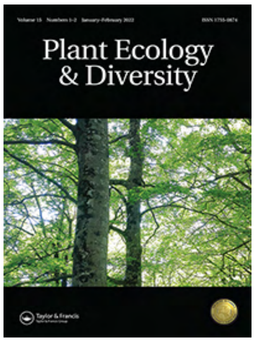

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# Changes in climate, grazing pressure and nutrient inputs affect the structural integrity and functioning of Andean shrublands

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# Changes in climate, grazing pressure and nutrient inputs affect the structural integrity and functioning of Andean shrublands

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**ABSTRACT**

**Background:** Changes in climate and the intensity of agriculture expansion can alter plant population dynamics and community composition and structure of dry shrublands.
**Aims:** We tested how temperature and moisture along an elevation gradient, grazing, and nutrient addition in soil affected demographic attributes of *Croton* shrubs and the composition and structure of plant species in an inter-Andean dry shrubland.
**Methods:** At three elevations, we installed grazing and exclusion plots, combined with four nutrient treatments: control, and addition of nitrogen (N), phosphorous (P) alone and in combination. We measured recruitment and survival of *Croton* seedlings, as well as survival, growth, fruiting of adult *Croton* and the composition and structure of neighbouring plants.
**Results:** Grazing exclusion improved adult survival of *Croton* at all three elevations. Grazing exclusion and addition of N and P increased adult growth of *Croton* at low and medium elevations. *Croton* seedling recruitment and survival decreased with distance to adult plants. The cover of *Croton* had a positive relationship with plant abundance and diversity.
**Conclusions:** Temperature, moisture, grazing and nutrient addition can alter the demography and cover of *Croton*, as well as the composition and structure of its neighbouring plants threatening the functioning of the inter-Andean dry shrubland.

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**KEYWORDS**
survival; growth; fruit yield; elevation; grazing; nitrogen; phosphorus; plant composition

## Introduction

Climate change, grazing and excessive nitrogen (N) and phosphorus (P) input can alter the structure and functioning of drylands around the world where water availability is a limiting resource (Westerband et al. 2015; Silva et al. 2021). In these environments, temperature increases, and moisture decreases at lower elevations (Richter and Moreira-Munoz 2005; Vélez-Mora et al. 2021). Changes in temperature and moisture along elevation gradients in dry ecosystems are not the only drivers that contribute to plant growth and reproduction, but also grazing (Eldridge et al. 2016), soil overfertilisation (Wassen et al. 2021) and the unpredictability of precipitation (Maestre et al. 2005; Ding and Eldridge 2021) may have important effects.

Positive interactions between facilitating (or nurse) plants and their facilitated plants during the drought season often increase survival, growth, and reproduction among plants (see Maestre et al. 2009; Cavieres and Badano 2010; Erfanzadeh et al. 2021). Moisture, nutrients, and cover (shading) in these environments are usually more accessible under adult plant canopies (nurse effect), favouring seedling survival and growth (Soliveres et al. 2010; Espinosa et al. 2019; Maestre et al. 2021). Favourable temperature and moisture conditions below facilitating plant canopies can promote plant associations (Scanlon et al. 2007; Howard et al. 2012) likely driving plant diversity (McIntire and Fajardo 2014; Mihoč et al. 2016; Erfanzadeh et al. 2021) and functioning (Maestre et al. 2016, 2021) in these semi-arid ecosystems. Existing studies suggest that the effects of plant–plant interactions tend to become more positive for biomass and biodiversity in ecosystems dominated by facilitating shrubs when aridity increases (Mazía et al. 2016; Rey et al. 2016; Berdugo et al. 2019; Erfanzadeh et al. 2021). A synthesis of community-level studies has found that more than 25% of species in drylands are spatially associated with facilitating plants (Soliveres and Maestre 2014). This illustrates the importance of understanding how plant interactions promote maintenance of plant diversity in extreme environments and how plant communities are affected by human activities that reduce plant biomass and cover such as livestock grazing (Maestre et al. 2016; Wu et al. 2021).

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Grazing is a driver of changes in composition and diversity of plant communities (Augustine and McNaughton 1998; Kutt et al. 2012; Eldridge et al. 2013). It directly influences the structure of a plant community by reducing plant growth (Daryanto et al. 2013; Eldridge et al. 2016) and in inter-Andean ecosystems has been shown to strongly affect both plant diversity and plant growth (Espinosa et al. 2013). Grazing also affects cycling and storage of N and P in the soil. In semi-arid grasslands in northern China, N storage (in aerial biomass, litter, roots, and soil) increased significantly due to grazing exclusion (He et al. 2008; Li et al. 2012), while in the northern highlands of Ethiopia, P storage in soil increased between 26% and 39% when grazing was excluded (Mekuria and Aynekulu 2013).

Changes in N and P inputs, mainly due to human activity, can have large effects on nutrient cycling within tropical ecosystems (Galloway et al. 2004; Elser 2011; Bejarano-Castillo et al. 2015; Craine et al. 2018). This nutrient imbalance occurs due to N deposition after burning, grazing and agricultural production (Jaramillo and Murray-Tortarolo 2019), and P loss through leaching and runoff because of heavy rains (Raghubanshi 1991; Rundel and Boonpragob 1995; Singh et al. 1997; García-Oliva et al. 2011; Hou et al. 2018). These changes in soil nutrients affect the primary productivity of the ecosystem (Peñuelas et al. 2013; Yuan and Chen 2015) and can also cause substantial alterations in biodiversity and the functioning of ecosystems (Carnicer et al. 2015). Despite its importance, our knowledge about the dynamics of N and P in tropical dryland ecosystems remains scarce (Waring et al. 2019).

Tropical dryland ecosystems are home to a wide diversity of species. They cover ca. 42% of tropical forests (Murphy and Lugo 1986) and contain 20% of global plant diversity hotspots (Davies et al. 2012; Maestre et al. 2021). These drylands play a key role in regulating global cycles of N (Tian et al. 2020), P (Delgado-Baquerizo et al. 2013) and water (Wang et al. 2012) and their plant communities provide various and important ecosystem services (Siyum 2020). Despite their enormous social and ecological importance, tropical dryland ecosystems are the most vulnerable and least protected ecosystems on Earth (Portillo-Quintero and Sánchez-Azofeifa 2010; Stan and Sanchez-Azofeifa 2019). Consequently, urgent action is required to halt their decline (Yao et al. 2020; Maestre et al. 2021).

The inter-Andean dry valleys are present in Colombia, Ecuador, Perú, and Bolivia (Pennington and Ratter 2006; Wood 2006; Linares-Palomino et al. 2011). In these ecosystems, shrubs represent a large portion of the diversity (43%; 12% are endemic), followed by herbs (36%) and trees (20%) (Quintana et al. 2016). Their main threats are extensive grazing (Iñiguez 2004), invasive grasses (Tapia-Armijos et al. 2015), nutrient deposition by burned biomass (Rollenbeck et al. 2013), high levels of human pressure (Tapia-Armijos et al. 2017) and climate change (Herzog et al. 2011; Cisneros et al. 2021). In these ecosystems, cattle forage mostly grasses along elevation gradients (Iñiguez 2004; Espinosa et al. 2013) while goats forage mainly at low elevations where there is greater abundance of shrubs and leguminous trees (Iñiguez 2004).

