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# Chronic disturbance alters seed dispersal traits and frugivores resources in a dry tropical forest

Carlos Iván Espinosa[1✉], Andrea Jara-Guerrero[1], Judith Castillo-Escobar[2], Jorge Cueva-Ortiz[3], Elizabeth Gusmán-Montalván[1], Bernd Stimm[3], Patrick Hildebrandt[3] & Adrián Escudero[4]

**Chronic disturbance is a major driver of biodiversity loss in seasonally dry tropical forests (SDTFs). However, its consequences on the functional dimension of diversity, particularly dispersal traits, remain unclear. We evaluated the effects of chronic disturbance on the functional traits of woody plant community and its potential effects for frugivores. We characterized eight traits related to seed dispersal and calculated the community weighted means and functional diversities for trees and whole woody community. We used GLMs to evaluate the effects of the chronic disturbance on these functional metrics, including the abundance and diversity of fruits as resources for frugivorous group. Chronic disturbance filtered traits related to dispersal, reducing the proportion of species with fleshy and heavier fruits, and producing more seeds per fruit. Functional richness and dispersion declined with disturbance. We found a general pattern of reduction in the availability and richness of fruits. Our results suggest that the changes in species richness and abundance are not random but result from environmental filtering on traits related to dispersal costs and stress tolerance. Changes in vegetation directly affected resources availability for frugivorous group, which in the medium term can affect the woody species persistence and catalyze the woody species loss.**

**Keywords** Drylands, Functional diversity, Frugivory, Seed dispersal, Dispersal syndrome

Understanding how anthropogenic disturbance affects biodiversity of tropical forests is a critical demand due to the dramatic deforestation and degradation rates[1,2]. Human-driven disturbance generates a sharp decline and homogenization of biodiversity[3–5]. This homogenization results from a reduction in the suitability of the habitat for certain species -losers- and a parallel increase in the abundance of others -winners-[6,7], depending on their environmental tolerances and requirements[8]. Although the underlining paradigm is a taxonomic homogenization after degradation[4,9], some authors suggested that it could also imply a functional simplification and convergence[6], increasing the vulnerability of entire species groups with particular functional traits[8,10].

Evidence also shows that certain critical dimensions of the plant trait architecture, such as those related to wood tissue[11] and leaf economic spectrum[12], suffer a decline in their natural variability in tropical forests after anthropogenic disturbance[13,14]. It is also expected that a third functional dimension of plant species related to dispersal and reproduction is also deeply affected by man-driven disturbance[10,15]. Even more, it is known that large-fruited and large-seeded species are especially sensitive after perturbation[16–18] which would have dramatic implications for animal-plant interactions, and community dynamics[10,15,19,20].

A considerable effort has been devoted to understanding the process of biodiversity loss after disturbance, including their functional and phylogenetic counterparts. However, most of those efforts have focused on deforestation and subsequent fragmentation as drivers of tropical forest diversity loss[4,10,16,21]. However, the effect of chronic disturbance (i.e. small scale extensive livestock farming and selective coppicing) are by far less known, despite their importance at a global scale[22]. Chronic disturbance implies a long history of low-intensity but constant human pressures without a significant loss in the extent of vegetation and tree canopy[23]. Often the forest extent is maintained whereas the biomass, structure, diversity, and ecosystem services decline[5,14,24].

[1]EcoSs_Lab, Departamento de Ciencias Biológicas y Agropecuarias, Universidad Técnica Particular de Loja, Loja, Ecuador. [2]Maestría de Biología de la Conservación y Ecología Tropical, Departamento de Ciencias Biológicas y Agropecuarias, Universidad Técnica Particular de Loja, Loja, Ecuador. [3]Department of Life Science Systems, Technical University of Munich, Freising, Germany. [4]Área de Biodiversidad y Conservación. Dep. de Biología, Instituto de Investigación en Cambio Global (IICG-URJC), Geología y Física Aplicada. ESCET URJC, Móstoles, Madrid, Spain. ✉email: ciespinosa@utpl.edu.ec

This maintenance of the forest extension makes difficult to assess chronic disturbance, a problem that can be aggravated by the interaction of different pressures acting together, as well as the differences in relation to the initial primary productivity of the forests[6,14].

One of the tropical ecosystems experiencing a higher pressure from chronic disturbance is the seasonally dry tropical forests (SDTFs)[25–27]. Chronic disturbance in SDTFs usually combines livestock grazing and small-scale timber extraction[28], which intensify stress through biomass depletion and, consequently, increased solar radiation and ground-level temperature and reduced soil content of water and nutrients[29–31]. Previous studies suggest that the stress induced in SDTFs by chronic disturbance drives a loss of plant taxonomic diversity[25,27,32], with the exclusion of species with particular ecological functions[14]. However, chronic disturbance could drive different changes at the community level, depending on the type of pressure exerted and consequences on the environment. For instance, it is expected that the establishment of species in these disturbed forests will be defined by functional traits related to stress tolerance[18], mainly due to increased drought[33]. On the other hand, Silva et al.[32] reported that the richness of species with fleshy fruits, and those with zoochoric dispersal were affected negatively by an increase in aridity but positively by the wood extraction or livestock grazing in SDTFs of the Caatinga region. Recent research at SDTFs in southwestern Ecuador showed that free-foraging goats in the forest disperse mainly legume seeds, particularly those of species with dry pods[34]; therefore, in chronically disturbed areas, where wild dispersers are almost excluded, those species with specialized traits for genuine dispersal by animals – i.e., fleshy fruits – may be adversely affected. On the other hand, Maza-Villalobos et al.[31] reported for SDTFs of Mexico that the presence of cattle negatively affected the size and weight of fruits, and the seed number per fruit, while the weight and size of seeds were positively affected. Considered collectively, this evidence suggests that chronic disturbance and aridity interact in complex ways, including synergistically[26], making predictions very difficult. Therefore, it seems necessary to clarify to what extent some functional traits are driving this plant diversity loss and functional homogenization because of chronic disturbance, and their effects at local scales.

SDTFs in Ecuador show a significant loss of tree diversity associated with chronic disturbance[27,35]. Thus, we are interested in assessing whether these changes in plant diversity generate a loss of functional diversity associated with seed dispersal, and the potential effects on the resource availability for frugivorous groups, considering both facultative and opportunistic species. With this in mind, we addressed the following specific questions; (i) how does the abundance of species with particular dispersal traits change with chronic disturbance? (ii) Are these changes in abundance the outcome of an environmental filtering on species with particular functional traits? (iii) What is the impact of those changes in the abundance and diversity of functional traits on the access to resources by frugivorous groups? We hypothesized that chronic disturbance limits the establishment of plants with fleshy fruits, large seeds, and dispersed by animals, because of their short period of seed viability, high water and nutrient requirements[36]. Disturbance may also limit establishment by changing the behavior of dispersers and changing the detectability of fruit for dispersers such as birds that reply on visual signals[37]. Consequently, we expected that the functional diversity of traits of fruits and seeds, will be negatively affected by chronic disturbance. Because trees show a higher loss of species richness than shrub species[27], these effects should be stronger in the case of trees than when the entire plant community, including trees and shrubs, is evaluated. Although the effects of chronic disturbance on shrubs are less understood, this group may be favored by low and medium levels of chronic disturbance species[27] because of the different and ampler requirements of water and light compared to trees[38]. Finally, we expected that those changes in functional diversity of the dispersal and reproductive traits negatively affect the variety and abundance of resources for frugivorous group, especially fleshy and large fruits.

