales-Armijo, et al., 2023; Schmera et al., 2018). Understanding the dominant drivers of the overall impact of rock-climbing activities would be crucial for comprehensive and efficient management of this popular recreational activity and better protection of cliff biodiversity.

Concern regarding climbing impact is heightened particularly if the new climbing routes are planned to be installed in protected natural areas and/or in cliff areas with dense or unique vegetation. For instance, ~62% of climbing routes in Spain are situated within protected natural areas (deCastro-Arrazola et al., 2021), posing a worrying threat to their biodiversity. Not surprisingly, there is a growing conflict between climbers and managers of natural areas. So far, measures implemented by land managers mainly involved restricting access to climbers during the breeding season of cliff-nesting birds. In the world-famous Margalef climbing area (Spain), located in the Sierra de Montsant Natural Park, technical reports also recommend monitoring the carrying capacity (i.e. the maximum number of climbers that the system can support; Stankey al., 1985) of cliff ecosystems and their surroundings, and encourage limiting access when exceeded. More drastic measures have even gone as far as a total ban on rock climbing in certain areas due to the impact on birds or cliff flora of high conservation value (e.g. *Petrocoptis grandiflora*, a narrow endemic plant of Serra da Enciña da Lastra Natural Park, Spain). Where such regulations and management protocols are absent, this may lead to the opening of new climbing routes on cliffs with abundant vegetation and endemic and/or threatened cliff flora. Therefore, land managers need guidance on when and how to implement effective conservation actions, as well as the monitoring strategies required to surveil cliff biodiversity.

Here, we assess for the first time the origin of the impact of the climbing activity on cliff ecosystems by temporally comparing the effects originating from the development of the climbing route with those from subsequent climbing ascents. To this end, we asked local route developers to establish and bolt new climbing routes on pristine cliff ecosystems in the popular climbing site and protected natural area of El Potrero Chico (Nuevo Leon, Mexico). Thereafter, we recorded cliff plants and lichens both before and after new routes were established, and after 10, 20 and 30 ascents. The pristine cliffs varied in vegetation density (densely versus sparsely vegetated), allowing us to assess whether the abundance of cliff vegetation before route development influenced the climbing impact. We hypothesized that (1) the opening of new climbing routes affects cliff plants more than subsequent climbers' ascents; and (2) the impacts of the climbing activity are stronger on cliffs with originally dense vegetation. The insights from this study enable us to develop a conservation management protocol to guide the management strategy and regulation of rock climbing, and ultimately aid in the conservation of cliff ecosystems and their unique biodiversit

2 | MATERIALS AND METHODS

2.1 | Study site

El Potrero Chico (Nuevo León, Mexico) is located close to Monterrey, in the northern periphery of the 'Sierra El Fraile y San Miguel' protected natural area, part of the Sierra Madre Oriental mountain range. It covers 23,506 hectares and elevation ranges from 800 to 2360 m a.s.l. This region is formed by Mesozoic sedimentary rocks, including shale and limestone cliffs that support rich and diverse cliff vegetation (INECC, 2017; Larson et al., 2000). El Potrero Chico has a semi-arid climate, featuring hot summers with average monthly maximum temperatures exceeding 40°C from June to August and moderate winter temperatures ranging between 7 and 16°C. Precipitation peaks in September and October, averaging between 70 and 130 mm per month (García, 2004; March-Salas, Morales-Armijo, et al., 2023). The dominant vegetation types in the study area are submontane vegetation and desert rosetophilous scrub, the latter having been classified as a conservation priority because of its high level of endemism (Estrada-Castillón et al., 2012).

Recognized as one of the most popular climbing destinations worldwide, El Potrero Chico offers around 700 climbing routes in 24 rock faces (Madden, 2022). Approximately, 100 of these routes have been opened between winter 2022/23 and winter 2023/24. Rock climbing began there in 1960, but its popularity as a climbing area greatly increased in the late 1980s. The preferred seasons for climbing are late autumn and early spring (between November and March) due to favourable temperatures and low/scarce precipitation. During the winter seasons of 2022–23 and 2023–24, there were 2312 and 2238 climbers in El Potrero Chico, respectively (information provided by the Tourism Secretary of Hidalgo).

2.2 | Field monitoring design

To understand whether cliff communities are more affected either by the opening of the new routes or by subsequent climbing, we recorded the vegetation of pristine cliffs before (pre-opening) and immediately after (post-opening) the opening of the climbing routes in September–October 2022 (please, note that no permits were required for the fieldwork activities). Thereafter, we recorded the cliff plant diversity and abundance and lichen cover after 10, 20 and 30 climbing ascents until January 2023. These five times when plants and lichens were recorded are hereafter referred to as 'measuring times'. We selected two cliffs situated 50 m apart from each other. Both had an average slope of 83°, were higher than 11 m, and were facing North. To assess whether the rock-climbing activity has variable impacts depending on the abundance of vegetation in the original unclimbed cliffs, one studied cliff has originally dense and the other scarce vegetation (Figure 1). Other criteria used for the selection of these cliffs included: the feasibility of descending from the top of the cliff before the opening of the new climbing route (rappelling), and easy access for the climbing community to foster their involvement in the study.

Following the recommendations from two local route developers, we delineated four climbing routes on the pristine cliff with dense vegetation (25°57′18″ N 100°29′07″ W; called 'Sotol-Plutonia' climbing sector), and three on the pristine cliff with scarce vegetation (25°57′16″ N 100°29′00″ W; called 'Agave' climbing sector) (see Table S1). A total of 42 plots of 3 m^2 plots and 504 subplots of 0.25 m^2 were surveyed at each of the five measuring times (see 'Field monitoring method' below). Climbing routes were at least 3.5 m apart from the next climbing route. To establish the climbing routes, the path of the upcoming climbing route was initially guided with tape. Cliff plants and lichens was then recorded by establishing three quadrats at different heights of the cliff face (see details in

'Field monitoring method'). This is the 'pre-opening' measuring time. For replicability in subsequent surveys, the positions of the corners of the quadrats in each of the measured areas were marked on the cliff using tape. Thereafter, the two local climbing route developers installed the bolts, performing all the usual actions for establishing the seven climbing routes, following the delineation marked by the tape. The day after each route was established and bolted, we re-recorded the cliff plants and lichens at exactly the same points of the cliff face as in the 'pre-opening' measuring time and was termed 'post-opening'. Finally, local climbers were contacted for climbing the studied routes. Once 10, 20, and 30 ascents were completed on each route, we subsequently recorded the same points as in the 'pre-opening' and 'post-opening' measurements (Figure 1).

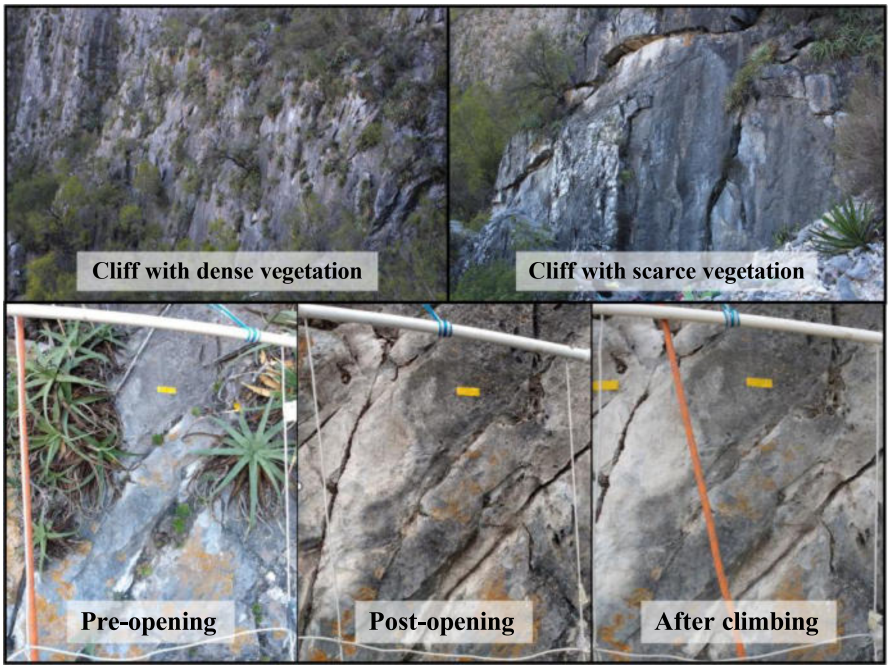


FIGURE 1 Example images of the studied cliffs. Cliffs with dense (top left) and scarce (top right) vegetation abundance were selected for the establishment of new climbing routes. Vegetation and lichens were recorded before (pre-opening) and after (post-opening) the establishment of the climbing routes. Subsequently, climbers ascended the routes 30 times, and cliffs were recorded after every 10 climbers' ascents.