This study developed from previous research on the population ecology and reproductive biology of *Croton* shrubs (a complex of interbreeding hybrids taxonomically unresolved) and on their interactions with other species in inter-Andean communities in Ecuador (Espinosa et al. 2013, 2019; Lara-Romero et al. 2017; Vélez-Mora et al. 2020, 2021). This research recognised the importance of changes in elevation on these communities and indicated the relevance of grazing pressure and nutrient input resulting from increasing agricultural development in neighbouring areas (Espinosa et al. 2013, 2019; Solano et al. 2018; Vélez-Mora et al. 2021). Here, we examine the demography of *Croton* in an inter-Andean dry valley to investigate experimentally the effects of current environmental and anthropogenic changes in such regions on dryland shrub communities. We present results of an experiment established in 2015 at different elevations involving grazing exclusion and nutrient additions to evaluate hypotheses derived from initial observational studies to better understand the consequences of anthropogenic changes on *Croton* and associated plants.

*Croton* is a dominant member of plant communities in inter-Andean regions of Ecuador (León-Yánez et al. 2011). Our study was conducted in the Andean Depression (Richter et al. 2009), a region between northern Perú and southern Ecuador (Richter and Moreira-Munoz 2005; Peters et al. 2014; Quintana et al. 2017). We utilised elevational changes in temperature and moisture as surrogates of potential current changes in climate (Sundqvist et al. 2013) across a narrow elevation range of 300 m (Vélez-Mora et al. 2020). Previous studies showed that grazing increased the facilitating effects of *Croton* on other species around 1550 m and reduced diversity and plant cover around

1950 m (Espinosa et al. 2013). They further showed that the facilitating effects of *Croton* canopy improved survival of conspecific seedlings (Espinosa et al. 2019) and that plant density and plant size of *Croton* increased seedling and adult survival and reproductive performance, while growth decreased due to intraspecific competition (Lara-Romero et al. 2017). Soil nitrogen stocks were also shown to increase with elevation (Solano et al. 2018). Based on these findings, we hypothesised that (1) under higher moisture and lower temperature conditions, without grazing and with higher availability of nitrogen and phosphorus, seedling and adult plant survival, growth and *Croton* fruit yield will increase; and (2) a reduction of density and cover of *Croton*, as a consequence of grazing and resource (moisture and nutrients) changes with elevation, will reduce the facilitating effect of *Croton* and consequently the richness and diversity of associated plants. To test these hypotheses, we evaluated the effects of climate variation in accordance with elevation, grazing exclusion, and nitrogen and phosphorus additions (1) on survival of seedlings and adult *Croton* plants, (2) on growth and fruiting of *Croton* plants, and (3) on the composition and structure of their associated plant species.

## Materials and methods

### *The dry shrubland of the inter-Andean valleys of southern Ecuador*

Several abiotic factors in the inter-Andean ecosystems provide stressful conditions for organisms. Seasonal and highly variable air and soil temperature extremes during the day, coupled with unpredictable and limited precipitation (Figure 1g and figure A1 in Espinosa et al. 2019) favour xeromorphic adaptations (Figure 2c,d). In addition, shallow and nutrient poor soils (Figure 1a, c and h) on very steep slopes (Figure 2a) exposed to erosion limit resources for growth and reproduction

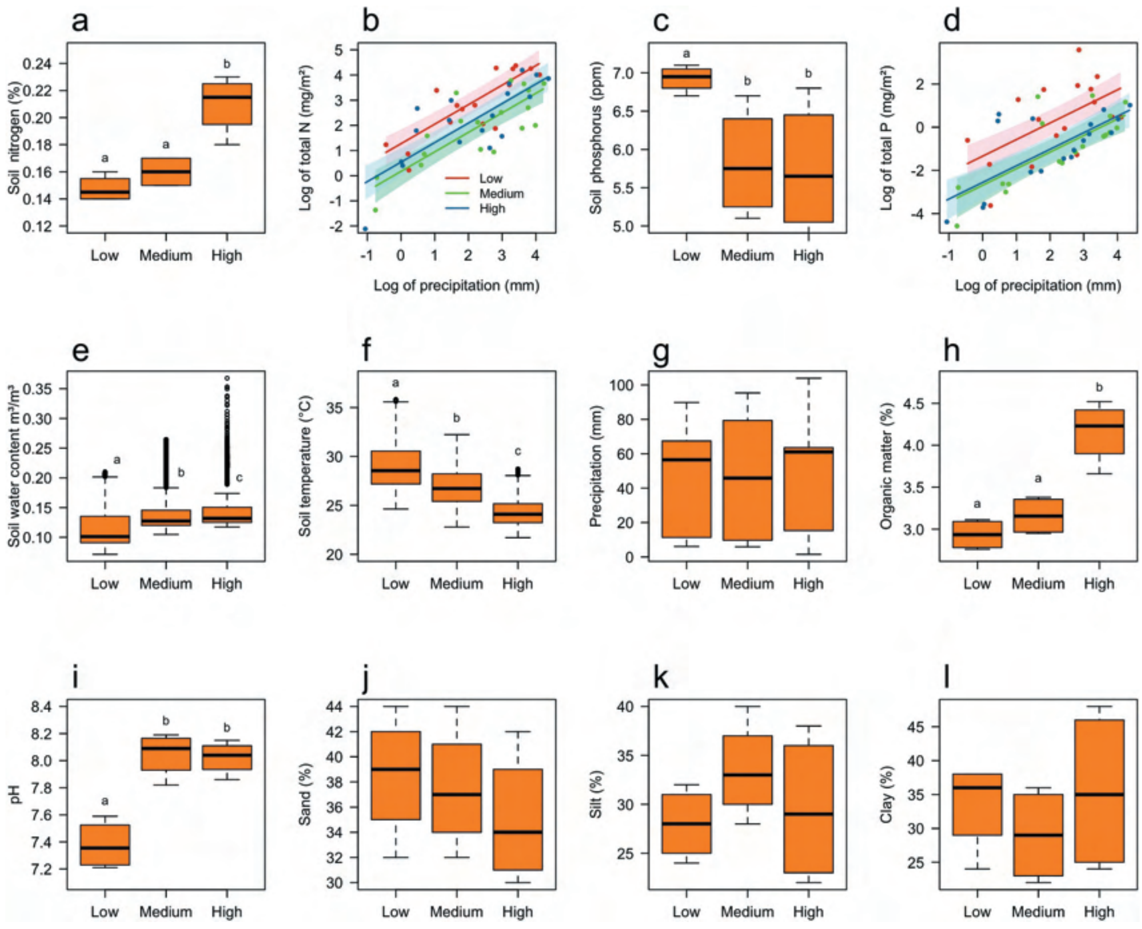

**Figure 1.** Summary plots of soil variables, climate, and N and P deposition in the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). a-c: concentrations of N and P from soil. b-d: wet deposition of N and P; observed values are indicated by different coloured points for each elevation as well as the polygons with confidence intervals to 95%. e-f: soil water content and temperature; g: precipitation during the rainy season November 2017 - March 2018; h-l: percent of organic matter content, pH, percent of sand, silt, and clay content of soil samples. Letters on box plots indicate statistically significant differences between elevations.