## Results

From the 100 woody species recorded in the plots, we obtained data for the 72 species distributed in 33 families and 59 genera (see Supplementary Table S1). These species represented 74% of the total abundance and 64% of the basal area of woody species in the study area. The families that presented the highest number of species and genera were: Fabaceae (22 species, 17 genera) and Malvaceae (6 species, 4 genera). Dry fruits represented the 64% (46 species), and fleshy fruits represented the other 36% (26 species). We distinguished seven types of fruits, the most common were pods ($n = 18$, 25%) and capsules ($n = 15$, 21%) related to autochory and anemochory. Other types of fruits were berries ($n = 11$, 15%), drupes ($n = 13$, 17%), samara ($n = 8$, 11%), in a smaller proportion achene ($n = 5$, 7%) and, syconium ($n = 2$, 3%). In addition, eight colors were recognized among fruits, being brown fruits the most common among the species ($n = 36$, 50%), followed by the yellow ones ($n = 10$, 14%), and green ($n = 9$, 14%). The dominant dispersal syndrome was zoochory ($n = 33$, 45%), followed by anemochory ($n = 23$, 31%) and autochory in smaller proportion ($n = 16$, 22%). From the autochory group, 5 species have been reported to be secondarily dispersed by ungulates (see Supplementary Table S2). Most of the zoochorous species showed traits related to dispersal by birds (22 species) and non-ungulate mammals (17 species). Other zoochorous species presented traits related to dispersal by reptiles (13 species), micromammals (11 species) and ungulates (10 species, including those primarily autochorous) (see Supplementary Table S2).

The first PCA axis of the chronic disturbance variables explained the 54% of the variation of the chronic surrogates and was positively associated with the number of goat feces, and negatively with the distance to human settlements and density of large trees (Supplementary Table S3).

### Changes in community weight mean of traits related to seed dispersal

The proportion of fruit types was affected by chronic disturbance in different ways. While pods were positively affected by CDI, the rest of fruit types were negatively affected. Only achene was not directly affected by CDI (Fig. 1, Supplementary Table S4). Our models showed a significant and positive effect of interaction CDI: E, which means that those negative effects of CDI on the proportion of berries, capsules, samaras, and syconium

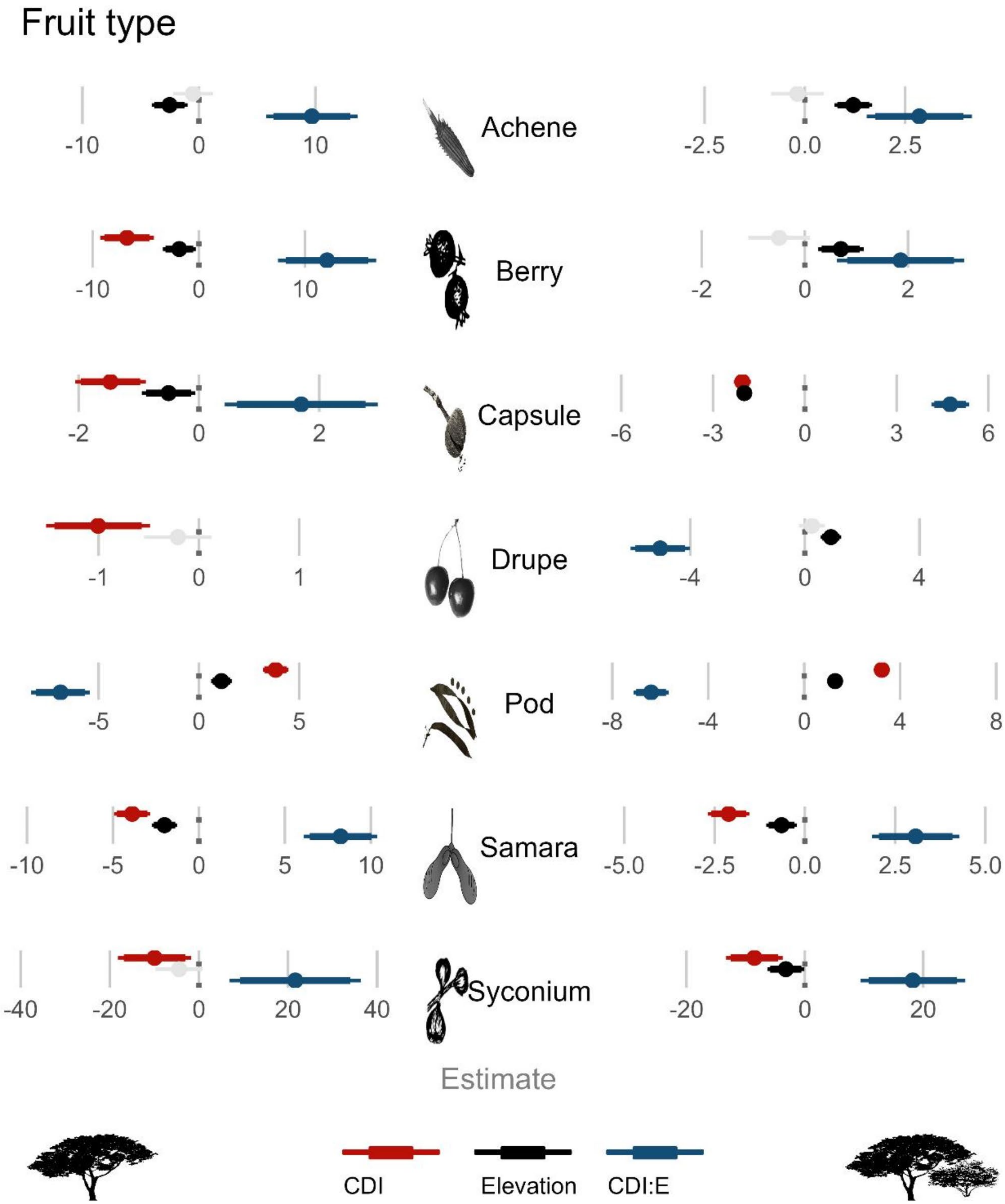

**Fig. 1**. Generalized linear model estimates of the proportion of fruit types for trees (left), and trees and shrubs (right). The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI : elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

were reduced as elevation increased (CDI: E positive effect). The CDI: E interaction also had a significant positive effect on achenes, indicating that the impact of CDI varies with elevation, showing a positive effect in higher-elevation areas. On the contrary, for pods, elevation reduced the positive effect of CDI (CDI: E negative effect). When we analyzed both trees and shrubs, the only change regarding trees was observed in berries and drupes, which did not show a direct effect of CDI on their proportions (Fig. 1). Still, the impact of CDI was dependent on elevation, showing that in higher-elevation areas the CDI increased the proportion of species with berry fruits, while reduced the proportion of drupes.