2.3 | Field monitoring method and data collection

To assess the strength and the origin of the climbing impact, we used a case–control design with a 3 m wide × 3 m high quadrat positioned at three zones of the climbing route (see March-Salas, Morales- Armijo, et al., 2023). The quadrat consisted of a central plot of 1 m width and 3 m height representing the central area of the climbing route (so-called 'within the climbing route'; as 'cases'); two imme- diately adjacent surveyed plots of 0.5 m width and 3 m height, as this area could be potentially used by climbers during their ascent, and therefore would not be exempt from being disturbed; two plots 1 m far from the centre of the climbing route of 0.5 m width and 3 m height on the left and right sides of the 3 × 3 m quadrat that served as 'controls', representing areas not reached by climbers and route developers (so-called 'near the climbing route'). This closely adjacent paired design was chosen to effectively assess the impact of rock climbing, minimizing variations in biotic or abiotic factors, such as aspect, inclination, microtopography, and insolation, as described in the methodological review by Boggess et al. (2021).

To characterize the spatial distribution of plants and lichens within each plot, both 'within' and 'near' plots were subdivided into 0.5 × 0.5 m subplots (12 subplots in each 'within' plot and 12 subplots in each 'near' plot). Photographs were taken from each subplot as part of the data collection process. To consider the physical microtopography of the cliff, we calculated the proportion of cracks (crevices) in each 0.5 × 0.5 m subplot using the 'ImageJ' programme (Rueden et al., 2017). This measurement helps to reduce potential bias when modelling the climbing effect, since the establishment and development of plants are more plausible with a higher percentage of cracks (Holzschuh, 2016). We identified all the plant species pres- ent in the plots (Velazco et al., 2011), and calculated the plant species richness in the 'within' and 'near' plots of each climbing route and quadrat, as well as the number of individuals per species (i.e. abundance). In addition, the area (in cm^2) of each individual vascular plant (i.e. plant cover), and the lichen and moss covers were calculated, also using the 'ImageJ' programme. Since mosses covered only 0.74% of the monitored cliffs, this variable was not analysed.

2.4 | Data analysis

We conducted all statistical analysis with *R version 4.0.3* (R Development Core Team, 2020). We assessed the origin of the climbing effect as well as the influence of the original cliff vegetation abundance on plant species richness, plant abundance, and vascular plant and lichen cover as response variables in four separate models. We used linear mixed-effects models (LMMs) implemented in the 'lme4' package and the 'lmer' function (Bates et al., 2015). Measuring time (five levels: pre-opening, post-opening, and 10, 20 and 30 as- cents), climbing route zone (two levels: within vs. near the climbing route), original cliff vegetation abundance (two levels: dense vs. scarce), and their two- and three-way interactions were modelled as fixed factors. Plot nested in cliff section and the climbing route was included as a random factor. In the models concerning vascular plants, the percentage of cracks was used as a covariate to control for the amount of micro-niches available for plant establishment and growth (Holzschuh, 2016).

After conducting 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. If the residuals were not normally distributed, we transformed the response variable (see transformations in Table 1). Whenever there was a significant effect in measuring time or significant interactions, we applied post hoc contrasts by Tukey tests using the 'lsmeans' package (Lenth, 2016).

TABLE 1 Results of the linear mixed-effects models (LMMs) investigating the origin of the climbing effect, and the influence of the vegetation abundance of pristine cliffs on plant abundance, plant species richness, and total cover of vascular plants and lichens.

Plant abundance[a]				**Plant species richness**		**Plant cover**		**Lichen cover**[b]	
Parameter	**df**	**Chi²**	***p*-value**	**Chi²**	***p*-value**	**Chi²**	***p*-value**	**Chi²**	***p*-value**
Percentage of cracks	1	2.254	0.133	0.672	0.412	2.319	0.128	—	—
Climbing route zone (zone)	1	38.631	<0.001***	18.898	<0.001***	55.735	<0.001***	8.078	0.004**
Measuring time (measuring)	4	101.888	<0.001***	83.267	<0.001***	66.171	<0.001***	28.847	<0.001***
Cliff vegetation (veg)	1	3.492	0.062•	9.376	0.002**	7.979	0.005**	0.314	0.575
Zone × measuring	4	10.337	0.035*	4.899	0.298	0.085	0.999	14.028	0.007**
Zone × veg	1	8.267	0.004**	2.969	0.085•	17.134	<0.001***	7.047	0.008**
Measuring × veg	4	2.169	0.705	12.729	0.013*	14.987	0.004**	0.201	0.995
Zone × measuring × veg	4	0.196	0.995	0.095	0.999	0.002	0.999	0.252	0.993

Note: LMMs included climbing route zone (near vs. within the climbing route), measuring time (pre- and post-opening the route, and 10, 20 and 30 climbers' ascents), cliff vegetation abundance, and their two- and three-way interactions, as well as the percentage of cracks. Transformations applied to the response variable are indicated below the table. Significance is indicated as $*0.05 > p \geq 0.01$; $**0.01 > p \geq 0.001$; $***p < 0.001$ and • reflects marginal effects ($0.1 > p \geq 0.05$). Transformations: *a*: log(x); *b*: $x^{1.5}$.

3 | RESULTS

Plant abundance, species richness, and both plant and lichen cover exhibited significant changes across the measuring times (Table 1). These changes depended on the climbing route zone for plant abundance and lichen cover (significant two-way interaction; Table 1; Figure 2), and on the original cliff vegetation abundance, specifically for plant species richness and cover (significant two-way interaction between measuring time and original cliff vegetation abundance; Table 1; Figure 3).

Plant abundance was significantly lower post-opening com- pared with before the opening of the new climbing routes, both within (post hoc test: $t = -5.889$; $p < 0.001$) and near (post hoc test: $t = -3.268$; $p = 0.043$) the transect bolted for climbing (Figure 2A). In contrast, no significant differences in plant abundance existed between the measurements post-opening and after 10, 20, or 30 climbers' ascents (Figure 2A). Lichen cover was not significantly dif- ferent before than after the opening of the climbing route, nor after 10 ascents (Figure 2B). Nevertheless, lichen cover was significantly lower after 20 ascents compared with the pre-opening measure- ments (post hoc test: $t = -4.445$; $p < 0.001$), and significantly lower after 30 ascents compared with the pre- (post hoc test: $t = -5.592$; $p < 0.001$) and post-opening (post hoc test: $t = -4.334$; $p = 0.001$) measurements (Figure 2B).

Plant species richness (Figure 3A) and total plant cover (Figure 3B) were significantly lower in the post-opening compared with the pre-opening measurements in initially densely vegetated areas (post hoc tests, for species richness: $t = -6.317$; $p < 0.001$; for plant cover: $t = -5.972$; $p < 0.001$). In contrast, there were no significant differences between the pre- and post-opening mea- surements in cliffs with initially scarce vegetation (Figure 3A,B). Climbing ascents did not significantly affect species richness or total plant cover, regardless of the amount of initial vegetation on the cliffs (Figure 3).

4 | DISCUSSION

As hypothesized, opening the climbing route is the most detrimen- tal phase of rock climbing for cliff vascular plants, but not for cliff lichens. To date, this impact was primarily attributed to an increase in climber frequency (e.g. Clark & Hessl, 2015; Lorite et al., 2017; Vogler & Reisch, 2011). However, we found that it is precisely dur- ing the opening when the greatest impact on cliff vegetation oc- curs, while the first 30 climbing ascents generate a relatively lower impact. Yet, the extent of this impact depends on the original veg- etation abundance of the pristine cliffs, and the decrease in lichens appears to be influenced by both activities: the opening of the new route as well as by the repeated friction produced by climbers dur- ing initial ascents. Considering the almost non-existent regulation of climbing route opening in most countries (Hanemann, 2000; March- Salas, Lorite, et al., 2023), and the significant negative effect of rock climbing on these habitats, we advocate and suggest clear conserva- tion management strategies to be implemented to control the estab- lishment of new climbing areas in cliff ecosystems.

4.1 | The origin and extent of climbing impact

The opening of new routes represents the phase with the strongest negative effect on cliff biodiversity, affecting not only the bolted area that will be directly used by climbers but also an extended area located 1–2 m away from the route, normally unused by climbers. However, after 30 climbing ascents, vascular plants in the areas away from the routes remained intact, indicating that the impact of the climbers themselves mainly occurs within the 1 m wide of the bolted route. Within the climbing route, actions carried out dur- ing route opening reduced cliff vegetation abundance by 60.6% (Figure 2A, right panel), whereas it decreased by 42.3% in the area near the climbing route (Figure 2A, left panel). After 30 ascents,