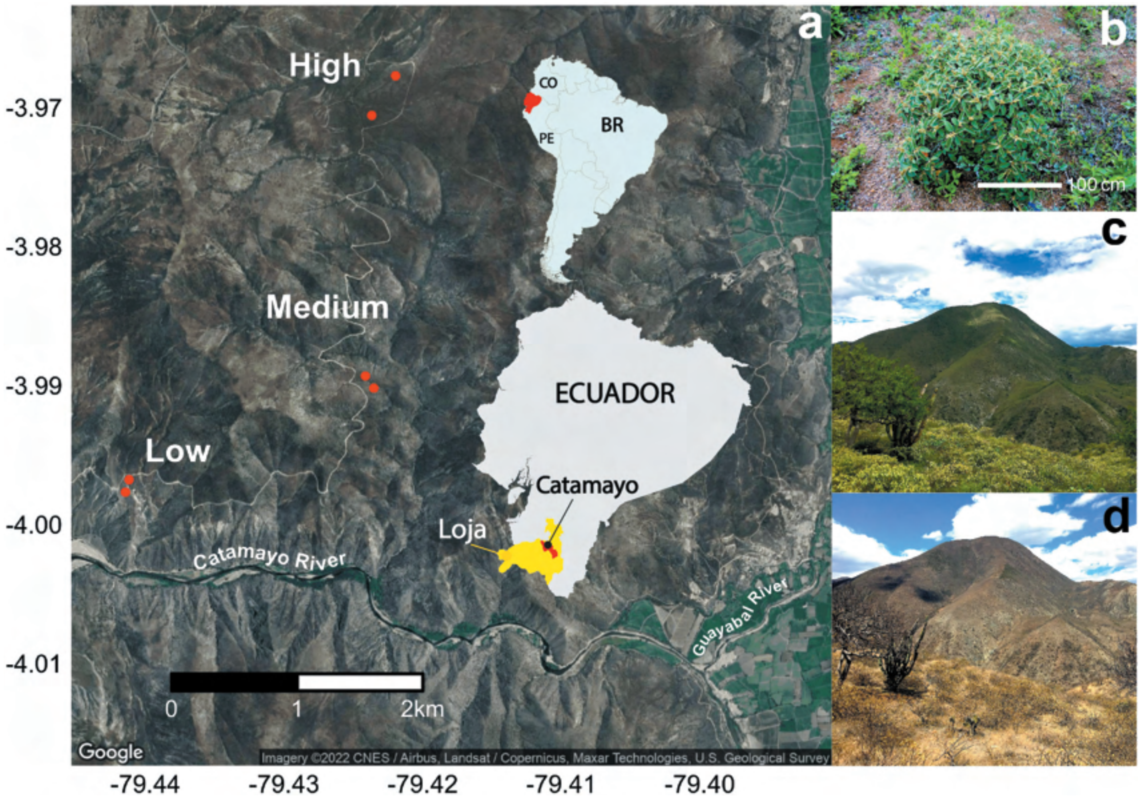

**Figure 2.** a: Paired grazed and grazing excluded study sites (red dots in satellite image) in the inter-Andean valley of Catamayo, Loja Province, Ecuador (inset) at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). The green areas at the right edge of the image are sugarcane plantations; b: *Croton* sp., the focal study species with its greenish-brown inflorescences; c: panoramic view near the site at 1400 m, April 2019; d: view of the same location in August 2019 during the dry season. The dry and leafless trees and shrubs reveal some cacti.

during restricted times when moisture is available (Arteaga et al. 2020). Furthermore, recent rising temperatures, increasing pressure from livestock (Figure S1) and reduction of water availability diverted for agriculture and human consumption have imposed further limitations on growth and reproduction (Fries et al. 2020).

### *Study site*

Our study was performed at an inter-Andean valley of the Catamayo Canton, Loja Province, Ecuador (Figure 2). This dry inter-Andean shrubland experiences an average annual temperature of 24.8°C, with an average annual precipitation of 317 mm and a prolonged dry season where 57% of the annual precipitation occurs between February and May (Espinosa et al. 2019; data from City Airport in Catamayo 2011–2015 located 6 km from our study site). In this valley, the dominant *Croton* shrubs are distributed continuously between 1100 and 2080 m of elevation (Espinosa et al. 2019). *Croton* varies in spatial aggregation that increases along the elevation gradient and decreases with grazing pressure levels (Espinosa et al. 2013). Patches of *Croton* form a matrix including sparse xerophytic and spiny vegetation co-dominated by tree perennials such as, *Vachellia macracantha* (Humb. & Bonpl. ex. Willd.), *Bursera graveolens* (Kunth), *Colicodendron scabridum* (Kunth), and shrubby perennials such as *Lantana canescens* (Kunth), *Agave americana* (L.), *Ipomoea carnea* (Jacq.) and *Opuntia quitensis* (Ulloa and Jørgensen 1995; Espinosa et al. 2013; Aguirre Mendoza et al. 2017).

We chose three elevations: 1700 m a.s.l. (high elevation; 3°58’07.90” S, 79°25’19.71” W), 1550 m a.s.l. (medium elevation; 3°59‘20.09“+S, 79° 25’28.64” W) and 1400 m a.s.l. (low elevation; 3° 59’40.15”S, 79°26’31.29” W). Along this environmental gradient, there was variation in soil temperature, moisture, and soil nutrient composition. We used generalised linear models with Gaussian distribution to evaluate the variation of total N (%) and total P (ppm) in the soil (%), precipitation (mm), organic matter (%), sand (%), and clay (%), soil water content ($m^3/m^3$), soil temperature (°C), and soil pH and silt (%) as a function of elevation (data were logarithmically transformed when necessary to meet model assumptions). We used a linear model to evaluate the variation of N (mg/m$^2$) and P (mg/m$^2$) deposition as a function of precipitation per elevation.

Total N concentration in the soil was lower at the low and medium elevations than at the high elevation (Figure 1a), although N deposition by rainfall was higher at the low elevation (Figure 1b). Total P concentration was higher at the low elevation compared to the medium and high elevations, both in the soil and deposited by rain (Figure 1c, d). Soil water content (recorded in winter between January and February 2019) was lower at the lower elevation (Figure 1e). Soil temperature (also recorded in winter between January and February 2019) was higher at the low elevation (Figure 1f). There was more organic matter at the high elevation (Figure 1h) and soil pH was more alkaline at the medium and high elevations than in the low elevation (Figure 1i). Precipitation in winter (between November 2017 and March 2018) was similar between these elevations (Figure 1g and Figure S2) as well as percentage of silt and clay in soil (Figure 1k,l). Percentage of soil sand decreased with elevation (Figure 1j).

At the regional level, dry weather and erosion at low elevations has led to the formation of Entisols characterised by sandy, stony, and rocky formations generating shallow, soils (Winckell et al. 1997; Moreno et al. 2018). At higher elevations, wetter climate has promoted development of clayey soils classified as Vertisols (Soil Survey Staff 2006; Moreno et al. 2018). Our soil analyses showed loam, clay, and clay-loam soils along the elevation gradient (Tables S1B and S2B). The topography is rugged with moderately steep slopes (Espinosa et al. 2019). These sites are visited by small herds of feral donkeys and horses. In recent years we have witnessed increasing goat and cattle herds in the area. According to local shepherds, cattle occasionally consume *Croton*. We also observed that livestock trample seedlings, small plants and damage the branches of *Croton* plants, mainly in winter (Figure S1).

At highest elevation (1700 m of elevation), maize is grown in association with pastures (Moreno et al. 2018), while at lowest elevations (1200 m of elevation), there is intense agricultural activity only in areas irrigated by the Catamayo River (Figure 2). The warm, tropical valleys are suitable for short-cycle crops such as sugarcane, banana, tomato, cucumber, pepper, zarandaja, beans and cassava, and perennials such as coffee and fruit trees (Moreno et al. 2018; Chamba-Morales et al. 2019). The Catamayo valley, located on flat land of recent alluvial sediments, accommodates the large *Ingenio Monterrey Azucarera Lojana CA* – MALCA and sugarcane fields irrigated with water from the rivers Catamayo and Guayabal (Winckell et al. 1997; Moreno et al. 2018; Figure 2a). Sugarcane cultivation covers an area of 2,172 hectares in the Catamayo Canton (Ochoa-Cueva et al. 2022). The extensive annual burning of sugarcane likely mobilises nutrients across the elevation gradient. Approximately five years ago, moringa (*Moringa oleifera*) cultivation was established near to our study site (Vélez-Mora personal observation).