Regarding the fruit color, the proportion of tree species with red, white, and yellow fruits was negatively affected by CDI, an effect that became weaker in higher-elevation areas (CDI: E positive effect, Fig. 2, Supplementary Table S4). The proportion of species with brown fruits was positively affected by CDI, although that effect reduced with elevation (CDI: E negative effect). The CDI: E interaction significantly influenced the proportion of species with black and green fruits. While this interaction positively affected species with black fruits at higher elevations, it negatively affected on species with green fruits in the same areas. When we analyzed trees and shrubs, the pattern of brown fruits was the opposite. For black and green fruits, the direct effect of CDI became significant for shrubs and trees. Specifically, CDI negatively impacted black fruits while positively affecting green fruits. However, at higher elevations, the influence of CDI was weaker for both types of fruits. Additionally, orange fruits were positively affected by CDI (Fig. 2).

We found that CDI significantly and positively affected the proportion of autochorous trees, and this effect increased at higher elevation (CDI: E positive effect). CDI negatively affected the proportion of zoochorous tree species, while in anemochorous tree species, this effect depended on the elevation, negatively affecting its proportion in higher elevation areas (CDI: E negative effect) (Fig. 3a, Supplementary Table S4). When combining tree and shrub species, the effect of CDI on autochorous species varied with elevation, increasing their proportion in higher-elevation areas (Fig. 3a). For anemochorous and zoochorous species, the effects observed for trees remained for trees and shrubs. We observed a significant and negative effect of chronic disturbance on fruit weight and seeds per fruit, both for trees and shrub and trees together. The negative effect of chronic disturbance reduced with elevation, except for fruit weight of trees (Fig. 3b). Chronic disturbance significangly affected the seed area of trees through elevation (CDI: E positive effect); the seed area was positively affected by chronic disturbance in higher-elevation areas. When considered shrubs and trees, the seed area was significant and negatively affected by chronic disturbance, with a weaker effect with elevation (CDI: E positive effect, Fig. 3c).

## Changes in functional diversity of traits related to seed dispersal

Chronic disturbance significantly affected functional diversity in its different components. For trees, chronic disturbance affected significantly and negatively the functional richness (FRic) of fruit color, as well as the functional evenness (FEve) of fruit color, fruit type, and dispersal syndrome, and the functional dispersion (FDis) of fruit type (Fig. 4, Supplementary Table S4). These effects were stronger at lower elevations (CDI: E positive effect), except for FEve of fruit type and dispersal syndrome, where elevation and CDI: E were insignificant. The CDI affected positively the FRic and functional evenness (FEve) of dispersal syndrome (Fig. 4, Supplementary Table S4). When analyzing trees and shrubs together, the majority of the negative effects of CDI observed in trees persisted. Differences were noted in the interaction CDI: E, which was not included in the model for fruit type and did not show significance for fruit color. Furthermore, the negative effect of CDI on the FRic and FEve of fruit color was not significant (Fig. 4, Supplementary Table S4).

The best models for quantitative fruit and seed traits (Fig. 5a-c, Supplementary Table S4) showed that chronic disturbance positively affected the fruit area, while the FEve and FDis of seed number per fruit were negatively affected, with a stronger effect at lower elevations (Fig. 5b,c). The FEve of seed area also showed a negative effect of CDI (Fig. 5c). The seed weight did not exhibit direct effect of CDI but the interaction CDI: E was positive for FEve and FDis, indicanting positive effects of chronic disturbance in higher-elevation areas (Fig. 5b,c). The effects of CDI were similar when analyzing the trees and shrubs together, except for FEve of fruit area, which became non-significant, and FDis of seed weight, which turned significant and was negatively affected (Fig. 5c, Supplementary Table S4).

## Changes in fruit availability for frugivorous groups

Chronic disturbance negatively affected the species richness of tree species dispersed by birds, reptiles, and non-ungulate mammals (Fig. 6, Supplementary Table S5). Those effects were stronger at lower elevations. When considering tree and shrubs together, these effects remained for species dispersed by birds and non-ungulate mammals, while the effects on species dispersed by reptiles disappeared. On the contrary, the richness of species dispersed by micromammals increased with the disturbance.

Chronic disturbance negatively affected the abundance of trees dispersed by birds, non-ungulate mammals, and ungulates. For species dispersed by non-ungulates mammals, this effect was stronger at lower elevations. When analyzing trees and shrubs together, the negative effect of chronic disturbance on the abundance of species dispersed by birds remained, although it was stronger at lower elevations (CDI: E positive effect). On the contrary, the negative effect on trees dispersed by ungulates and non-ungulate mammals was diluted. On the other hand, the effect of chronic disturbance on species dispersed by micromammals and reptiles became significant and negative (Fig. 7).

# Discussion

Seasonal tropical dry forests are highly endangered due to chronic anthropogenic disturbance[23,39]. Although the reach and spatial extension of this chronic disturbance are not easy to assess, it is known that forests suffering this pressure support lower species richness than less disturbed forests[14,25,28,35,36]. Our results revealed that a reduction in the presence and abundance of species with particular seed dispersal traits accompanies this loss of