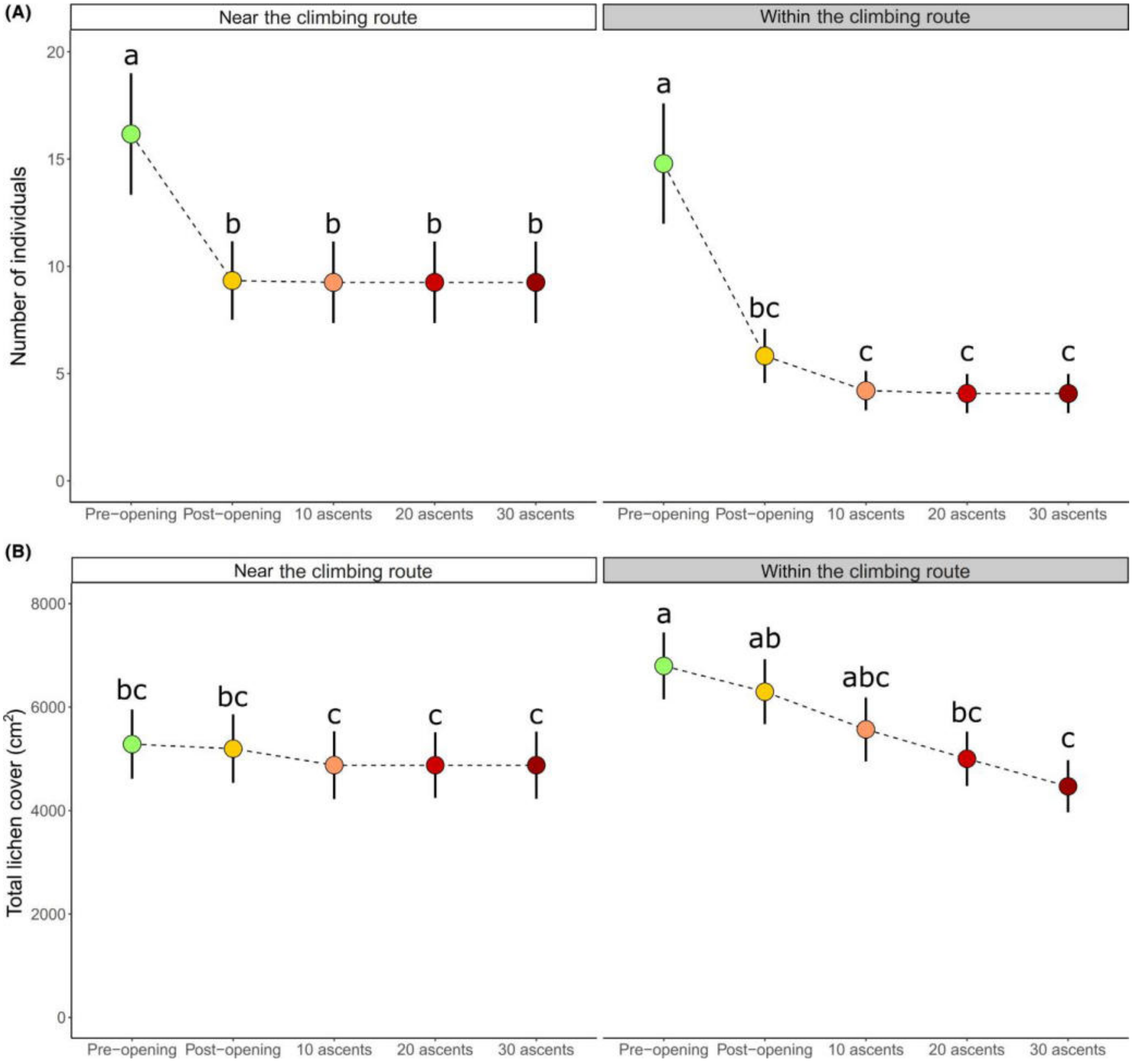
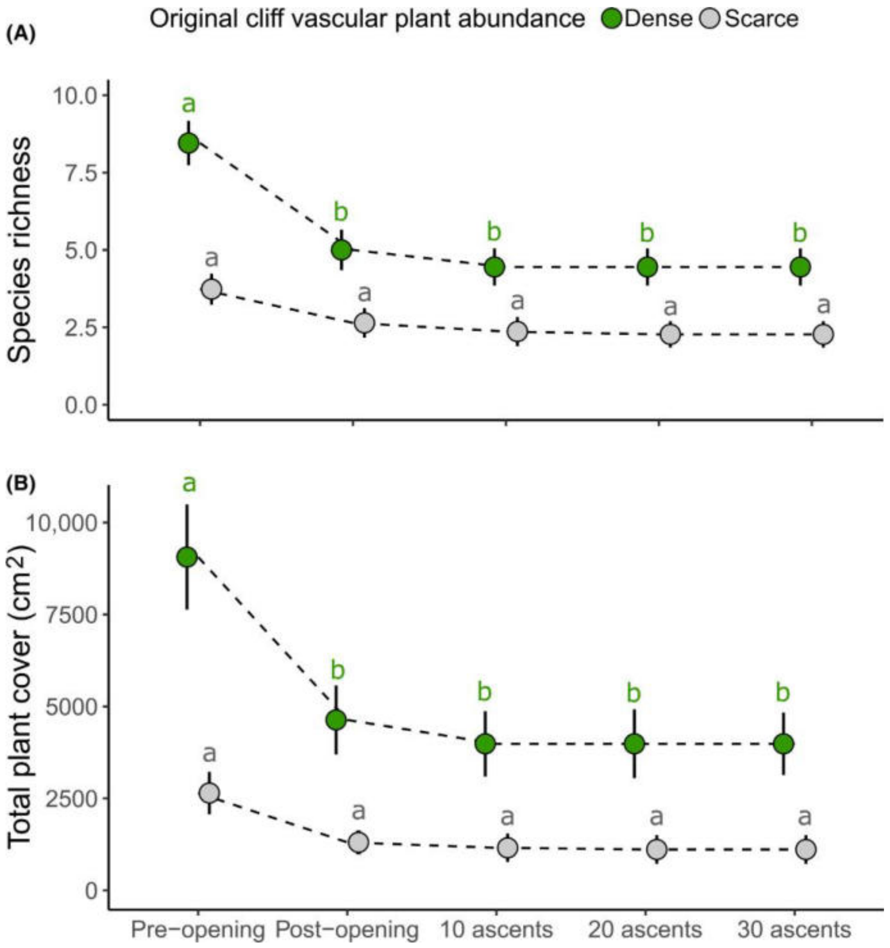


FIGURE 2 Differences in plant abundance and total lichen coverage between pristine cliffs and different phases of climbing activity. Mean ± standard error (SE) in the number of individuals (A) and the total lichen coverage in the studied cliffs (in cm^2; B) measured before (pre-opening) and after (post-opening) the opening of the new climbing route are displayed as well as after 10, 20 and 30 climbers' ascents are shown for the area near (panel on the left) and within (panel on the right) the climbing routes. Significant differences in post hoc contrasts among the measuring times are indicated with different letters, and colours represent the increased climbing pressure over time.

30.2% of the remaining cliff vegetation after route opening was lost within the route, although this decrease was not supported statistically (Figure 2A, right panel). This decrease is equivalent to the loss of around two plant individuals per climbing ascent, mostly occurring during the first 10 ascents. This is in line with the results of Schweizer et al. (2021), which revealed that climber impacts occur mostly during the climbers' first ascents. Route developers typically remove loose rocks that might pose a safety risk for climbers. During route cleaning, they also remove plants and soil from cliff crevices that could obstruct climbers' progress. Moreover, if mosses or lichens on the cliff could potentially cause climbers to slip, route developers often use metal brushes to remove them. These actions explain the strong impact of the opening of new climbing routes. We also found a gradual decrease in lichen cover, indicating that saxicolous cliff-dwelling lichens are affected by both the route opening and subsequent ascents (Figure 2B, right panel). Significant differences in lichen cover were observed after 20 ascents compared with the pre-opening monitoring, and after 30 ascents compared with the post-opening monitoring, resulting in an overall reduction of 34.6%. These findings also align with the results of Schweizer et al. (2021), who reported a strong reduction in lichen cover within the first 50 ascents, with no significant decreases afterward. However, lichen cover was constant in the nearby area of the route (Figure 2B, left panel), indicating that climbers can greatly impact lichens, as previously observed (e.g. Adams & Zaniewski, 2012; Clark & Hessl, 2015; Tessler & Clark, 2016). This gradual impact may be attributed to the above-mentioned activities during outfitting and the repetitive friction during the first ascents. Fine-scale studies identifying rare and unique cliff lichen species (e.g. Boggess et al., 2017) emphasize the importance of considering lichens and cliff erosion in conservation planning.

FIGURE 3 Plant species richness (A) and total vascular plant cover (B) between the pre-opening of the climbing route and different phases of the climbing activity in cliffs that originally hold dense (green) or scarce (grey) vegetation abundance.

Mean± standard error (SE) are shown, and significance of post hoc contrasts among measuring times within dense and scarce



It is worth noting that the extent of the impact from the opening depended on the abundance of vegetation in the pristine cliffs. The opening of the new routes significantly impacted plant species richness and total plant cover in those cliffs with originally dense vegetation, while weaker effects were observed in cliffs with originally scarce vegetation (Figure 3). Species richness decreased by 40.9% and 29.2% in cliffs with originally dense and scarce vegetation, respectively, whereas total plant cover was reduced by 48.9% in cliffs with originally dense vegetation, and 50.6% in those with originally scarce vegetation. However, climbers' ascents showed minimal effects on species richness and plant cover, with reductions of 11%–14.9% in all cases (Figure 3).

