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# Title: The effect of small-scale topography on patterns of endemism within islands

Running title: The effect of small-scale topography on endemism

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## Abstract

**Abstract.** Topography influences evolutionary and ecological processes by isolating populations and enhancing habitat diversity. While the effects of large-scale topography on patterns of species richness and endemism are increasingly well documented, the direct effect of local topography on endemism is less understood. This study compares different aspects of topographic isolation, namely the isolating effect of deep *barrancos* (ravines) and the effect of increasing isolation with elevation in influencing patterns of plant endemism within a topographically diverse oceanic island (La Palma, Canary Islands, Spain). We collected plant presence–absence data from 75 plots in 8 barrancos on the northern coast of La Palma, spanning an elevation gradient from 95 to 674m a.s.l. Using mixed-effects models, we assessed the effect of barranco depth and elevation on the percentage of single-island endemics, multi-island endemics, and archipelago endemics. We found that percent endemism was not significantly correlated with barranco depth and correlated negatively with elevation within barrancos (rather than the expected positive relationship). The topographic barriers associated with the deep island barrancos thus appear insufficient to drive speciation through isolation in oceanic island plants. The decrease in endemism with elevation contradicts findings by previous broader-scale studies and it may reflect local influences, such as high habitat heterogeneity at low elevations.

**Keywords:** Isolation, barranco, ravine, La Palma, topography, endemism, elevation, islands.

**Highlights:**

- Small-scale variation in topography may favour endemism if it causes species to be persistently isolated
- La Palma (Canary Islands) has many deep, steep-sided *barrancos*, containing unique habitat with many endemic plant species
- The proportion of endemic plants on barranco floors decreases with elevation, while the co-linear increase with barranco depth is not significant
- Local topography may complicate broader-scale relationships between endemism and elevation, and this requires further research

## Introduction

Topography is a key factor influencing the evolutionary and ecological processes that generate and maintain the diversity of life on Earth (Irl et al. 2015, Tukiainen et al. 2017, Godinho & da Silva 2018). It influences species diversity via two main mechanisms. First, topographic complexity drives local variation in climate across a small area through alterations in slope, elevation, and cold-air drainage (Dobrowski 2011), increasing the co-occurrence of species with different climatic tolerances (Lenoir et al. 2013). This contributes to habitat diversity, which positively correlates with species diversity (Kohn and Walsh 1994, Hortal et al. 2009, Tews et al. 2004). Secondly, topography causes isolation, acting as a dispersal barrier between populations (Janzen 1967). Topography may restrict species physically, for example by riverine barriers (Moraes et al. 2016). But species can also be restricted by their physiological tolerances, for example to low temperatures at high elevations. Topographic barriers limit gene flow through isolation, which leads to divergence, providing the conditions required for allopatry (Coyne and Orr 2004). Additionally, the isolation provided by topographic structures can create refugia for many species by supporting relict populations and protecting them from the spread of competing species (Harrison and Noss 2017). The ability of species to track their climate niche during climatic changes further decreases the extinction risk of species in topographically diverse areas (Sandel et al. 2011). Climatic fluctuations can lead to repeated isolation and reconnection and may act as a ‘species pump’ (Gillespie and Roderick 2014, Steinbauer et al. 2016). Topography thus positively influences species richness and endemism by enhancing evolutionary processes as well as by preventing extinction. As a result, areas with larger variation in elevation are thought to have higher speciation and endemism rates (Godinho and da Silva 2018).

The effect of large-scale topography, such as mountain ranges, on patterns of species richness, speciation rates, and endemism are increasingly well documented (Thomas et al. 2008, Steinbauer et al. 2012, Verboom et al. 2015, Steinbauer et al. 2016, Xing and Ree 2017), but the direct effect of local topography, such as steep-sided *barrancos* or ravines, is less well understood. In contrast to mountains, deep valleys or barrancos are only rarely discussed as barriers to gene flow (Janzen 1967, Ghalambor 2006, Steinbauer et al. 2016), and few studies have considered barranco beds as isolated habitats which are themselves separated from each other by dispersal barriers, creating divergence between resident populations (Zhao and Gong 2015). Barrancos (or ravines) are deep gorges with steep sides and very narrow beds. They can harbour different, often milder, climates from their surroundings, while the barranco walls may represent extreme environments, which are rocky, extremely steep, and severely lacking in soil. This means that species at the bottoms of barrancos could be physically and ecologically isolated from equivalent environments (other barranco bottoms). If populations located on highland areas separated by lowland are considered to be disconnected, then, by analogy, a population within a deep barranco may be disconnected from a population in another barranco, depending on the connectivity of the lowland environment. If some barrancos are isolated habitats, then they may have the potential to harbour relatively high levels of endemism. This is true of the valleys in the

Hengduan Mountain Region of China: they host a high diversity of plant species, of which 37% are endemic, and some species are endemic to specific valleys (Zhao and Gong 2015). This mechanism is taxon dependent, whereby more vagile species are less affected.