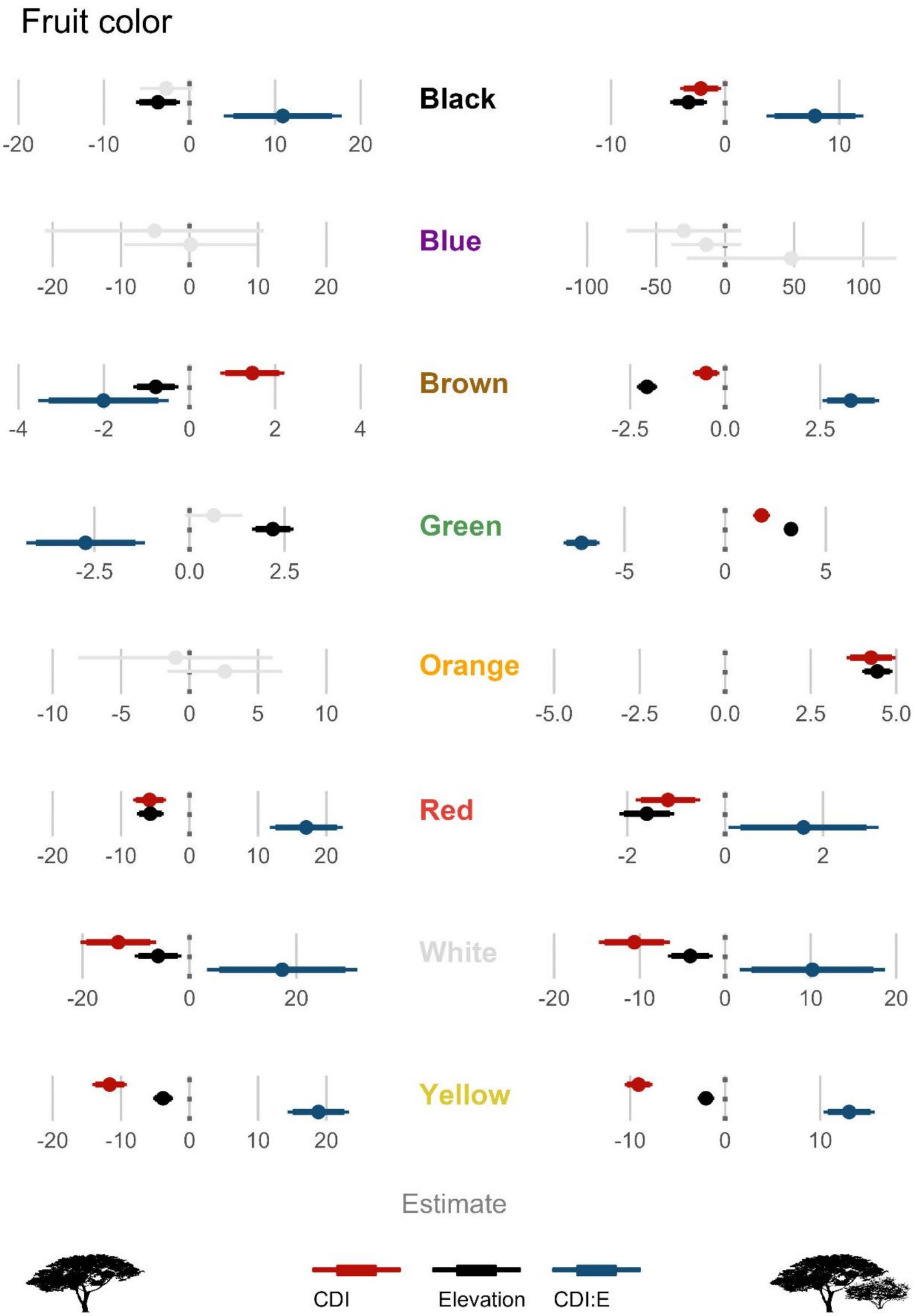

**Fig. 2**. Generalized linear model estimates of the proportion of fruit color for trees (left), and trees and shrubs (right). The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI : elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

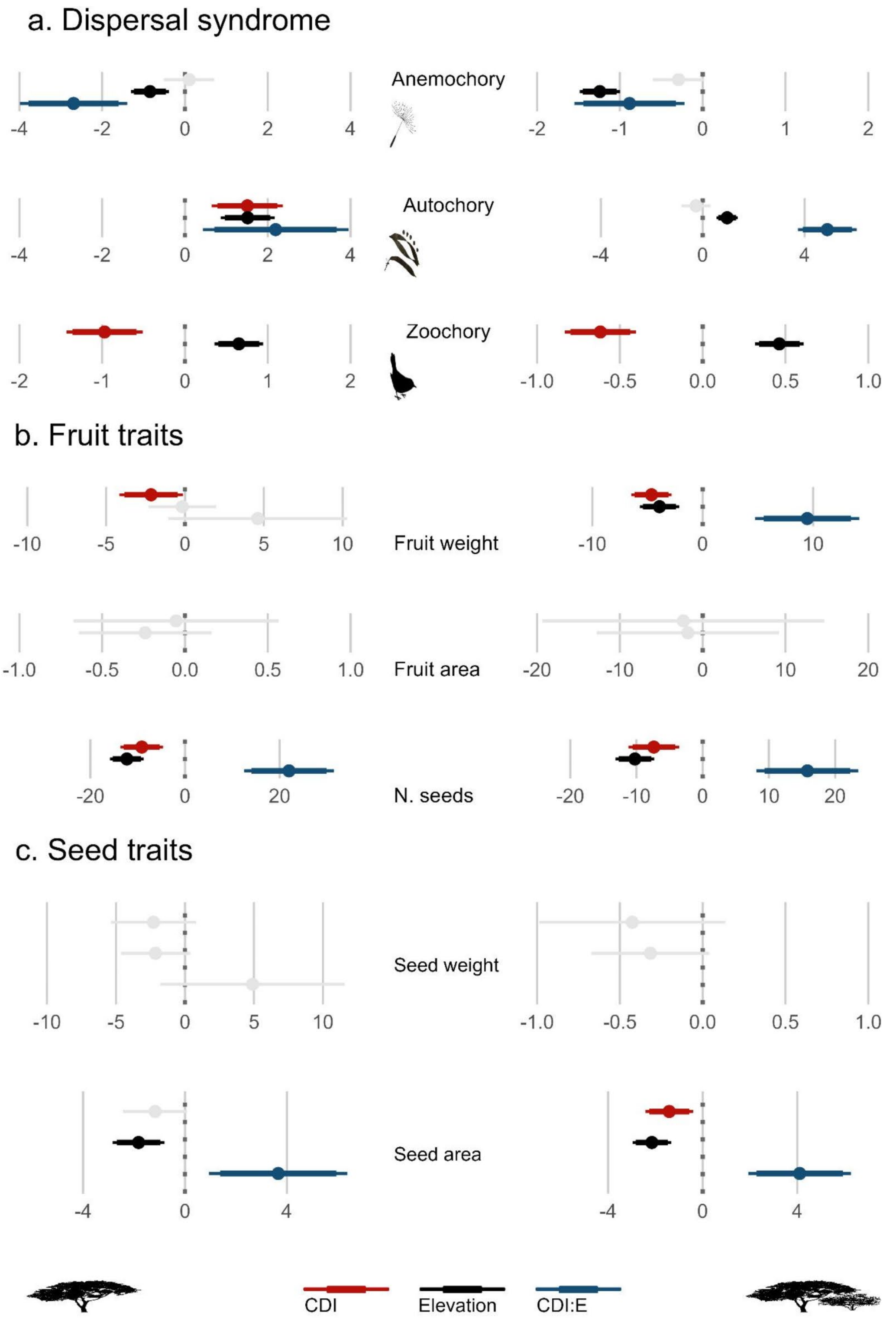

**Fig. 3**. Generalized linear model estimates of the proportion of dispersal syndromes, fruit and seed traits for trees (left), and trees and shrubs (right). The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI: elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