Both Farris (1995) and Kuntz and Larson (2006) suggested that route developers select cliffs with scarce vegetation, avoiding heavily vegetated cliffs that could hinder the establishment of new climbing routes. However, cliffs with scarce vegetation may harbour plants of high conserva- tion value, such as rare, endemic, or even endangered species. Thus, regardless of the abundance of vegetation on the pristine cliffs, an exhaustive species inventory should be conducted before establish- ing new routes, as indicated in our management protocol (Figure 4). This is especially demanding in the case of very narrow specialists that occur in small areas of one cliff (i.e. *Borderea chouardii*, a very ancient Dioscoraceae living on a unique cliff in Pyrenees; see García et al., 2012) or some specialists of overhanging cliff habitats, such as *Sarcocapnos pulcherrima* (Lorite et al., 2017).

Route developers also tend to select dry areas for route open- ing, as wet rocks may be uncomfortable and hazardous for climbing (Boggess et al., 2021). Dry cliff areas usually have lower vegetative abundance but otherwise may be more densely covered by lichens (Boggess et al., 2021). This trade-off between vegetation or lichen cover is also suggested by the measurements we obtained near the climbing route (see Figure 2A,B). In addition, route developers likely prioritize the removal of lichens that are less firmly attached to the rock, such as leafy foliose and fruticose species, while crustose lichens are likely removed due to continuous friction from climbers' ascents, as our results suggest (Figure 2B). Although it may be thought that lichens or other organisms may be less relevant for conservation compared with plants and vertebrates (Rubio-Salcedo et al., 2013), Reding (2019) found that endolithic and rare lichens are understudied but may have a significant presence on cliffs. Moreover, the erosion generated by repeated ascents may negatively affect other cliff organisms such as soil and rock-dwelling fungi, algae, cyanobacte- ria, invertebrates, mosses or different seed dispersers and pollina- tors (Baur et al., 2017; Coleine et al., 2021; Cooper, 1997; Gerrath et al., 2000; Horath & Bachofen, 2009; Krah & March-Salas, 2022; Schmera et al., 2018), also causing indirect negative effects on cliff plant communities.

Furthermore, our study provides a new interpretation of results from previous studies on this topic. Our findings on the effect of route opening within and in the areas close to the climbing routes suggest that the climbing effects previously found in other stud- ies with closely paired designs showed conservative results (e.g. Boggess et al., 2017; Clark & Hessl, 2015; March-Salas et al., 2018; March-Salas, Morales-Armijo, et al., 2023; Reding, 2019; Tessler & Clark, 2016). They used as controls nearby areas that considering our results, may be more or less equally affected by the route development compared with the climbing route area. Therefore, the climbing impact found afterward in these studies should then be primarily attributed to the repeated ascents rather than to the opening of the climbing route, which is clearly the bottleneck of the detrimental process. Yet, considering that only seven new routes were investigated and that popular climbing routes support many more than 30 ascents per year, future studies should include a larger number of study areas and a longer temporal scale with more climbing ascents in order to increase precision in the assessment of long-term climb- ing impacts. Future studies can also consider the assessment of the effect of sports climbing on cliff edges and talus areas. Furthermore, since our results showed that the areas near the climbing routes are affected by route opening, future studies should include transects on cliff faces that are untouched by climbing as additional controls.

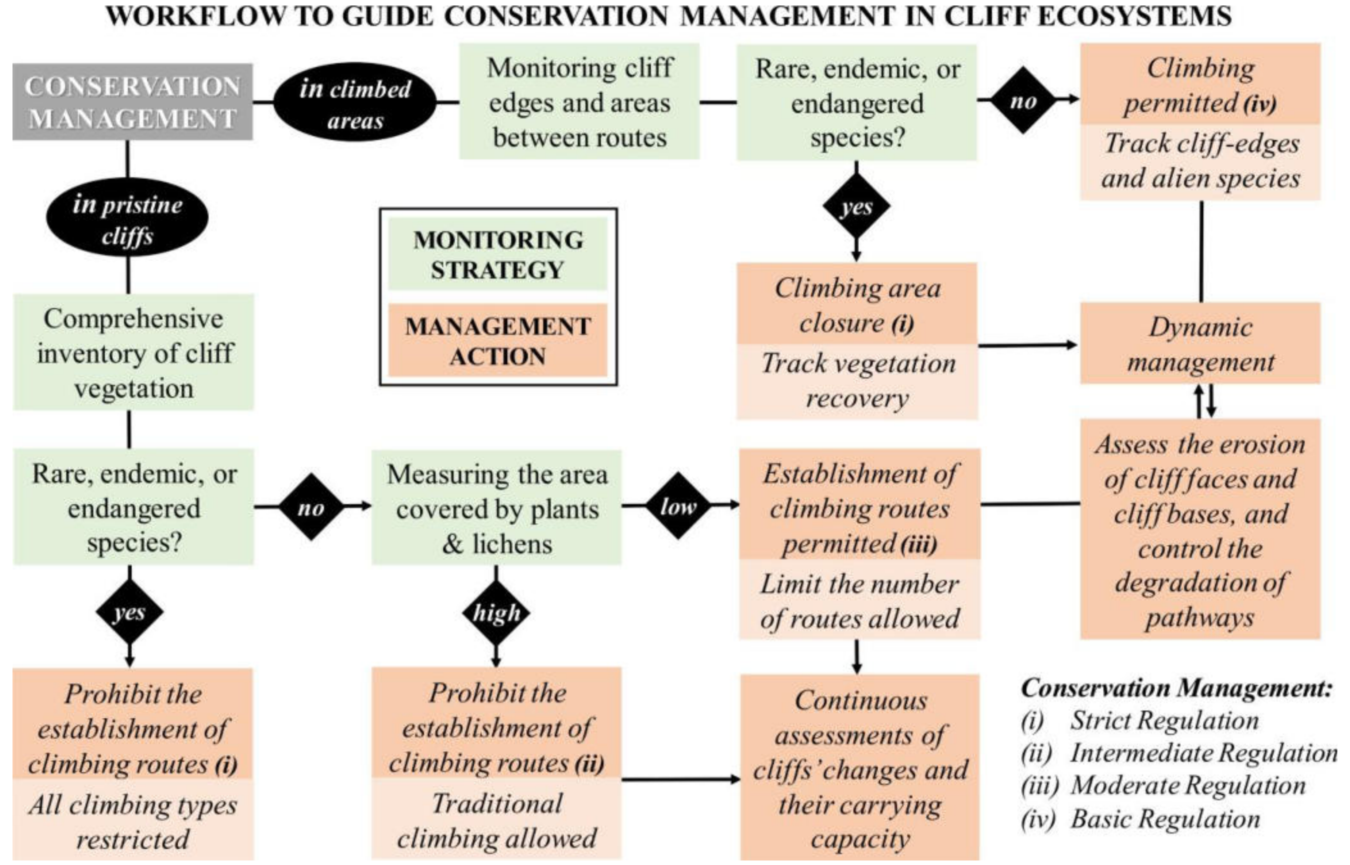


FIGURE 4 Workflow diagram as guidance for implementing conservation management actions in both pristine and climbed cliffs. The green boxes represent the associated field monitoring strategy to gather adequate information for decision-making, while the orange boxes represent the management actions to be implemented in each scenario. The light orange boxes show a complementary action to be implemented. The type of regulation to be implemented for each action is also highlighted and categorized into strict (i), intermediate (ii), moderate (iii), and basic (iv) regulation.

4.2 | Conservation management in cliff ecosystems

Despite its growing popularity, rock climbing is a recreational activity with few management guidelines (March-Salas, Lorite, et al., 2023). Regulations and accepted practices regarding the opening of new climbing routes are almost non-existent, or ambiguous and differing among countries and regions. Our results clearly indicate that this is an important issue to consider by conservation managers. However, it is also true that recently, the U.S. National Park Service (NPS) and U.S. Forest Service (USFS) identified environmental hazards associated with the opening and bolting of new routes for sport climbing. In January 2024, they proposed to ban fixed anchors in wilderness areas, unless granted special permission (National Park Service, 2024). In Ireland, guidelines have been developed to strive for a balance between the development of new climbing areas, the consideration of the natural environment, and climbing ethics (Mountaineering Ireland, 2023). Except in cases of cliffs with rare or endangered species, these guidelines consist solely of non-mandatory recommendations, such as removing only as much soil as necessary from cliff crevices, considering pruning rather than tree removal, or removing plants only after ensuring they are not rare or protected (Mountaineering Ireland, 2023). Therefore, there are still no protocols that can help authorities and practitioners follow standardized management and monitoring strategies in cliff ecosystems.