### *Study species*

The taxonomy of *Croton* in our study area remains problematic and we opted to be cautious on its classification and refer to it as *Croton* (Euphorbiaceae). *Croton* is a 0.5–1.5 m tall monoecious shrub that inhabits a wide variety of habitats, mostly semi-arid and often in secondary vegetation (Ulloa and Jørgensen 1995; Van Ee et al. 2011; Figure 2b). Plants reach reproductive maturity in 2–3 years and can survive for several years (Espinosa et al. 2019). Recent studies indicate clear morphological variation in leaves and inflorescences among forms at different elevations and suggest that there is incipient reproductive isolation between local populations of *Croton* occurring at local elevation extremes (Vélez-Mora et al. 2021).

### *Experimental design and treatments*

In July 2015, we initiated a field experiment along an elevation gradient to evaluate the effects of climate (temperature and moisture) variation, grazing, and N and P addition to the soil on *Croton* survival, growth, fruit yield, seedling survival, and on associated plant diversity. Average annual temperature (°C) at the high elevation was 20.68 (standard error [SE] = 0.01), at the medium elevation 21.90 (SE = 0.01) and at the low elevation 22.87 (SE = 0.01). We observed that winter rains generally start in October and end in April (see Figure A1 in Espinosa et al. 2019) and decided, therefore, to measure precipitation in the period of likely greatest rainfall from November 2017 to March 2018. At each elevation, we obtained a weekly rainfall average during this period and summed these weekly averages to obtain monthly precipitation (Figure S2). Average precipitation during this winter period was 49.12 mm (SE = 12.38) for the high elevation, 47.25 (SE = 17.99) for the medium elevation and 46.25 (SE = 16.24) for the low elevation.

Two pairs of 10 m × 10 m plots (at least 100 m apart) were established at each elevation. In each pair, one plot was excluded and the other not excluded from grazing. In total, we established 12 plots. Plot assignment was established randomly. Plots excluded from grazing were fenced with four lines of barbed wire at a maximum height of 1.5 m in July 2015, while those in which grazing was allowed had only wooden posts placed at the four corners. Wire was replaced when damage was observed, and all old posts and wire were replaced by new material in February 2019. For the nutrient addition treatments, subplots of 3.5 m × 3.5 m were established within the 10 m × 10 m plots, separated from each other by 1 m (see Figure S3). On 18 March 2017, 10 March 2018, and 19 April 2019, N and P were applied to subplots within each plot. Nutrients were applied depending on the previous availability of these nutrients in the soil of each subplot. One replicate of each treatment (control, N, P and N+P) was applied per plot. (Calculations and exact amounts applied of N and P by subplot are shown in Tables S1 and S2). On average, 346.81 g of urea (N) and 506.24 g of triple superphosphate (P) were applied per treated subplot at the high elevation; 382.20 g and 503.76 g at the medium elevation, and 391.05 g and 467.24 g at the low elevation. Also, a subplot without nutrient addition was assigned as control treatment in each plot. In steep areas, this was positioned at the top end of a plot to minimise nutrient cross-contamination from other subplots. We considered that a 10 m × 10 m plot size as suitable for the experiment due to high density of *Croton* across the elevation gradient (20.75 plants on average ±1.55 SE per plot).

### Survival, growth, fruit yield by inflorescence and seedling survival

We recorded in July 2015, shortly before plots were fenced, the height, length, and canopy width of each *Croton* plant greater than 15 cm in height to estimate their volume (see Vélez-Mora et al. 2020). In July 2019, the same measurements were repeated, and live and dead plants were recorded to evaluate the survival of plants initially recorded in July 2015. Plant size (canopy length, canopy width, and plant height as in Vélez-Mora et al. 2020) was recorded in July 2017 and July 2019. We used these measurements to estimate *Croton* growth. Sample sizes for each demographic variable are in Table S3.

We recorded *Croton* fruit yield monthly from September 2017 to September 2019. We randomly chose five plants per nutrient subplot and on each plant, we randomly chose five inflorescences to count the number of fruits per inflorescence. When fruits had dispersed or fell and the inflorescence withered, we chose another group of five inflorescences after the onset of winter (between December and January). Fruit yield per inflorescence was estimated as the maximum number of fruits counted in any month during each annual reproductive season. We considered number of fruits produced per inflorescence on a plant as an indicator of the reproductive condition of the plant (Data in Espinosa et al. 2019 can be used to estimate the total number of fruits per plant).

During August and November 20 February 201920, and March 2021, we recorded the number of *Croton* seedlings recruited in each subplot at each elevation, noting their status (dead/alive), height, and distance (cm) to their nearest (supposed) maternal plant.

### Vegetation sampling

In June 20 May 201617, and June 2021, we recorded and taxonomically identified every plant with stems >10 cm in each plot at each elevation at the end of the rainy season. From these records, we calculated the total number of standing stems of all species, species richness, and the Shannon diversity index per plot.

### Data analysis

We used generalised linear models to evaluate plant growth, survival, and seedling survival variation as a function of elevation, grazing exclusion, nutrient addition (N and P), and for the analysis of two-way interactions. The logarithm of plant volume was considered as the most informative plant size variable (see Vélez-Mora et al. 2020) and its initial value was included as a covariable in these models if relevant (expressed as linear or quadratic terms). We used a logit link and a binomial distribution to evaluate *Croton* adult and seedling survival and used normal errors and the identity link to evaluate plant growth. Random effects by replicated site by elevation were negligible and we dropped these variables from the models. A generalised linear mixed-effects model (*lme4* R package;

Bates et al. 2015) with a logit link and a binomial distribution was used to evaluate fruiting probability per inflorescence as a function of plant volume and elevation (plant volume and elevation as fixed factors and plants as random factors). We used a generalised linear mixed model with negative binomial errors and a logarithmic link to evaluate fruit yield by inflorescence (annual maximum number of fruits) as a function of plant volume and the interaction between elevation with nutrient treatments (plant volume, elevation, and nutrient treatments as fixed factors and plants as random factors). Generalised linear models with Poisson distribution were used to assess the influence of *Croton* cover on number of total standing stems of all species and species richness (*vegan* R package; Oksanen et al. 2020) in 2016 and in 2021. Cover was summarised as the sum of canopies of each *Croton* individual (see Vélez-Mora et al. 2020) per plot. To assess the influence of *Croton* cover on Shannon diversity (*vegan* R package) in 2016 and in 2021, we used a linear model. For this model we used the logarithm of Shannon diversity. All analyses were performed in version 4.1.1 of R software (R Core Team 2021).

## Results

### *Effects of elevation, grazing exclusion and N and P addition on survival, growth, and fruit yield*

Elevation, grazing, nutrient addition to the soil, and plant volume affected survival, growth, and fruit yield of adult *Croton* individuals. Survival increased with plant volume (Figure 3, Table S4). We used the average of logarithm of plant volume from 2015 (11.66) to standardise by size survival probabilities and facilitate the description of comparisons among treatments. At each elevation, low, medium, and high, *Croton* survival increased in non-grazed plots without addition of nutrients (low: 0.93 ± SE 0.59; medium: 0.97 ± SE 0.68 and high: 0.91 ± SE 0.53 elevations) compared to control grazed plots (0.86 ± SE 0.80; Figure 3). At low elevation, survival decreased (0.53 ± SE 0.53; Figure 3) in non-grazed plots with added P, compared to the control. At medium elevation, there was a reduction in survival (0.79 ± SE 1.08) in non-grazed plots with added of N+P, compared to control non-grazed plots with no added nutrients (0.97 ± SE 0.68; Figure 3; Figure S4). At high elevation, we observed the lowest survival (0.42 ± SE 0.53; Figure 3; Figure S4) in grazed plots (control treatment).