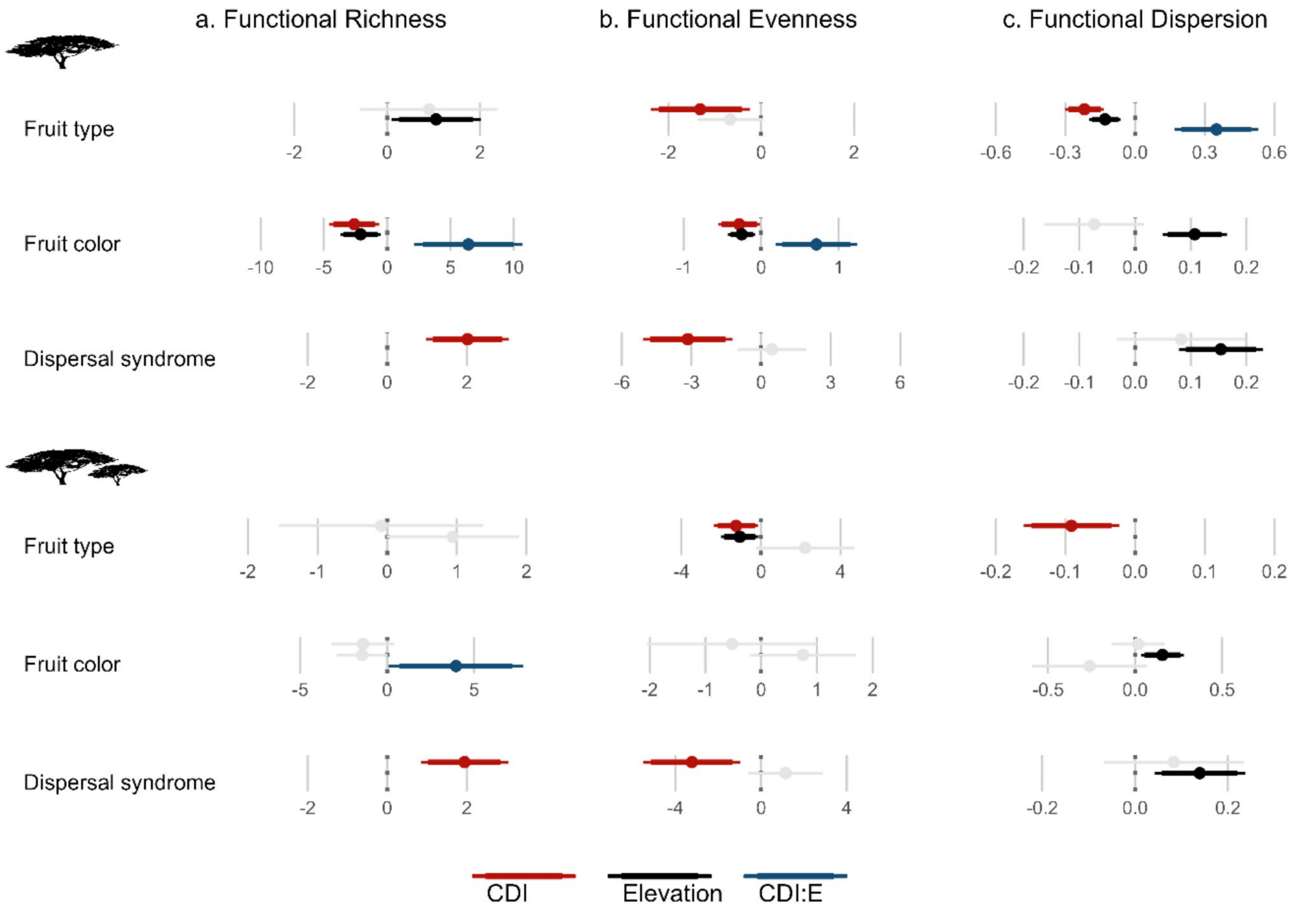

**Fig. 4**. Generalized linear model estimates of functional diversity of qualitative traits for trees (top) and trees and shrubs (bottom). The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI: elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

woody richness. Additionally, those areas with lower water availability (i.e. located at lower elevations), support the strongest effects of chronic disturbance on the abundance and diversity of functional traits. Previous studies indicated that the loss of forest species generated by chronic disturbance is initially defined by the loss of species with vegetative traits that allow the avoidance of water loss, such as hard and small leaves[2,14]. Moreover, there is pressure from livestock, especially goats, a generalist herbivore, that controls the recruitment of new plants[40].

As hypothesized, chronic disturbance also affects the structure and composition of the vegetation by filtering certain traits associated with dispersal, limiting the establishment of species with heavier fruits, more seeds per fruit, and associated with dispersion by animals. In this way, the pressures that generate the disturbance would be limiting the species regeneration through different paths, with the zoochorous species with fleshy fruits being the major losers. Although there is not microenvironmental information for our forests, some studies in SDTFs have reported that the loss of forest density associated with chronic disturbance increases stress due to greater exposure of the soil to radiation, which, together with greater evaporation, generates an increase in water stress[14,41]. Considering the competitive advantage of large-seeded species on harsh environments[42], those novel conditions in SDTF under chronic disturbance can explain the negative effects on species with more seeds per fruit, which tend to be small-seeded[43]. Furthermore, there is evidence that these changes in microenvironmental conditions are related to the loss of most tree forest species[27], changes in plant-animal interactions[44] and in species composition[45], as well as with increases in genotoxic damage in birds[46]. Similarly, micro-environmental changes behind chronic disturbance can limit plant access to essential resources required for producing expensive fruits, thereby reducing their persistence in disturbed areas. In this line, more studies are needed to evaluate the impact of chronic disturbance on fruit production and clarify the process behind, either the abundance of individuals bearing fruits or the per capita fruit production[15].

On the other hand, autochorous woody species were the winners. This result is not a surprise since autochorous species have been shown to be opportunistic pioneers and, consequently, more common in disturbed habitats[47], but also some of them are secondarily dispersed by goats[48]. In our study area, most of autochorous species are legumes with seeds covered by hard coats[49,50] that led them to tolerate drought and survive not only the dry season but even larger periods waiting for adequate germination windows.

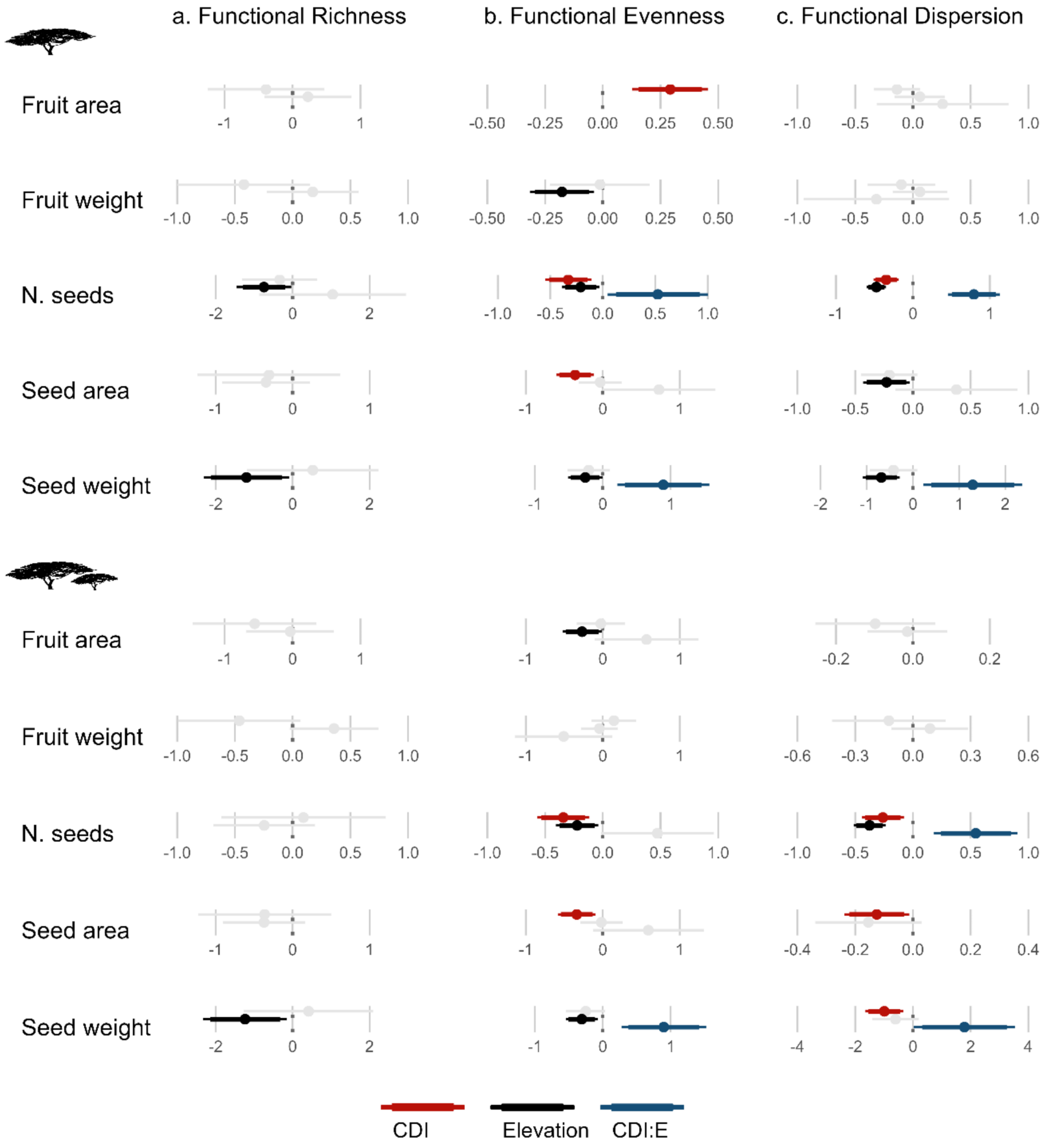

**Fig. 5**. Generalized linear model estimates of the functional diversity of quantitative fruit and seed traits for trees (top) and trees and shrubs (bottom). The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI : elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