We propose a conservation management protocol that includes data collection and monitoring that would allow gathering information on cliff ecosystems over time for adequate decision-making, plus management actions (Figure 4). Monitoring strategies would offer an opportunity for managers to promote environmental stewardship of cliffs and define specific regulations to be implemented. We categorized these regulations into *strict* (i) regulation due to the presence of singular species (i.e. rare, endemic, endangered, or millennial-old species); *intermediate*; (ii) and *moderate* (iii) regulations for pristine cliffs with respectively dense or scarce non-protected vegetation abundance; and *basic* (iv) regulation for already-climbed cliffs with no singular species in the cliff edges or in areas between the climbing routes (Figure 4). For *basic* management, the unintentional introduction of seeds of ruderal or even invasive species, which can change the species composition and overcome cliff-specialist plants (Rusterholz et al., 2011), should receive particular attention. If *intermediate* (ii) and *moderate* (iii) conservation management is applied, traditional (i.e. climbing that does not use fixed gear and anchors in the cliff, and that does not always follow a clear previously-established route) or low-intensity climbing may be allowed in pristine cliffs. Then, the maximum number of new climbing routes should be evaluated, considering the ecosystem carrying capacity, and establishing *Limits of Acceptable Change* (a framework that quantitatively defines acceptable ecological conditions on a system used for recreation activities, and the appropriate management actions to prevent further changes; March-Salas, Lorite, et al., 2023; Stankey et al., 1985). In light of the results of our study, this would ideally require long-term monitoring of biodiversity changes, listing species, assessing site conditions over time, and comparing those data to the initial state of the pristine cliff (Schatz et al., 2014). Particularly, this should include direct measurements of population size, tracking singular species, and assessing the erosion of cliff faces (e.g. lichen cover, changes in cliff physical features, signs of rock erosion, or marks of exces- sive use of climbing chalk), as well as their surroundings such as cliff bases, cliff edges and the pathways to the climbing area, since they can hold important diversity (Boggess et al., 2021; Fragnièreet al., 2024). Moreover, in these management scenarios, further is- sues should be contemplated: quantifying the climbing frequency is a critical factor to determine the climbers' impact (Boggess et al., 2021); moreover, the climbing time-period (seasonal or year- round climbing) should be considered not only for birds, but also for vascular plants, since the impact can be strongest if seeds that ac- cumulate in cliff fissures are cleaned-up, when plants are emerging, or if climbers can disturb the pollination activity. Guiding agencies and local climbing organizations may be able to provide information regarding route use.

Since there are no benchmarks for each management scenario, we should conduct adaptive strategies before having ranges of thresholds that describe desired conditions, acceptable climbing pressures, and data on the cliff status (Webb et al., 2020). Therefore, when these benchmarks are surpassed, it should trigger the imple- mentation of previously defined management actions, raising the conservation management level, and probably requiring additional data collection (Harrison et al., 2024; Webb et al., 2020). All this will require revisiting the climbed cliffs and conducting continuous mon- itoring and assessments, so agencies should require and increase investment in management support.

5 | CONCLUSIONS

Our study shows that the climbing-related action with the strongest impact on cliff plant communities is the opening of new climbing routes. Yet, more routes investigated over a longer temporal scale with more climbing ascents should be considered to draw more reliable conclusions about the impact that climbers themselves can generate over time. Certain cliffs are likely among the last pristine ecosystems in many countries. These pristine cliffs, especially those harbouring unique species —whether endemic, rare, or threatened— must be protected, which may require banning the establishment of new climbing areas. In cases of pristine or climbed cliffs with no unique or singular species, dynamic management actions (i.e. those that can vary over time, such as less restriction in non-reproductive seasons of birds or plants) and continuous monitoring should be implemented, including setting maximum numbers of climbing routes to be established in each cliff and defining *Limits of Acceptable Change* as climbing intensity increases. We also advocate for a framework that mandates an environmental assessment prior to the opening of new climbing areas, in addition to providing route developers with best practice guides and training in cliff nature conservation. Protecting cliff ecosystems from human disturbance is crucial to slow down biodiversity loss, but this requires increased conservation efforts based on detailed guidelines for effective management.

AUTHOR CONTRIBUTIONS

Felipe Morales-Armijo and Martí March-Salas designed the study, and Martí March-Salas, Felipe Morales-Armijo and Juan Lorite designed the field-monitoring methodology. Felipe Morales-Armijo conducted the field surveys and gathered the data with the help of Andrea Sobrevilla-Covarrubias and inputs from Martí March-Salas, while Eduardo Estrada-Castillón helped to identify the cliff plant species. Martí March-Salas analysed the data and wrote the original draft of the manuscript, with interpretation of the data, review, and editing by Adrián Escudero, J. F. Scheepens, and Juan Lorite. All authors approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.g1jwstr0z (March-Salas et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Information about the newly established climbing routes, including the name we chose for the climbing sector and climbing route, the amount of vegetation of each climbing sector, the climbing difficulty (measured with the Yosemite Decimal System—YDS grades, and using a quality approach: moderately difficult, difficult, fairly difficult, very difficult), and the route height (in m). The routes were developed in September–October 2022, and all climbing routes were oriented to the North.

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3 CHAPTER 3

Assessment of vegetation using drones in climbed cliffs: A comparative analysis of sampling methods

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ABSTRACT

1. Cliff ecosystems are critical refugees of biodiversity, providing habitat for unique and endemic species that have adapted to extreme environmental conditions. However, these ecosystems are increasingly threatened by anthropogenic pressures, including habitat destruction, invasive species, and recreational activities such as climbing.

2. Traditional in situ sampling methods, such as rappelling and climbing-based vegetation surveys, have been the standard for studying cliff ecosystems. While effective in providing high-resolution data, these methods are often constrained by logistical challenges, cost, and safety risks, limiting their applicability to small areas and increasing the potential for disturbance to fragile habitats.

3. The advent of drone technology has revolutionized ecological research, offering a non-invasive, efficient, and scalable alternative to traditional methods. Drones enable comprehensive aerial surveys, capturing high-resolution imagery of vegetation structure, species distribution, and microtopographic features, thereby overcoming many of the limitations of ground-based techniques.

4. This study explores the comparative strengths of traditional and drone-based sampling methods in assessing species richness, vegetation cover, and lichen distribution in cliff ecosystems, highlighting their respective roles in capturing micro- and macro-scale ecological data.

5. Our results show that drones consistently outperform traditional methods in terms of spatial coverage and efficiency, particularly in capturing variations in plant abundance and species richness near climbing routes.

6. The integration of drone technology with other tools, such as multispectral imaging and geospatial analysis, can enhance the ability to monitor ecological changes over time, providing a comprehensive framework for conservation management.

7. From a conservation ethics perspective, the use of drones represents a commitment to reducing human impact on fragile ecosystems while maximizing data quality, offering an innovative approach to balancing ecological preservation with sustainable human use of cliff environments.

8. This study underscores the transformative potential of drones in advancing ecological research, advocating for their integration into monitoring and management strategies to ensure the long-term protection of cliff ecosystems and their unique biodiversity.

Keywords: Cliff ecology; Conservation management; Drones; Lichens; Sport climbing.

INTRODUCTION

Cliffs are among the most challenging ecosystems to study due to their inaccessibility, steep terrain, and harsh environmental conditions. These ecosystems are vital for biodiversity conservation, as they often provide refugia for species that have adapted to survive in rugged and extreme environments. Many cliffs are home to unique and endemic species, including vascular plants, which are increasingly threatened by human-related impacts such as habitat destruction, invasive species, and anthropogenic climate change. Given their ecological significance, it is essential to develop effective methods for monitoring and conserving cliff ecosystems (Larson, Matthes, & Kelly, 2000; Bader et al., 2018, Harrison et al., 2024). However, traditional methods for ecological sampling in these environments are limited by logistical complexity, cost, and safety risks to researchers and the habitats being studied (Schwilk et al., 2021).

Traditional in situ sampling methods, such as rappelling, climbing, and climbing-based vegetation surveys, have long been the standard approaches for studying cliff ecosystems. These methods offer high levels of spatial resolution and allow for direct interaction with the environment, crucial for understanding species composition, vegetation structure, and ecological processes (March-Salas et al., 2023; Holmes & Parmenter, 2016). However, in situ methods are often constrained by the challenging physical terrain of cliffs, which restricts the areas that can be surveyed effectively. For example, rappelling can only provide access to certain vertical portions of cliffs, limiting the spatial extent of the survey. Additionally, these methods are time-consuming, physically demanding, and involve significant risks, including falls and injuries, especially in remote and dangerous locations (Bollinger & Rousselle, 2022). Moreover, traditional techniques can cause disturbance to the fragile ecosystems being studied, potentially altering plant growth patterns or disrupting wildlife habitats (Hughes La Vigne et al., 2022).

Given these challenges, there is an urgent need for more efficient and safer methods for ecological sampling in difficult-to-access environments like cliffs. One promising technological advancement is the use of Unmanned Aerial Systems (UAS), more commonly known as drones. Drones have become an invaluable tool in ecological research, providing researchers with a non-invasive, cost-effective, and efficient means of gathering data from hard-to-reach areas (Nyberg et al., 2024). Equipped with high-resolution cameras, thermal imaging sensors, and geospatial technology, drones allow for comprehensive aerial surveys that capture both vegetation structure and species distribution over large, otherwise inaccessible areas (Nyberg, 2019; Stoychev et al., 2019; Hoffrén & García, 2023). The ability to operate at great heights and cover wide areas in a short period of time makes drones an ideal tool for cliff ecosystems, where in situ sampling methods are often limited by vertical and horizontal accessibility (McKinley et al., 2020).