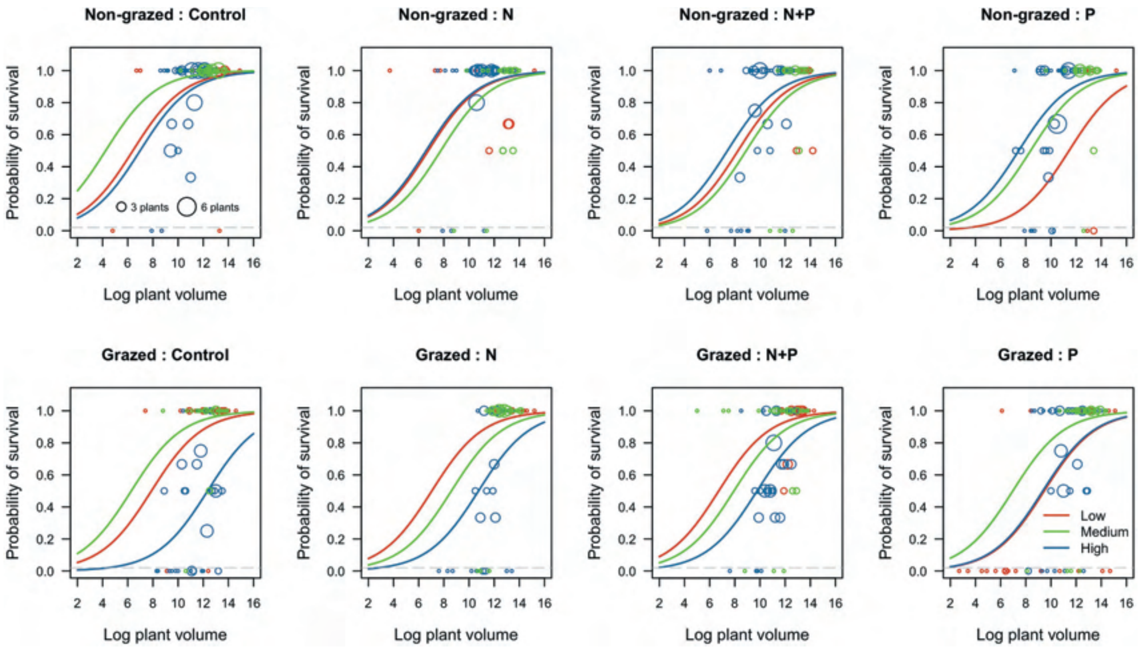

**Figure 3.** Plant volume, elevation, and the interaction between elevation, grazing exclusion, and nutrients on the survival of *Croton* plants in the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a binomial fit of plant survival probability by elevation, grazing/no grazing, and nutrients according to plant volume. Coloured empty circles indicate the number of plants (see top left panel for legend) included in a binned treatment category. Grey horizontal dashed line is a reference (model intercept = 0.02) to distinguish survival among the three elevations, and between exclusion and nutrient additions. The $R^2$ value of survival model was 0.21.

*Croton* growth increased and then decreased with plant volume (Figure 4, Table S5). We used the average of logarithm of plant volume from 2015 (145.06; only surviving plants) to standardise growth. At each elevation, low, medium, and high, *Croton* growth increased in the non-grazed plots with added N+P (low: 12.85 ± SE 0.15; medium: 12.69 ± SE 0.15; and high: 12.07 ± SE 0.15 elevations) compared to controls (Figure 4). However, at high elevation, growth decreased with only P addition in non-grazed plots (11.40 ± SE 0.16; Figure 4; Figure S5).

Fruiting probability of *Croton* increased with plant volume (Figure 5, Table S6) and was not influence by elevation (Figure S6). *Croton* fruit yield also increased with plant volume (Figure 6). We used the average of plant volume from 2019 (12.88) to standardise fruit yield. At low elevation, fruit yield was highest in plots with added N (8.79 ± SE 0.10 Figure 6). At medium elevation, fruit yield increased with added N+P (7.39 ± SE 0.14; Figure 6, Table S7), and at high elevation fruit yield was lower with N addition (4.63 ± SE 0.14) compared to plots without nutrients addition (control treatment; Figure 6; Figure S7).

### *Effect of canopy on seedling survival*

*Croton* seedling survival decreased with distance from the closest supposed maternal plant (Figure 7, Table S8). The effect of elevation on *Croton* seedling survival was inconclusive, but there was weak evidence of lower survival at low elevation (Figure 7; Figure S8). We did not have enough data to evaluate the effects of nutrient addition on seedling survival.

### Effect of *Croton* cover on abundance, richness, and diversity

There was a clear positive relationship between the sum of *Croton* canopies per subplot and total number of standing stems in both evaluation years, 2016 and 2021 (Figure 8, Table S9). In 2021, there was a higher number of total standing stems recorded. No clear relationship between the sum of *Croton* canopies and species richness was evident in either 2016 or 2021. However, in 2016 there was a clear positive relationship between the sum of *Croton* canopies and Shannon diversity (Figure 8). We documented a clear reduction in *Croton* cover in 2019 especially at high elevations (Figure S9).

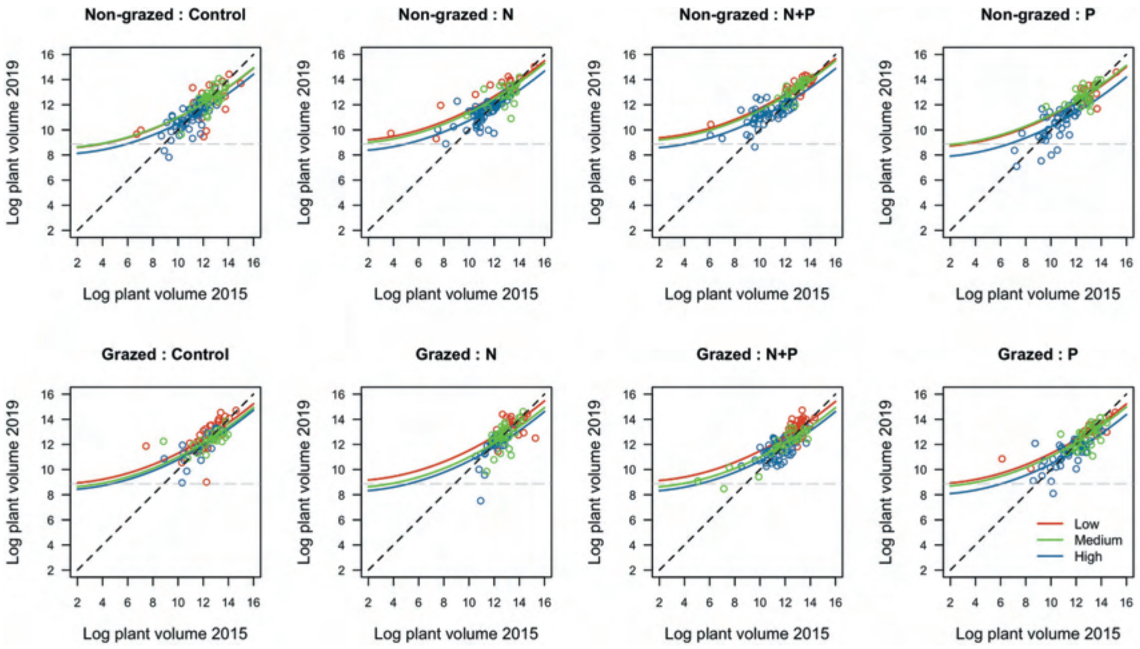

**Figure 4.** The relationship between *Croton* plant volume in 2015 and in 2019 in the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a quadratic fit showing plant growth for elevation, grazing exclusion, and nutrient addition between initial (2015) and final plant volume (2019). Circles represent each plant surveyed. Plants (open circles) above dashed diagonal line indicate growth, and plants below indicate decrease. Grey horizontal dashed line is a reference (model intercept = 8.87) to distinguish growth among the three elevations, between grazing and exclusion, and between nutrient additions. The $R^2$ value of growth model was 0.70. Elevation and interaction between exclusion and nutrients, and elevations and nutrients were related to the growth of *Croton* plants.