Barrancos can differ from each other as well as from the surrounding landscape. The environments within barrancos may become more similar to their surroundings as barrancos become shallower and less steep. Thus, topographically different barranco forms may possess very different ecological characteristics and different degrees of isolation. In addition to being more isolated, deeper barrancos (i.e., with increasing elevational difference between the barranco ridge and the barranco floor) have higher habitat heterogeneity within a small area, from the shady, relatively moist barranco bed to the steep, rocky, sun/wind exposed cliffs. Habitat heterogeneity is a well-known factor governing diversity and speciation (MacArthur and Wilson 1967, Stein et al. 2014).

Oceanic islands provide informative systems for studying the effect of topography on endemism because of their disproportionately large numbers of endemic species, many of which have evolved *in situ* (Whittaker and Fernández-Palacios 2007). Oceanic islands tend to have long topographic and climatic gradients relative to their size, which have been linked to endemic species richness (Irl et al. 2015). Substantial volcanic activity means that many high-elevation oceanic islands are topographically complex, with lava flows, land slips, and high rates of erosion carving out deep, steep-sided barrancos, and the barranco mouths are often separated by high cliffs.

Here, we analyse the effect of small-scale topography on patterns of endemic species richness in a set of barrancos on the island of La Palma (Canary Islands). La Palma is a highly suitable study site in this context because, within a small area, the topography varies drastically (Carracedo et al. 2002, Irl and Beierkuhnlein 2011) and the Caldera de Taburiente volcano complex possesses, on its outer flanks, many similar, adjacent barrancos of varying depths. Past sea-level fluctuations mean that these barrancos were once extended when the sea level was lower: with rising sea level, the open ends of the barrancos at the coast became disconnected from similar habitats, creating large cliffs and perhaps hindering dispersal between barrancos at lower elevations.

We investigate **percent endemism**, defined as the percentage of native species that are endemic (following Steinbauer et al. 2016), within different barrancos and assess its relationship with elevation and barranco depth. We use percent endemism instead of endemic richness to control for overall species richness. We focus mainly on endemism defined at the archipelago level (archipelago endemics, or AEs) but also differentiate between single-island endemics (SIEs – species that are endemic to La Palma) and multi-island endemics (MIEs – species which are endemic to the archipelago and found on at least one island other than La Palma; MIE + SIE = AE). We contrast two competing effects of topography-driven isolation on evolutionary dynamics, as follows. First, in line with recent findings (Steinbauer et al. 2016) at a larger scale (grain size), we may expect an increase in percent endemism with elevation (above sea level) of the barranco floor due to increasing isolation leading to higher speciation rates on the island and the archipelago as a whole. This predicts that (1) the floors of deeper barrancos will have lower speciation rates and lower percent endemism because they are at lower elevations. Alternatively, the isolating effect of deep barrancos may favour specialist or endemic species adapted to unique environments, whilst enhancing the survival of relict species. This would predict (2) higher percent endemism in deeper barrancos.

## Materials and Methods

### *Study area*

La Palma is located within the Canary Islands archipelago (Fig. 1). It is 708 km$^2$ in area and its highest elevation is 2426 m a.s.l. (Irl and Beierkuhnlein 2011). The climate is mild and stable all year round, but, spatially, it changes quite drastically between the north-east and south-west of the island because the trade winds approach from the north-east (Irl and Beierkuhnlein 2011). The northern part of the island is approximately 1.8 million years old and topographically complex, which is due to high levels of erosion that have formed many deep barrancos (Carracedo et al. 2002, Iohnson 2008). In contrast, the southern part of the island is much younger and subject to more recent volcanic eruptions, so the barrancos are less developed. For these reasons, our sample sites were located in the northern and north-eastern part of the island where there is a set of barrancos of varying depths, which possess similar climates and have lush vegetation on their beds. There is an abundance of endemic species on the island, most of which are well documented (Muer et al. 2016). The island contains approximately 115 vascular plant species endemic to the archipelago (AEs), 371 native non-endemics, and 238 exotics. Of the archipelago endemics, 40 are single-island endemics and 75 are multi-island endemics (Muer et al. 2016). It should be noted that there are no recorded SIEs that are endemic to a single barranco, though one species, *Echium bethencourtii*, is known to be endemic to the barranco floors of the study area.