Drones offer several advantages over traditional sampling methods, including increased spatial resolution, higher efficiency, and reduced ecological impact. Unlike in situ methods, drones can survey entire cliff faces, from the base to the summit, and cover areas that would otherwise be unreachable due to verticality or remoteness. This is particularly beneficial when studying large cliff systems or remote locations that require significant time and resources to access using traditional methods (Michez et al., 2021; Gao et al., 2024). In addition, drones can capture high-quality imagery in a fraction of the time it would take to conduct a traditional vegetation survey, greatly improving the efficiency of data collection (Bishop et al., 2022). Furthermore, the non-invasive nature of drone surveys minimizes disruption to the environment, reducing the risks of plant damage, soil erosion, or disturbance to wildlife habitats. This makes drones particularly useful for conservation efforts, where minimizing human impact is a key objective (Bollinger & Rousselle, 2022; La Vigne et al., 2022).

One of the most significant advantages of drone technology is its ability to integrate with other emerging technologies, such as aerial manipulators. Aerial manipulators are robotic arms or platforms attached to drones that can interact directly with the environment, enabling tasks such as plant sampling, data collection, and environmental monitoring (La Vigne et al., 2022. These systems represent a major leap forward in drone-based ecological research, as they allow researchers to collect samples or conduct analyses in areas that were previously difficult or dangerous to reach using traditional methods (Ollero et al., 2018).

In addition to its efficiency and precision, drone technology also offers the potential to reduce the cost and risk associated with fieldwork in hazardous environments. Traditional in situ methods often require significant financial investment in equipment, personnel, and logistical support, particularly when accessing remote cliff habitats. Drones, on the other hand, are relatively low-cost, especially when compared to other aerial survey methods, such as helicopter-based surveys (Nyberg, 2019; Bishop et al., 2022). Moreover, drones can be operated remotely, reducing the need for researchers to physically access dangerous cliff faces, thereby mitigating the risks of injury or fatality. This makes drones an attractive alternative to traditional methods, particularly for conservation projects where safety and cost-effectiveness are critical factors (Stoychev et al., 2019; Hughes La Vigne et al., 2022).

Despite the numerous advantages of drones, the transition from traditional in situ methods to drone-based surveys require careful evaluation and comparison to determine which method provides the most accurate and reliable data for ecological research. While drones have demonstrated their effectiveness in surveying large areas and capturing high-quality imagery, there is still a need to assess how they compare to in situ methods in terms of precision, efficiency, and cost (Ribeiro et al., 2020). Some researchers have raised concerns about the limitations of drone technology, such as the potential for lower resolution in some cases or difficulties in capturing fine-scale ecological details that can be observed with direct interaction in the field.

In this chapter, we compare two widely used methods for vegetation sampling on cliffs: traditional climbing-based methods and drone-based imagery. We evaluate both methods based on key metrics such as precision, cost, time, and ecological impact. The primary objective of this comparison is to assess whether drone-based data capture can provide higher spatial resolution and more comprehensive coverage than traditional in situ sampling, particularly in challenging environments like cliff ecosystems. Additionally, this study aims to evaluate whether drone-based methods can identify both the number of individuals and the species with the same accuracy as conventional sampling techniques. We hypothesize that drone data capture will offer superior accuracy in terms of species abundance, richness, and vegetation cover, especially in areas that are difficult or dangerous to access with traditional methods, while reducing the ecological impact associated with the presence of researchers in these sensitive environments.

MATERIAL AND METHODS

Study site

El Potrero Chico, located in Nuevo León, Mexico, is situated near Monterrey on the northern boundary of the 'Sierra El Fraile y San Miguel' Natural Protected Area, part of the Sierra Madre Oriental Mountain range. This region spans 23,506 hectares and ranges in elevation from 800 to 2,360 meters above sea level. It is characterized by Mesozoic sedimentary formations, including shale and limestone cliffs, which support a rich and diverse array of cliff vegetation (Larson et al., 2000; INECC, 2017). The area experiences a semi-arid climate, with hot summers featuring monthly maximum temperatures often exceeding 40 °C between June and August, and moderate winters with temperatures ranging from 7 to 16 °C. Rainfall peaks in September and October, averaging between 70 and 130 mm annually. The dominant vegetation types include submontane forests and desert rosetophilous scrub, the latter recognized as a conservation priority due to its high level of endemism (Estrada-Castillón et al., 2012).

El Potrero Chico is internationally recognized as one of the most prominent climbing destinations, offering over 700 climbing routes across 24 sectors (Madden, 2022). Although climbing activities in the area began in the 1960s, its popularity surged significantly during the late 1980s. The prime climbing seasons occur in late autumn and early spring (November to March), when temperatures are favorable, and precipitation is minimal. Recent records from the Tourism Secretary of Hidalgo indicate that during the 2022-23 and 2023-24 winter seasons, the site welcomed 2,312 and 2,238 climbers, respectively.

Field sampling design

We conducted the first comparative assessment on the cliff vegetation between a drone-based versus climbing-based method. Between August and October 2024, we captured aerial images with one of the most affordable drones on the market, the DJI Mini pro 3 - 48 MP, which at 5 meters away from the wall was able to capture photos with a resolution of 1 cm.

We delineated three climbing routes on the cliff with high vegetation (25°57'18" N 100°29'07" W; so called ‘Sotol-Plutonia’ climbing sector) (see information of the climbing routes in Table S1). A total of 20-3 m2 plots and 238-0.25 m2 subplots were surveyed at each of the two-sampling method (see ‘Field sampling method’ below). Climbing routes were at least 3.5 meters apart from the next climbing route. Cliff vegetation was then recorded by establishing three sampling quadrats at different heights of the cliff face (see details below in the 'Field sampling method').

The first sampling corresponds to in situ sampling, setting up a fixed anchor and using the rappel technique to descend. To capture the drone photographs, we used the upper part of the in situ sampling quadrat, positioning it at the same height as the previous quadrats, respecting the previous or in situ sampling. After adjusting the 3m horizontal rod, with alternating red colors every 50 cm, which will then give us the downward projection of the subplots to be analyzed (see Figure5. drone image below).

Field sampling method and data collection

To test the accuracy of both methods, we used a case-control sampling design with a 3 m wide × 3 m high quadrat located in three areas of the climbing route (see Morales-Armijo et al. 2024). The quadrat consisted of: a central plot 1 m wide and 3 m high representing the central area of the climbing route (referred to as “Inside the climbing route”); two immediately adjacent surveyed plots 0.5 m wide and 3 m high, as this area could potentially be used by climbers during their ascent and thus would not be free of disturbance; two plots 1 m from the center of the climbing route 0.5 m wide and 3 m high to the left and right of the 3 × 3 m quadrant that served as controls, representing areas not reached by climbers.

To characterize the spatial distribution of plants within each plot, both "within" and "near" plots were subdivided into 0.5 m × 0.5 m subplots (12 subplots in each "within" plot and 12 subplots in each "near" plot). Photographs were taken of each subplot as part of the data collection process. The indirect method, which consists of capturing a maximum quality photograph (48Mp) with a drone at 5 meters from the wall. To position the scale on the photograph, we use as a reference the upper part of the quadrant, which corresponds to a PVC pipe painted red every 50 cm. Subsequently, in the program 'ImageJ' (Rueden et al. 2017), we made the grid 50 cm x 50 cm (see Figure 5) to then obtain the abundance, richness and vegetation covers within each subplot.

To consider the physical microtopography of the cliff, we calculated the proportion of cracks (i.e., crevices) in each 0.5 × 0.5 m subplot using the program 'ImageJ' (Rueden et al. 2017). This measurement helps to reduce potential bias when modeling the climbing effect, as plant establishment and development are more plausible with a higher percentage of crevices (Holzschuh 2016). We identified all plant species present in the plots (Velazco et al. 2011) and calculated richness in the plots "within" and "near" each climbing route and quadrat, as well as the number of individuals per species (i.e., abundance). In addition, we calculated the area (in cm2) of each individual vascular plant (i.e., vegetation cover), and lichen covers, also using the program "ImageJ".

Data analysis

We performed all statistical analyses with R version 4.0.3 (R Development Core Team 2020). We evaluated and compared plant abundance, species richness, vegetation cover and lichen cover as response variables.

Linear mixed-effects models (LMM) implemented in the 'lme4' package and the 'lmer' function (Bates et al. 2015) were used. The sampling method (two levels: climbing-based and drone-based methods), the climbing route area (two levels: within vs. near the climbing route), and their two-way interaction were modeled as fixed factors, and the climbing route was included as a random factor. In the models concerning vascular plants, the percentage of cracks was used as a covariate to control for the amount of microniches available for plant establishment and growth (Holzschuh 2016).

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. If the residuals were not normally distributed, we transformed the response variable (*see* transformations in Table 1).

RESULTS

Plant abundance, species richness, and both plant and lichen cover exhibited changes depending on the sampling method and the climbing route zone (see Table 1; Figs. 1–4). The observed differences varied significantly with the interaction between the climbing route zone (within vs. near) and the sampling method (climbing-based vs drone-based methods), highlighting differential patterns in vegetation communities in response to climbing activity.