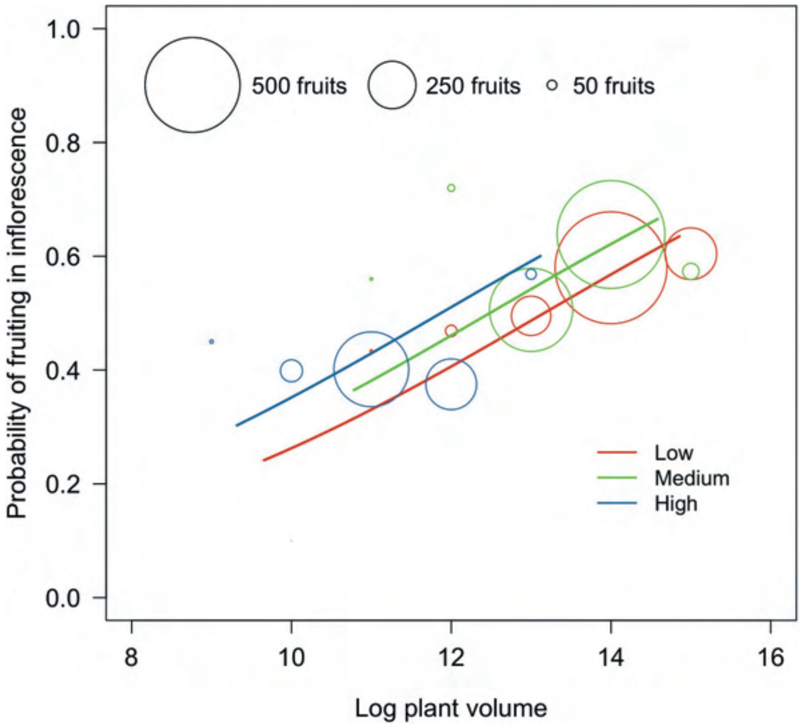

**Figure 5.** The relationship between plant volume and the probability of fruit yield per inflorescence of *Croton* sp. By elevation in the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a binomial fit of probability of fruiting per inflorescence per elevation by plant volume. Circles are the number of fruits observed by inflorescences per elevation. The $R^2$ value of probability of the fruiting model was 0.22.

## Discussion

During the last decade we have observed an intensification of agricultural and livestock activities (cows and goats) in our study area (Leon-Velarde et al. 2000; Quintana et al. 2019). These activities have increased the nutrient load of soils and diverted water from the few local streams (Minga-León et al. 2018; Arteaga et al. 2020). Simultaneously, the frequency of extremely dry years and annual number of days without rain have also increased. Climate change, grazing and nutrient addition are a widespread threat for species persistence and sustainable community functioning in dry ecosystems (Ulrich et al. 2014; Smith et al. 2016; Maestre et al. 2021) and appear to be magnified in mountain areas such as the inter-Andean valleys (Coppus et al. 2003; Zehetner and Miller 2006; Murgueitio et al. 2011). Our experimental work showed how variation in climate (temperature and moisture) along a narrow elevation gradient, the availability of N and P, and grazing influenced overall species interactions and abundance, as well as survival, growth, and fruit yield of *Croton*, a key species of the inter-Andean dry shrubland.

There is evidence that native ungulates were more abundant and widespread in South America in the past. Thus, it is likely that the reintroduction of large ungulates after the arrival of European colonisers may have restored some ecological functions lost after the extinction of the American megafauna in the late Pleistocene (Lundgren et al. 2020). There is also indirect evidence that ungulates play an important ecological and evolutionary role in many communities (Janzen 1984, 1986), especially those containing grasses or short-cycle plants (Belsky et al. 1993; Archibald et al. 2019). We do not know how important the past presence of ungulates in the region we studied may have been. Given the seasonality of local weather and lack of continuous vegetation cover, we suspect that the local presence of ungulates was relatively scarce. However, a previous study comparing grazed and ungrazed sites in the same area found evidence of negative effects of grazing on plant cover and interactions (Espinosa et al. 2013).

Our study suggests that grazing is a critical stressor of *Croton* demography. Although consumption of *Croton* by livestock in the region is relatively low, the tendency of cows and goats to browse pods and young shoots of acacias in winter (Iñiguez 2004; Espinosa et al. 2013), in addition to consuming grass in the area in recent years, could cause trampling of shrubs and seedlings, affecting *Croton* persistence especially at high elevations. *Croton* survival may have benefited by grazing exclusion, since without fences and with smaller *Croton* plants at the high elevation (Vélez-Mora et al. 2021), it is easier for livestock to roam for food at