Contrary to what we expected, chronic disturbance did not cause a generalized loss of functional richness. However, we found important changes in the functional configuration of the woody community related to a reduction in functional evenness and dispersion. The reduction in functional evenness suggests that in SDTFs facing chronic disturbances, some niches may be empty or underutilized by woody species, while others are heavily occupied. Additionally, the reduction of functional dispersion suggests a narrower distribution of species in the functional space of traits. Chronic disturbance reduces the functional evenness across most of

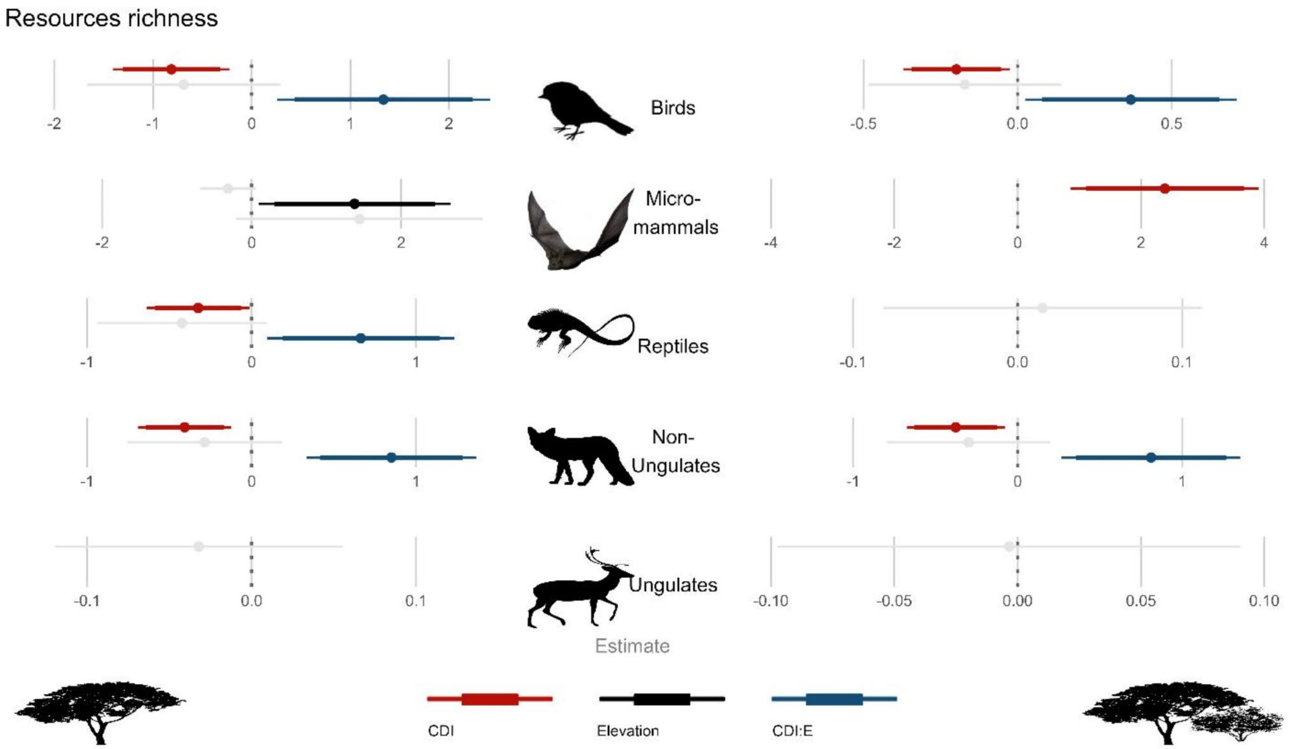

**Fig. 6.** Generalized linear model estimates of the species richness of trees (left), and trees and shrubs (right) as subrrogate of resources richness. The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI : elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

the traits assessed. The negative effects of CDI on FEve of fruit type could be explained by how different fruit types respond to CDI. While naturally rare fruit types decrease in abundance with increasing CDI, common fruits in the community, such as pods, are positively affected. These opposite responses would result in a loss of evenness at the community level as chronic disturbance increases. On the other hand, the disturbance reduced fruit colors such as red, white, and yellow, frequently low-abundant and associated with zoochorous species, that in these forests represent 35% of the abundance of individuals[49]. According to Silva et al.[32], chronic disturbance has resulted in changes in the functional structure of the Caatinga dry forests, leading to a reduction in the Rao's index of reproductive functional groups. Our results support this finding and suggest that chronic disturbance may similarly modify the functional structure of the woody plant community. However, it is worth noting that our study area represents an intermediate of the disturbance gradient, which is quite far from severely degraded areas in which trees are really scarce[28]. It is possible that in those areas with higher level of disturbance the filtering processes implies an even higher loss of functional richness.

Shrubs play an interesting role by blurring the negative effects of chronic disturbance on the proportions of dispersal syndromes and fruit types, particularly berries and drupes. According to Jara-Guerrero et al.[27], the openness of canopy in these forests leads to an increase in the density of shrubs which find an opportunity for actively recruit new individuals under more sunny conditions. Thus, to some extent, shrubs can help maintain a certain offer of dispersal traits in degraded forests. However, the negative effect of chronic disturbance on fruit color remains when considering both shrubs and trees. This effect may result from changes in the availability of effective dispersers[51], or an increase in their conspicuousness to inappropriate seed dispersers, seed predators, and fruit parasites[37,52,53] as tree density reduces. If visual dispersers decrease, brightly colored fruits may be displaced by more neutral or cryptic fruits, such as brown ones, that rely on generalist dispersers or other dispersal mechanisms. This finding suggests that chronic disturbance imposes novel selective pressures on fruit color as a trait, potentially affecting negatively colors that are more dependent on specific dispersal agents[51,52]. For example, brightly colored fruits such as red, yellow and white, that attract birds, may become scarcer. However, a more thorough analysis based on objective measurements of fruit color and disperser behavior in disturbed environments is needed considering the intricate interactions between dispersing animals and fruits, including the varying color perceptions of birds.