Plant abundance was significantly higher near the climbing routes compared to within the climbing routes (Table 2; Fig. 1). However, no significant differences were found between the sampling methods in either of the zones (Table 2).

Species richness was significantly influenced by the interaction between climbing route zone and the sampling method (Table 2). Near the climbing routes, richness was notably higher when using the drone sampling method (Fig. 2).

Plant cover was significantly higher near the climbing routes than within the routes (Table 2; Fig. 3). No significant differences in plant cover were observed between the sampling methods (Table 2).

Lichen cover was significantly influenced by the sampling method (Table 2; Fig. 4), being consistently higher when using the climbing-based method compared to the drone-based method, regardless of the climbing route zone. No significant interaction was detected between the climbing route zone and the sampling method for this variable (Table 2).

DISCUSSION

The results confirm the breadth of new opportunities offered by drones, it is possible to project the use of this equipment for the monitoring and evaluation of these cliffs in the world. (Nyberg et al., 2024). . Drones have revolutionized the ability to monitor these impacts by providing a combination of precision, coverage, and safety that surpasses traditional methods, paving the way for a more comprehensive understanding of these fragile ecosystems (Nyberg et al., 2024).

The differences in plant abundance and species richness observed between the climbing-based method and drone-based methods highlight the distinct strengths and limitations of each method in capturing ecological patterns. The drone method consistently detected higher plant abundance and species richness, particularly in areas near the climbing area, highlighting its sensitivity to microhabitat-level variation (Graham & Knight, 2004; Morales-Armijo et al., 2024). The gradual decrease in lichen cover in climbing areas, captured more accurately by the climbing - based method, underscores the importance of human field observations for detecting microscale ecological changes, such as lichen erosion caused by climbing activities (Harrison et al., 2022; Boggess et al., 2017). Taken together, these methods offer complementary perspectives, highlighting the need for integrated approaches to cliff ecosystem conservation

From a conservation ethics perspective, the intrusion of climbing activities into cliff habitats raises questions about the balance between recreational use and ecological preservation. Now we know about de effects on cliff biodiversity, which can reduce vegetation cover significantly within climbing routes, exemplifies how human intervention often prioritizes short-term utility over long-term ecosystem integrity (Clark & Hessl, 2015; Morales-Armijo et al., 2024). This reflects a broader philosophical tension in conservation: the anthropocentric tendency to value ecosystems primarily for their utility to humans rather than as intrinsically valuable entities.

Aldo Leopold's land ethic, which advocates a moral responsibility to maintain the health and integrity of the land, resonates strongly in the context of the impacts of cliff climbing. These ecosystems, which harbor endemic and rare species, are not mere recreational landscapes, but critical components of biodiversity (March-Salas et al., 2023; Larson et al., 2000). The lack of regulations governing rock climbing as a recreational and ecotourism activity in many countries further highlights a moral oversight that requires urgent rectification (Hanemann, 2000; March-Salas et al., 2023). The use of drones also introduces an intriguing dimension to conservation ethics, bridging the gap between technological intervention and ecological stewardship.

The drone-based findings also corroborate ecological theories of microhabitat specialization. The uneven distribution of lichens and plants across cliffs, influenced by microtopographic factors such as crack density and slope, highlights the ecological complexity of these systems (Cooper, 1997; Holzschuh, 2016). This underscores the necessity of fine-scale ecological data, which drones provide with unprecedented accuracy.

Drones are reshaping ecological research by offering a non-invasive means of assessing inaccessible habitats. Their ability to map vegetation at a centimeter-scale resolution facilitates the detection of subtle ecological changes, such as shifts in plant health or lichen abundance, which are critical for monitoring the long-term impacts of climbing (Nyberg et al., 2024). Furthermore, drones enable the integration of advanced analytical tools, such as photogrammetry and multispectral imaging, which can quantify ecological parameters, including plant vigor and soil erosion, with high precision.

Future research should focus on integrating drone data with other technologies, such as LiDAR and hyperspectral imaging, to develop comprehensive ecological models of cliff ecosystems. Additionally, longitudinal studies tracking the recovery trajectories of vegetation and lichens post-disturbance would provide valuable insights into the resilience of these ecosystems under varying management regimes.

In conclusion, the integration of ecological insights with cutting-edge drone technologies offers a transformative approach to understanding and conserving cliff ecosystems. By combining precision monitoring with ethical stewardship, we can balance recreational use with the imperative to protect these biodiverse yet fragile habitats, ensuring their preservation for future generations.

CONCLUSIONS

Cliff ecosystems are vital biodiversity reservoirs, harbouring unique and often endemic species that thrive in these challenging environments. Despite their ecological importance, they remain understudied due to their inaccessibility and the logistical complexities associated with traditional research methods. This study underscores the transformative potential of drone technology in overcoming these challenges and advancing ecological research and conservation efforts.

In our study, drones showed accuracy in capturing the ecological data planned for our research, such as species richness, vegetation cover, However, the complementary strengths of traditional methods cannot be overlooked. human-based method remain indispensable for fine-scale analyses and provide critical insights into microscale interactions, such as the dynamics of lichen and vascular plant communities. These findings highlight the importance of integrating both methodologies to achieve a holistic understanding of cliff ecosystems. The integration of drone technology into ecological research also aligns with broader conservation principles. By minimizing direct human interaction with fragile habitats, drones reduce the risk of physical disturbances to ecosystems. This approach exemplifies an ethical commitment to conservation that prioritizes minimizing harm while maximizing the quality and scope of data collected. Furthermore, drones facilitate the monitoring of human impacts, such as those from recreational climbing, offering valuable insights into how these activities affect vegetation and biodiversity over time.

By embracing innovation and collaboration, we can develop robust strategies to safeguard cliff ecosystems. These biodiverse yet fragile habitats are not only vital for ecological integrity but also for maintaining the broader environmental health of the regions they inhabit. Investing in such forward-thinking approaches ensures the preservation of these ecosystems for future generations, reinforcing their role as a cornerstone of biodiversity conservation.

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Author’s contributions

FMA and MMS designed the study, and FMA designed the field-sampling methodology. FMA conducted field surveys and gathered the data with the help of AS, while EEC helped to identify the cliff plant species. MMS and FMA analyzed the data. FMA wrote the original draft of the manuscript, with review and editing by all authors.

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Data availability

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

Tables

Table 1: Results of the Linear Mixed-effects Models (LMMs) comparing sampling method and its influence on plant abundance, species richness, and total cover of vascular plants and lichens. LMMs included climbing route zone (near vs. within the climbing route), sampling method (climbing and drone), and their two-way interactions, as well as the percentage of cracks. Transformations applied to the response variable are indicated below the table. Significance is indicated as * $0.05 > P \geq 0.01$; ** $0.01 > P \geq 0.001$; *** $P < 0.001$, and • reflects marginal effects ($0.1 > P \geq 0.05$).

		Plant abundance			**Species richness**			**Plant coverage**			**Lichen coverage**		
Parameter	**df**	**Chi^2**	***P-value***		**Chi^2**	***P-value***		**Chi^2**	***P-value***		**Chi^2**	***P-value***	
Percentage of cracks	1	0.1805	0.6709		0.274	0.524		0.002	0.960		-	-	-
Climbing route zone (Zone)	1	5.3550	0.0206	*	8.673	0.003	**	5.936	0.014	*	1.676	0.195	
Sampling method (Method)	1	0.1114	0.7385		12.347	<0.001	***	0.102	0.749		14.284	<0.001	***
Zone × Method	1	0.0729	0.7872		4.569	0.032	*	0.054	0.816		0.400	0.526	

transformations: boxcox(x)

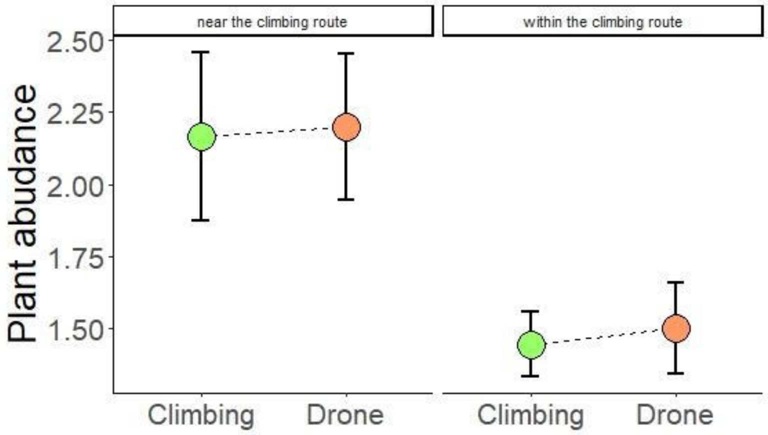

Figure 1: Differences in plant abundance between the climbing - based and the drone-based method. Mean ± standard error (SE) in the number of individuals sampled before (climbing) and after (drone) are shown for the area near (panel on the left) and within (panel on the right) the climbing routes.