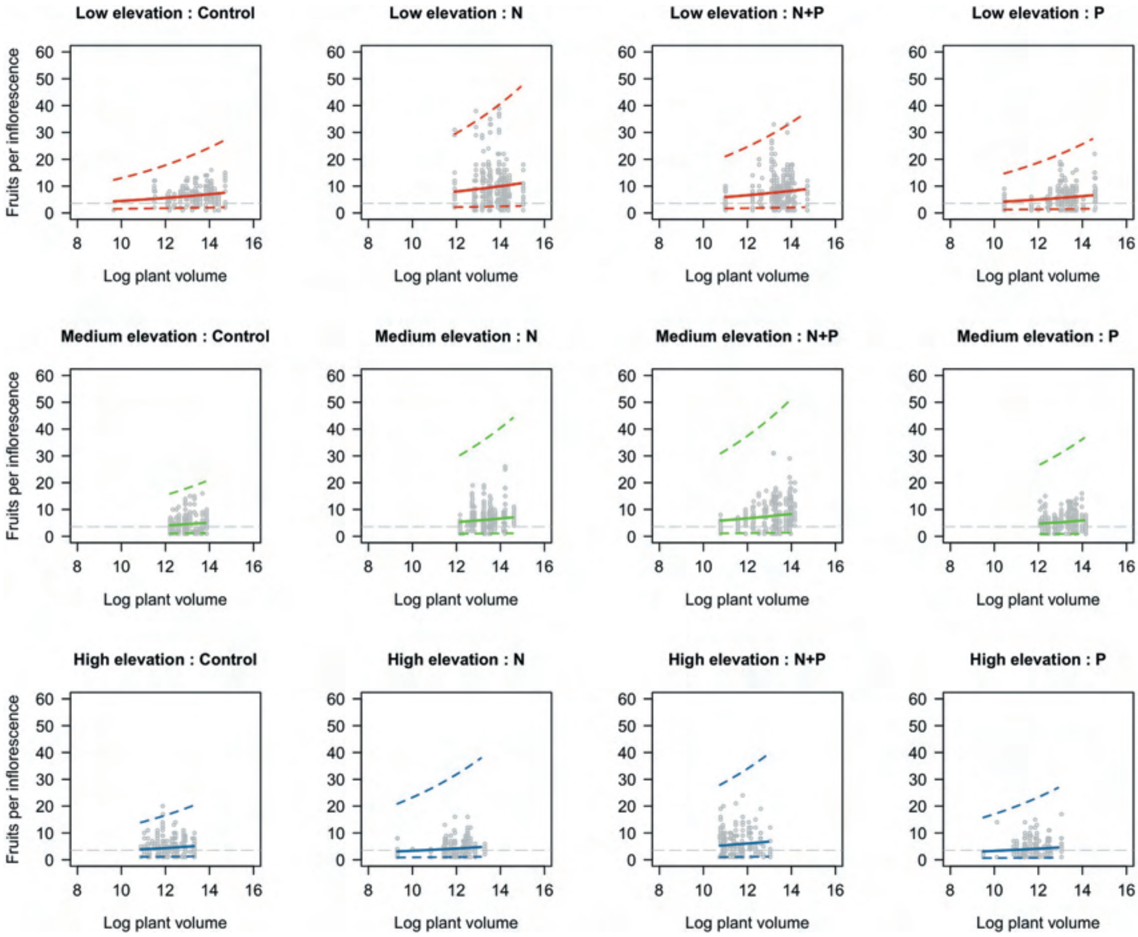

**Figure 6.** The relationship between plant volume and fruit yield per inflorescence as a function of elevation and nutrient addition in *Croton* sp. In the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a negative binomial fit of fruit yield per inflorescence for elevation, grazing exclusion, and added nutrients according to plant volume. Grey circles represent annual maximum number of fruits per inflorescence. Dashed lines are 95% confidence intervals. Horizontal grey dashed line is a reference (model intercept = 3.57, with plant volume = 8) to facilitate distinguishing fruit yield (number of fruits) among elevations, and between nutrients. The $R^2$ value of fruit yield model was 0.30.

this elevation. As in other dry ecosystems, reduction of livestock may improve *Croton* plant survival. In western New South Wales, Australia, grazing by sheep and rabbits (non-native herbivores), and kangaroos (native herbivores) increased mortality of four perennial grasses (Grice and Barchia 1992). For these species (*Aristida browniana*, *Enneapogon avenaceus*, *Monachather paradoxa* and *Panicum laevinode*), mortality rates were higher with grazing, regardless of whether this was caused by native or non-native herbivores. In semiarid woodlands in eastern Australia, recent grazing by livestock (sheep, goats and cattle), and rabbits similarly affected survival of young shrubs, mainly *Eremophila longifolia* (Travers et al. 2019). Since shrubs in dry ecosystems regenerate relatively slowly, grazing has the potential to alter such systems over the long term (Dawson and Ellis 1996). Therefore, a decrease in survival of *Croton* due to grazing may severely alter their population structure and consequently reduce vegetation cover that protects their congeners and other species of the dry inter-Andean shrub systems (Espinosa et al. 2013, 2019).

Our study also revealed that soil nutrient concentrations affect *Croton* survival at different elevations. At the low elevation, plants in ungrazed plots to which P was added had lower survival, compared to control plots. Addition of N+P at the medium elevation also reduced survival compared to controls. These reductions in survival at low and medium elevations in ungrazed plots but with nutrient addition can, at least partially, be attributed to increases in plant competition. At the low elevation, average interspecific density in ungrazed plots without added nutrients (control treatment) was 75 individuals in 2021 but rose to 94 individuals with P added. However, at the medium elevation, such changes in density were not evident in ungrazed plots to which both N and P were added. Background availability of N at low and medium elevations was lower compared to that at the high

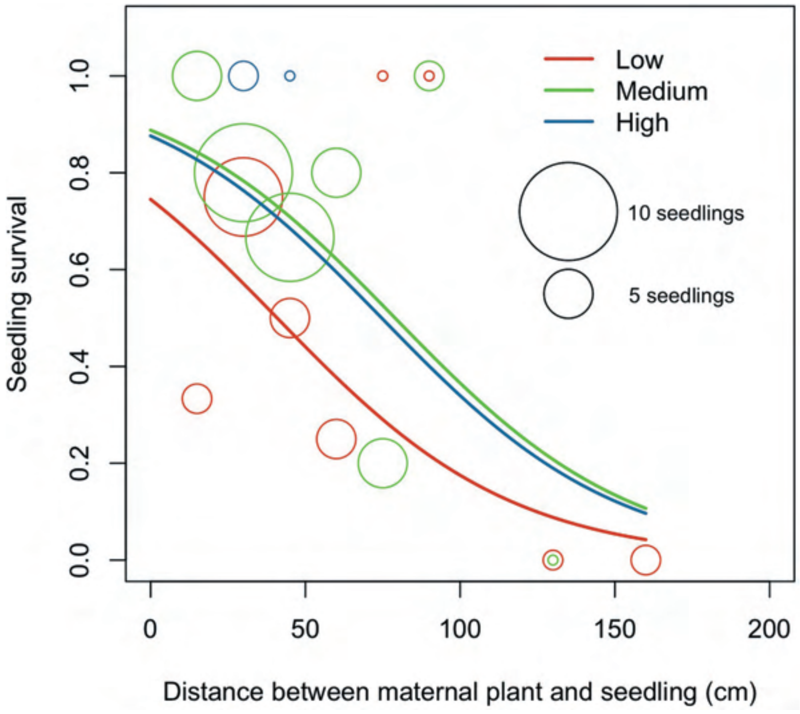

**Figure 7.** The relationship between the distance between seedlings and their maternal plants of *Croton* sp. In the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a binomial fit of seedling survival probability for elevation by distance between maternal plant and seedling. Circles are the number of seedlings per elevation. The $R^2$ value of this model was 0.17.

elevation while availability of P was higher at low elevations. Addition of N and P to ungrazed plots could have increased interspecific density (especially at the low elevation), generating a decrease in *Croton* survival. The continuous contribution of N through volatilisation and runoff of fertilisers from nearby crops (Moreno et al. 2018; Larios-González et al. 2021), cattle excrement (Scharpenseel et al. 1996), ash deposition from sugarcane burning (Granli and Bøckman 1995; Jaramillo 2011; Guamán et al. 2012), and the almost absence of organic matter and low water availability at the low elevation (Figure 1e–h, respectively) could threaten *Croton* survival at this elevation (Gallego-Zamorano et al. 2022). Other studies have also reported negative effects of interspecific density on shrub survival after nutrient addition. For example, in the Cape Floristic Region, South Africa, NPK fertiliser increased weed density, decreasing the survival of shrubs (Holmes 2001) that are sensitive to high P levels (Stock and Allsopp 1992).

In terms of the effects on growth, addition of N +P without grazing improved *Croton* growth at all elevations, whereas the addition of P decreased growth at the higher elevation. This suggests that grazing exclusion and availability of both P and soil water (Schulte-Uebbing et al. 2021) can improve growth of *Croton* if the effects of nutrients do not conflict with a potential increase in interspecific density. Further study should better answer how nutrient addition (artificially or by natural deposition) can promote growth among species in this ecosystem (Xu et al. 2021). Fertilisation could support growth of other species, such as grasses that could be limiting *Croton* growth, particularly at high elevations. In recent years, we have observed an increase in density of grasses surrounding the *Croton* shrubs at high elevations (Figures S10, S11 and S12). At this elevation, there are low concentrations of P in the soil (Figure 1c). An increase in P availability in soil can favour growth of certain grass species (Wassen et al. 2005; Siddique et al. 2010; Daws et al. 2021). Adaptation to low P availability can be considered a stress-tolerant strategy that gives certain plant species, such as *Croton*, a competitive advantage over other species. Therefore, to promote *Croton* growth it is essential to consider a balanced supply of N and P according to the needs at each elevation together with controlled grazing.