Another valuable finding is that the environmental filtering generated by chronic disturbance was stronger at lower elevation. In STDFs, lower elevations support the lower precipitation rates and higher mean temperatures[35], being under higher risk in the face of climate change[54]. Thus, those species with capsules, samaras and fleshy

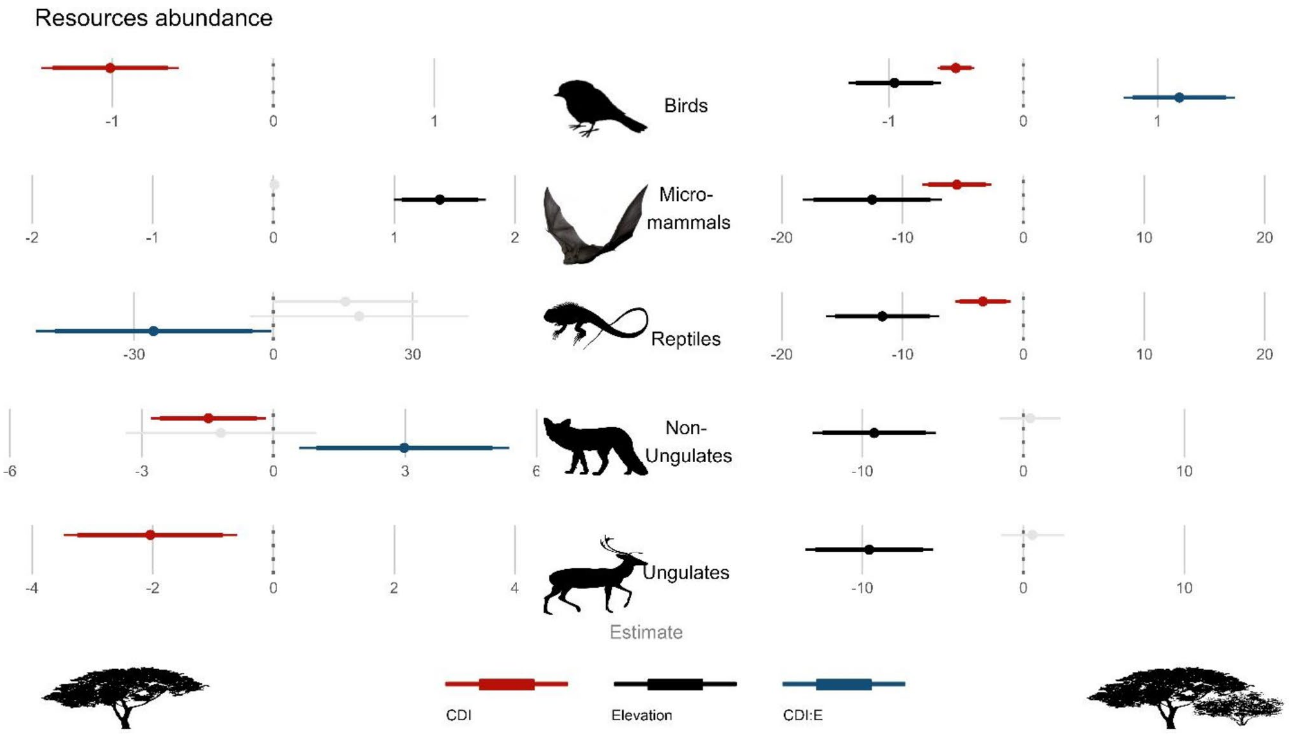

**Fig. 7**. Generalized linear model estimates of the abundance for trees (left), and trees and shrubs (right) as subrrogate of resources abundance. The plot shows the estimates for each variable as dots and the confidence interval of the estimator as lines, with thin line at 95% and thick line at 90%. The variables are listed from top to bottom: CDI, elevation, and the interaction of CDI: elevation. Significant effects are shown with colored lines, while non-significant effects are shown with gray lines. Each plot includes only the variables considered in the best model.

fruits, particularly those with red, yellow and white fruits can be lost with the chronic disturbance. Additionally, the availability of fruits associated to frugivorous species is also strongly affected at lower elevations.

Since a high diversity of functional fruit traits can sustain a larger community of frugivores[19,55], the observed changes in the functional traits of the woody community have direct effects on the availability of resources for frugivorous species[55] and represented a potential cascading effect on the whole ecosystem[25]. This is especially significant for those species with red, white and yellow fruits, which are related to consumption by birds and mammals. Thus, the loss of these resources can explain the reduction of richness and abundance reported for some groups such as bats[56] and birds[57] in these forests.

On the other hand, we found a low effect of disturbance on the abundance and diversity of resources for ungulates. One of the main ungulates is the deer (*Odocoileus virginianus*) which is known as a disperser of several species with pods that were thought to be only dispersed via autochory[58]. Thus, the abundance of pods in degraded areas can explain why the richness of species dispersed by ungulates were not affected by the chronic disturbance.

In conclusion, species were filtered based on traits related to dispersal costs and their subsequent ability to withstand the environmental stress induced by the disturbance. The observed changes in vegetation have a direct effect on the availability of resources for frugivorous species, which in the medium term can generate a cascading effect on the whole forest ecosystem[8,59]. Although zoochory and plant regeneration dynamics are recognized as key processes to ecosystem functionality, there is need to aid them in the development of a risk assessment approach for the ecosystem[60]. Understanding the broader implications of these functional shifts is vital for informing management practices. Chronic disturbance not only exacerbates biodiversity loss but also reduces the ecosystem's ability to buffer future environmental stressors, including climate change. By integrating insights from this study into a framework of adaptive management and restoration, we can enhance the resilience of SDTFs and contribute to aligning conservation efforts with the challenges posed by these highly vulnerable ecosystems.

## Materials and methods

### Study area

Our study was conducted in Southwestern Ecuador (Loja province, Zapotillo, Macará and Celica counties; between latitudes 4°19'39 " and 4°01'40" S and between longitudes 80°19'00 " and 79°41'40" W). This is part of the Tumbesian region and comprises some of their largest and best-preserved SDTFs. The altitude ranges from 120 to 1100 m a.s.l. The annual mean temperature is between 20° and 26° C, and the annual mean precipitation ranges from 300 to 700 mm[35]. There is a dry season from May to November and a rainy season from December to April. Dominant tree species were *Cochlospermum vitifolium* (Cochlospermaceae); *Handroanthus chrysanthus* and *H. bilbergii* (Bignoniacea); *Ceiba trichystandra*, *Eriotheca ruizii* (Bombacaceae); *Guazuma ulmifolia* (Malvaceae) and *Muntingia calabura* (Muntingiaceae)[35]. These forest remnants are mainly used for extensive grazing of goats and cattle and sporadic wood extraction[27,28,35,48].

Although the guild of seed dispersers has not been extensively studied, this area hosts some potential seed dispersers[56] such as at least two frugivorous bat species (*Artibeus fraterculus*, *Sturnira bakeri*) and other two omnivorous bats (*Lophostoma occidentalis*, *Phyllostomus discolor*)[61]. Two deer species that inhabit this SDTFs have also been reported feeding fruits, *Odocoileus virginianus*[58,61] and *Mazama americana*[61,62]. Other omnivores feeding on fruits are fox *Lycalopex sechurae*, *Pecari tajacu* and some rodents (e.g. *Sciurus* spp. and *Proechimys decumanus*)[62]. Moreover, this area is widely recognized by the diversity of bird species, some of which are well-known for their potential as seed dispersers[63]. Although saurochory is likely the least studied interaction in this area, the effectiveness of lizards as seed dispersers has been reported in other SDTFs in the Neotropics[64].