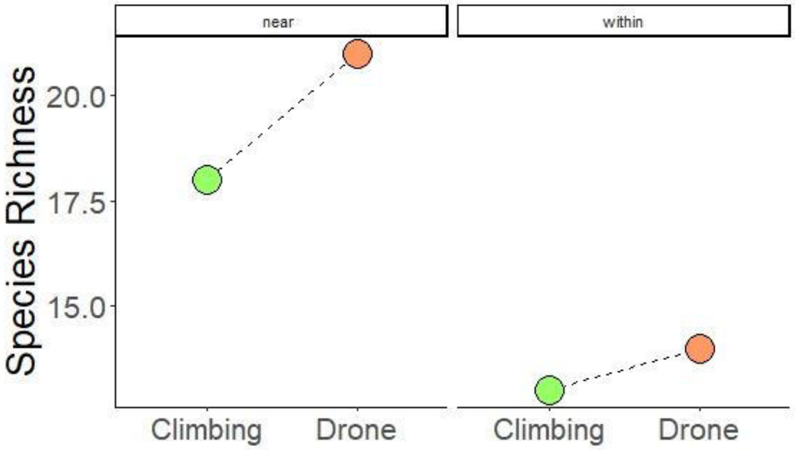

Figure 2: Plant species richness between the climbing method and drone method and near climbing route and within. Mean ± standard error (SE) is shown.

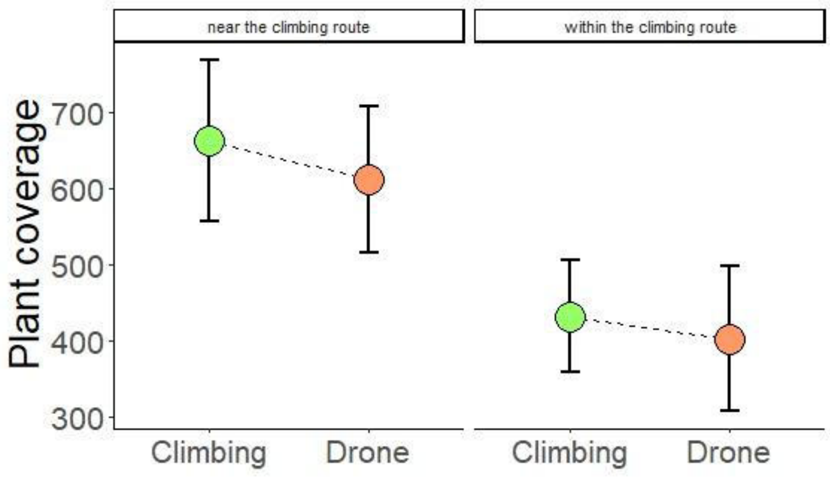

Figure 3: Differences in plant coverage between climbing method and drone method. Mean ± standard error (SE) in the number of individuals sampled before (climbing) and after (drone) are shown for the area near (panel on the left) and within (panel on the right) the climbing routes.

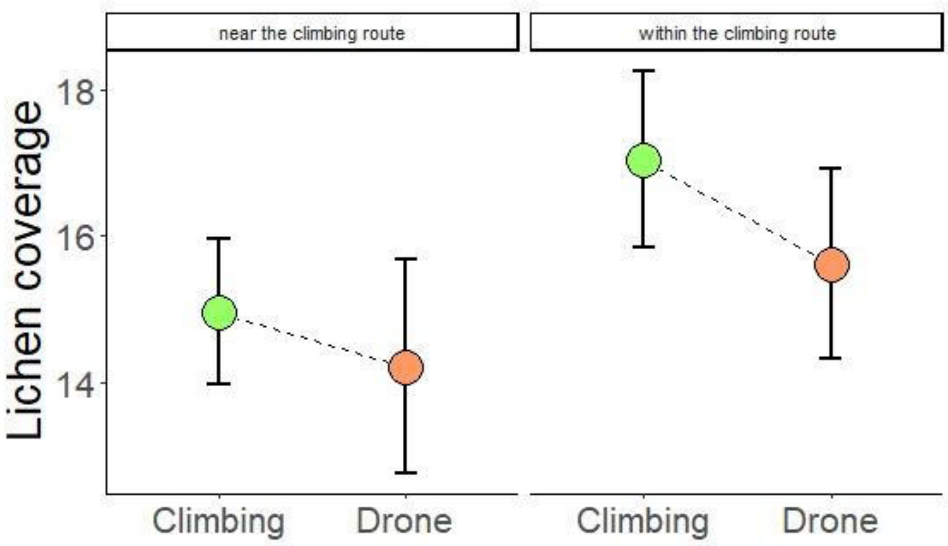

Figure 4: Differences in lichen coverage between climbing method and drone method. Mean ± standard error (SE) in the number of individuals sampled before (climbing) and after (drone) are shown for the area near (panel on the left) and within (panel on the right) the climbing routes.

Supplementary material

Table S1: Information about the sampling routes, including the name we chose for the climbing sector and climbing route, the climbing difficulty (measured with the Yosemite Decimal System – YDS grades –), and the route height (in m). All climbing routes were oriented to the north.

Sector	Route name	Difficult	Height
Plutonia-Sotol	Mitlan	5.11b	29
	Entre agaves y sotoles	5.10c	20
	En memoria	5.10b	21

Figure 5: Images of the 'Drone-based Method', representing digitally the same plots and subplots surveyed.

4 GENERAL CONCLUSIONS

Cliff ecosystems are among the most biodiverse and ecologically distinct habitats on Earth, providing refuge to species uniquely adapted to extreme conditions (Larson et al., 2000; Schwilk et al., 2021). However, the rapid growth of recreational climbing presents significant challenges to their conservation (deCastro-Arrazola et al., 2021; Harrison et al., 2022). The research I developed during my PhD highlights the critical need for a multifaceted approach that balances recreational use with the ecological preservation of these fragile habitats. By examining the impacts of climbing on cliff communities, the destructive effects of new climbing route development, and the transformative potential of drone technology, this work provides a comprehensive framework for sustainable management and biodiversity conservation.

The research conducted through my first chapter clearly indicates that climbing activities have profound consequences for the biodiversity and ecological stability of cliff ecosystems. We found a reduction in species diversity and the disruption of positive species associations due to climbing, which underscore the growing vulnerability of these habitats (Lorite et al., 2017; March-Salas et al., 2018). These findings emphasize the need to preserve ecological networks for maintaining the community stability and biodiversity in cliff ecosystems (Gray et al., 2021). Our results highlight that conservation efforts must move beyond focusing solely on emblematic or rare species to also include dominant and common species, as their loss can destabilize entire ecosystems (Avolio et al., 2019). Biodiversity hotspots such as cliffs, where ecological interactions are most at risk, should be prioritized to protect the intrinsic value and functional integrity of cliff ecosystems (Calatayud et al., 2020).

Importantly, in my second chapter we showed that, among the potential impacts from climbing activities, the development of new climbing routes is likely the most ecologically destructive phase. These impacts are particularly severe in areas with dense vegetation, where the removal of plants can destabilize ecological networks and increase the likelihood of local extinctions for rare and specialist species (Clark & Hessl, 2015; Morales-Armijo et al., 2024). To mitigate these impacts, it is essential to conduct pre-emptive biodiversity assessments before route development and to provide ecological training for those involved in creating and maintaining climbing routes. These proactive measures can prevent irreversible biodiversity losses while promoting sustainable climbing practices that balance recreation and conservation (deCastro-Arrazola et al., 2021).

In my third chapter, we conducted a comparative assessment to evaluate whether drone technology is a comparable and even beneficial solution for monitoring cliff ecosystems. Previous research already anticipated that drones enable high-resolution, large-scale imagery with minimal environmental disturbance, providing detailed data on vegetation structure, species distribution, and microtopographic features (Nyberg, 2019; McKinley et al., 2020; Nyberg et al., 2024). In our comparative assessment, we confirmed the precision and high applicability of drones for monitoring cliffs and conclude that while traditional in situ methods remain indispensable for analyzing fine-scale ecological interactions, drones complement these efforts by enabling researchers to monitor extensive and otherwise inaccessible cliff faces (Bishop et al., 2022). By integrating drone technology with ground-based methods, conservationists can gain a comprehensive understanding of ecosystem dynamics, assess the impacts of climbing activities efficiently, and develop evidence-based management strategies.

The research I conducted during my PhD Thesis underscores the urgent need for a holistic conservation framework that integrates scientific research, sustainable recreational practices, and technological innovation. Prioritizing biodiversity hotspots, conducting thorough impact assessments, ensuring sustainable route development, and leveraging advanced monitoring technologies are essential steps to protect these unique habitats. Collaboration between scientists, climbers, local communities, and policymakers is vital to achieving these goals, ensuring that conservation strategies balance ecological preservation with the recreational and cultural value of cliffs.

By adopting these strategies, the long-term preservation of cliff ecosystems can be secured, allowing them to thrive amid increasing human pressures. This integrated approach serves as a model for managing the coexistence of human recreation and ecological conservation, promoting a sustainable future for both nature and society.

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