*Croton* fruit yield improved at the low elevation with addition of N and at medium elevation by addition of N and P. Low elevation had lower

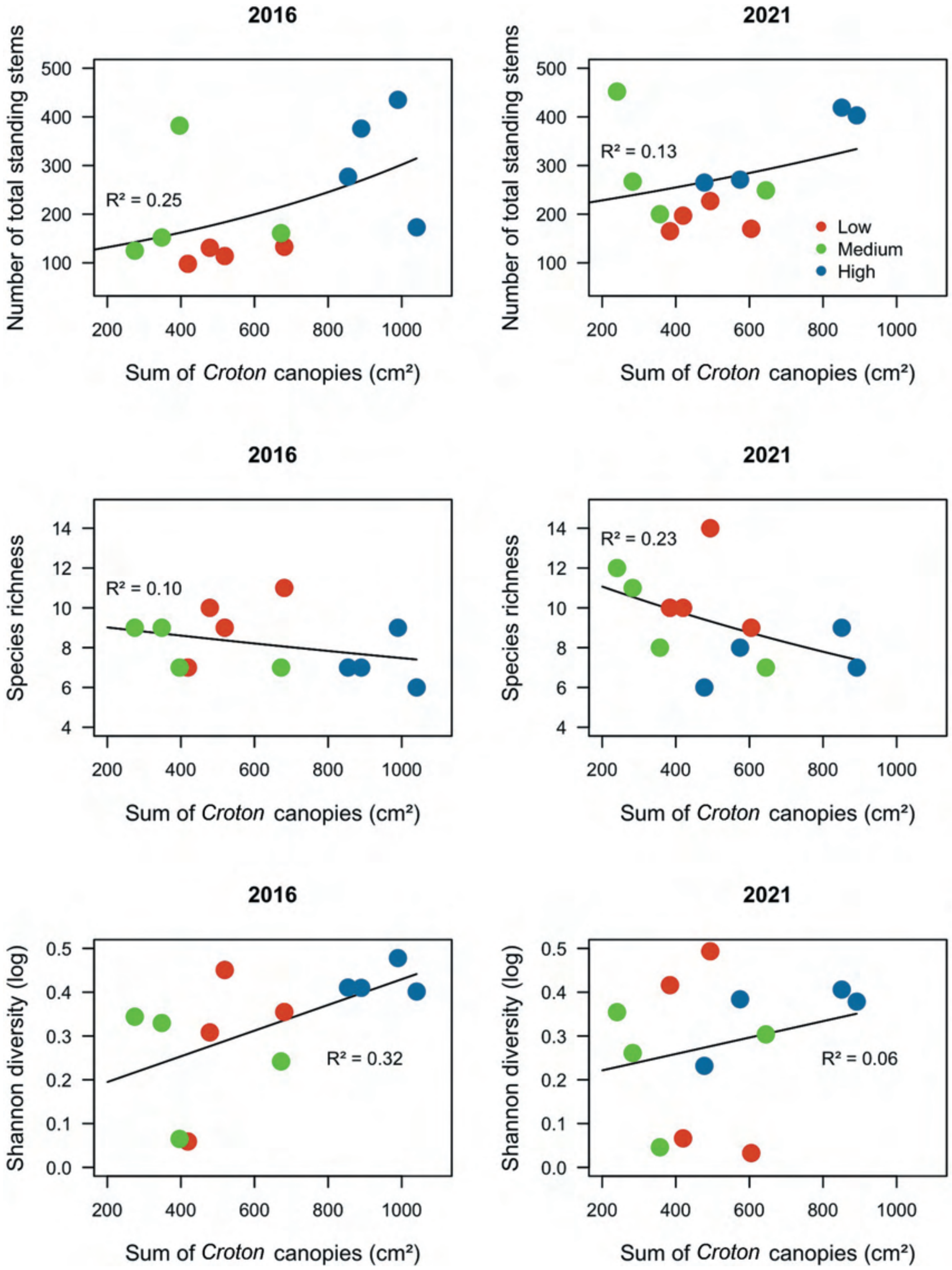

**Figure 8.** The number of total standing stems (abundance), species richness and Shannon diversity in 2016 and 2021 as a function of *Croton* canopy cover in the inter-Andean valley of Catamayo, Loja Province, Ecuador at elevations of 1400 m a.s.l. (low), 1550 m (medium), and 1700 m (high). Solid lines are trend lines for a Poisson fit for both number of total standing stems of all species and for species richness and a linear fit for Shannon diversity. There was no clear evidence of association between richness and *Croton* canopy cover in 2016 and 2021, nor for Shannon diversity in 2021.

concentrations of N (Figure 1a) and higher concentrations of P in the soil compared to concentrations at high and medium elevations (Figure 1c). Balancing the availability of soil N and P is important at these elevations to improve fruit yield and seed quality (see Kramer and Kozlowski 1979; Drenovsky and Richards 2005). We have observed at the low and medium elevations that fruit yield and seed size are relatively high without N and P application (Vélez-Mora et al. 2021). Perhaps N and P application would be necessary for improved production and seed quality and to ensure establishment and survival of *Croton* seedlings, or perhaps the main limitation is the availability of soil water (Figure 1e; Trindade et al. 2020). This question could be answered with experiments of balanced addition of N and P at each elevation, exclusion of long-term grazing, and water availability. In the Great Basin Desert in western North America, addition of N and water balanced their availability in relation to P, improving seed production and quality in the native shrub *Sarcobatus vermiculatus* (Drenovsky and Richards 2005). At Northeast Normal University, Jilin Province, China, *Chloris virgata* increased the reproductive production (mass of seeds produced) with an intermediate level of N (2.5 g $m^{-2}$) (Wang et al. 2016). Our study stresses the importance of balancing levels of N and P for adequate yield of *Croton* fruits in sites co-limited by these two nutrients.

We confirmed that the survival of *Croton* seedlings decreases as they shift away from the canopy of their maternal or facilitator plant. *Croton* canopy is critical for seedling establishment and recruitment in extreme environments due to less evaporation from soil by shade promoting density-dependent community plant associations (Lara-Romero et al. 2017; Jonge et al. 2021). We further suspect that drivers, such as grazing, intensification of drought at low elevations and disproportionate enrichment of nutrients, can change plant composition (Siddique et al. 2010; Espinosa et al. 2019; Daws et al. 2021). These drivers can also jeopardise facilitation offered by *Croton* canopy and consequently reduce recruitment of both *Croton* and other species. Long-term experiments are necessary to understand the interactive effects (climate change, nutrients, and grazing) on recruitment regimes and seedling establishment in this and other dry tropical environments (see Bhadouria et al. 2016, 2017, 2020).

## Conclusions

*Croton* cover is essential to promote abundance and plant diversity in the inter-Andean dry shrubland. The presence of *Croton* in this dry shrubland not only guarantees permanence of *Croton* species, but also of the plant community. The positive interaction between *Croton* and their facilitated species should be considered in restoration and conservation plans to ensure the functioning and services that this ecosystem provides, especially at high elevations. Four years from starting our study, we observed a general reduction in *Croton* cover at high elevations (Figure S11). We suspect that the main causes of this reduction were extensive grazing (cows and goats), addition of nutrients (N and P) and increased abundance of herbaceous plants. Trampling and excrement from livestock alter the physical and chemical properties of soil, moisture, and nitrogen content (Pulido et al. 2018; Zhan et al. 2020), affecting the composition and diversity of plant communities (Koerner et al. 2018; Lyseng et al. 2018). In addition, an increase of N through atmospheric deposition, which further favours the growth of nitrophilous grasses, causes competitive exclusion of key ecosystem species such as *Croton* (Bobbink et al. 1998; Figure S12).

The above changes, along with climate change, can degrade the structural attributes of the inter-Andean shrubland preventing these communities from providing critical environmental services, such as the provision of water and control of erosion. We are convinced that wise landscape planning and the search for alternative productive options to grazing goats and cows, and small-scale commercial crops, should be a priority for the local society. Further research aimed at identifying the limits to ecological and social resilience and resistance of communities in these ecosystems will help in the development of more environmentally compatible human use of resources in these regions.

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## Disclosure statement

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