## Data sampling

Within an area of 1800 $Km^2$, we randomly selected 24 locations covering a wide gradient of chronic disturbance resulting from grazing and logging of SDTF over different periods and intensities of use[28]. In each locality, we placed an L-shape cluster of three plots of $60 \times 60$ m separated 200 m from each other. In these plots we recorded all trees with a diameter at breast height (DBH) $\geq 10$ cm. Shrubs with DBH $\geq 5$ cm were also registered in a sub-plot of $20 \times 20$ m established in one corner of each plot (see Cueva Ortiz et al. 2019 for details). Plots covered an altitudinal range from 234 to 1037 m asl.

## Morphology and dispersal traits

Between January and June 2017, we collected fruits and seeds directly from fruiting trees. With these samples, we made a morphological characterization recording weight, length and width of fruits and seeds, number of seeds per fruit, and three qualitative traits: fruit type, fruit color and dispersal syndrome. We measured a minimum of 10 fruits and 50 seeds per species from at least five healthy individuals. We calculated the projected area of fruits and seeds as the area of an ellipse, i.e. the product of *Pi* by the radius of the length and radius of the width. For those woody species that did not produce fruits during the study time traits were obtained from bibliographic information or collections of seeds stored in the germplasm bank of Universidad Técnica Particular de Loja. We assigned a color to fruits of each species taking as reference Wheelwright & Janson[52] and Galetti et al.[19], which consider nine colors according to human perception: black (including dark red), red (including pink), yellow, orange, brown, gray, green, white and blue (including purple). Following Van der Pijl[65], we categorized all the species in three primary dispersal syndromes: anemochory (wind), zoochory (animals) and autochory (explosion or gravity) (see Supplementary Table S1 for the dispersal assignation). Lately and based on bibliographic information and personal observations we assigned each of these zoochorous species to a group of dispersers: birds, bats, non-ungulate mammals, ungulate mammals and reptiles (Supplementary Table S2).

## Data analysis

Chronic disturbance was defined based on three variables known to be surrogates of anthropogenic perturbation: (1) distance to the nearest human settlements, which vary from hamlets to villages. Considering that the free foraging activities of the goats intensify in the surroundings of the human settlements, the increase in the distance implies less disturbance[35,66]. (2) Biomass of goat feces in the plot[35,66], and (3) number of tree individuals with DBH > 20 cm, because a decrease of big trees is indicative of high disturbance[67]. These predictors of chronic disturbance were integrated in a principal component analysis (PCA). For the rest of analyses, we selected the first axis of the PCA as a chronic disturbance index. We used the "rda" function from the "vegan" package[68] to adjust this PCA.

To evaluate the effects of chronic disturbance on the abundance of species with particular dispersal traits, we calculated the community weighted mean (CWM) by using the density of individuals for each species. For the qualitative traits, the CWM was calculated as the proportion of each trait's level in the plot. To evaluate the changes in functional diversity with chronic disturbance, we calculated three measures of functional diversity separately for each trait; functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis)[69]. These three metrics measure different properties of the functional space. FRic evaluates variations in the functional space. For a single continuous trait, it is measured as the range within that functional space. For nominal traits, FRic is determined by the number of unique combinations of trait values present in a community. FEve assesses the distribution degree of traits abundance along of functional space, while FDis quantifies the mean distance of individual species to the centroid of all species in the community[70]. In our case, when analyzing the FDis for each individual trait, the centroid is the average value of the functional trait weighted by the abundance of each species. For qualitative variables, each category was transformed to a binomial presence-absence variable, the Gower dissimilarity matrix was calculated, and a principal coordinate analysis (PCoA) was used to place the species in a continuous functional space. The centroid was obtained as the weighted average of the coordinates of each species in that space[70]. The functional metrics were calculated by using the abundance (density) of each species and were estimated both for the trees and for the entire community, i.e. trees and shrubs. Because the trees and shrubs were measured in a different sized area, we calculated the density per hectare for shrubs and trees separately and then pooled the data. The functional diversity measures were calculated through the "dbFD" of the "FD" package[70].

Since functional richness is affected by covariates, such as species richness and abundance, it was necessary to remove those effects by using null models. The values were expressed by observing the index as a value relative to the null model[71,72]. The null model was calculated by randomizing the abundance of the matrix by keeping the rows fixed (productivity of the plots of land) and the columns (the dominance of the species)[73]. The null models were built using the "randomizeMatrix" from the "spicy package" and applying the "independswap" which preserve the columns abundances (site abundances) and so the richness[74]. The transformed index was defined as a standardized size effect (SES, sensu[75]).

$$SESFD = \ FD_{obs} - meanFD_{sim}/sdFD_{sim}$$

The $\mathrm{FD}_{\mathrm{ods}}$ refers to the diversity index (FRic) of the observed data, $\mathrm{FD}_{\mathrm{sim}}$ correspond to the average value of the FRic of each of the 999 randomizations of the community and $\mathrm{sdFD}_{\mathrm{sim}}$ the standard deviation of the FRic of these randomizations.

We built generalized linear models for the metrics of each trait by using the CWM and functional diversity including the proportion of fruits as response variables, and the chronic disturbance index (CDI), elevation as a foreseeable proxy of climate variation to partial out the effect of climate on the plant community, and the interaction between chronic disturbance and elevation (CDI: E) as explanatory variables. We used elevation as a proxy of climate because it can provide a more accurate indication of local climatic variations than available climate grids (see[76]). Additionally, the correlation between changes in the plant community and elevation has been extensively acknowledged[33,34,77].

To analyze qualitative traits, we adjusted Generalized Linear Models (GLMs) using a binomial error distribution. To evaluate quantitative traits and functional diversity indices, we tested several families of error distributions for use in our GLMs, as the distribution of these variables does not always fit a normal distribution. Gamma distributions have been used to model continuous variables that are always positive and have skewed distributions. We utilized four error distributions: Gamma error distribution with three link functions (square root, logarithmic, and inverse) and the Gaussian error distribution. For each measured trait, we adjusted three model structures: (i) complete model; it is a model with CDI, elevation and CDI: E, (ii) model without interaction; CDI and elevation, and (iii) reduced model; only CDI. We used the AIC statistics to detect the best adjustment among the 12 models (4 error distribution x 3 structure of models).

To evaluate the effects of chronic disturbance on the availability of resources for frugivorous group, we also applied GLMs by using the basal area and species richness of plants as proxies for the abundance and richness of available resources, respectively. These were evaluated for different groups of dispersers, which served as response variables. In order to standardize the variables for each disperser group, we divided the basal area of resources by the highest value of the plot. We followed the same procedure used to evaluate the best model in the dispersal trait analysis (see above) but using the quasipoisson error family for count data. All of the analyses were implemented in the R environment[78].

## Data availability

All data generated or analyzed during this study are included in this published article and its supplementary information files.

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## Author contributions

CE and AJ-G conceived and designed the research and analyzed the data. JC-E and JC collected the data. AJ-G, CE, AE and JC-E wrote the original draft. All co-authors discussed the results and commented and approved the final manuscript.

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## Declarations

## Competing interests

The authors declare no competing interests.

## Additional information

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**Correspondence** and requests for materials should be addressed to C.I.E.