### *Data Collection*

Species presence–absence data were recorded in 75 plots across 7 different barrancos. We attempted to sample barrancos only in the north of the island, but as many were too difficult to access on foot, we included an additional barranco in the north east (barranco 7, fig 1b). The number of plots varied between barrancos due to the difficulties of access (see Table 1). Within each barranco, 2m x 11m plots were placed along a transect following the barranco bed and were placed on alternate sides of the barranco where possible (fig 2). The length of the transect depended on the accessibility of the barranco: transects were sometimes cut short, usually because of large cliff faces eroded by waterfalls. Once we determined the length of the transect, we then set out plots that were evenly spaced. Plots were situated just above the barranco floor. We avoided the riverbed so as to exclude the disturbances associated with occasional river flows (the barrancos are dry most of the time). From the coast inwards, the barranco floors follow an increasing elevational gradient; thus, across all barrancos, we were able to sample an elevation gradient from 95m to 674m. Elevation was recorded at each plot using a handheld GPS (Garmin Oregon® 600). Most species were identified in the field, but for those about which there was any doubt we collected specimens and identified them within three days, with the help of experts. There were 5 individuals for which we could not get an accurate ID, so we removed these from the data set (this made no detectable change to our results). Species were categorised as SIE (single-island endemic), MIE (multi-island endemic), and AE (archipelago endemic, i.e., either SIE or MIE) using Muer et al. (2016). Species richness and percent endemism (pAE, pSIE and pMIE) were calculated for each plot and barranco (Table 1.).

### *Barranco metrics*

Barranco depth was calculated as the difference between the barranco floor and the lowest ridge using the elevation profile in Google Earth. This was calculated in four different ways. First, we calculated depth as a single average measurement for each barranco by measuring depth at 10 evenly spaced points along the barranco, starting at the coast and ending at approximately 600m in elevation (as this is the highest elevation we could reach with our plots) and taking the median value. We refer to this as average barranco depth. Second, because our plots span different ranges in each barranco, we calculated average depth using only the area of the barranco that was sampled by the plots. Again, we measured depth at 10 evenly spaced points along the barranco, but this time only between the first and last plots in each barranco, and used the median value. We refer to this as average sample depth. Thirdly, we measured depth at each individual plot and refer to this as plot depth. Finally, we used the maximum depth value for each barranco. Maximum depth was obtained by using the highest depth value for each barranco that was calculated from any of the above measurements. Thus, we have four measurements for barranco depth: average barranco depth, average sample depth, plot depth, and maximum depth (see Figure 2).

As an alternative measure of isolation, we quantify barranco shape using the height to width ratio (HWR), where higher HWR indicates narrower or steeper-sided barrancos, which we assume are more isolated. The HWR was calculated using following formula adapted from Bull and McFadden (1977):

$$HWR = log_{10}\left(\frac{arh}{2dr}\right)$$

where $arh$ = average height of both ridges and $dr$ = the distance between the left and right ridges. These parameters were calculated using elevation profiles in Google Earth. Cross-sections were placed at 10 points along each barranco to get a topographical profile, and the measurements were extracted, and an average value calculated for each barranco. Narrow, deep barrancos have high HWR values, whereas broad, shallow barrancos have low values. Post-field work, we were able to calculate barranco depth at every plot, except barranco 3 where GPS coordinates are missing. HWR was scaled before further analysis. HWR was highly correlated with barranco depth ($r$=0.98, $P$<0 .001), indicating that the barrancos are all very similar with respect to how shape relates to depth, so we do not consider it further.

*Statistical Analyses*

We tested the hypothesised effects of barranco depth and elevation on pAE, pMIE, pSIE, and species richness using four generalised linear mixed-effects models with binomial family errors for proportions (pAE, pMIE, pSIE) and Poisson errors for count data (species richness). We tested each barranco depth metric separately in the models. The influence of elevation on percent endemism was calculated for all barrancos combined, so, here, the sampling unit is the barranco. Therefore, each plot represents a pseudoreplicate within each barranco. For this reason, we used barranco as a random effect, allowing the intercept to vary. Depth and elevation were scaled and included as predictor variables in the models. For the plot depth measurement, barranco 3 was also removed as no GPS points were available for this barranco to accurately calculate depth for the plots. Pearson's product moment correlation (r) was used to check the correlation between plot depth and elevation within each barranco.

As the number of plots varied between each barranco, we wanted to be sure that this would not affect our results. Therefore, as the minimum number of plots in a barranco was 6, we ran the above analysis using only 6 plots per barranco (for barrancos with more than 6 plots, we randomly sampled sets of 6 from the available ones). See Supplementary Table S2. All analysis were performed using R version 3.4.2 (R Core Team 2017). Mixed effects models were performed using the R package 'lme4' (Bates et al. 2015). The amount of variation accounted for by the predictor variables was quantified using pseudo-$R^2$ as calculated using the function r.squaredGLMM in the R package 'MuMIn', which returns a revised statistic based on (Nakagawa et al. 2013).

## Results

Overall, we recorded 180 species in the 75 plots, of which 67 were endemic to the Canary Islands (AE; 10 SIE and 57 MIE), 105 were native but not endemic, and 8 were exotic. The total number of native plant species on La Palma is 486. Therefore, we captured a considerable proportion of the entire flora in a small sampled area of the spatially rare habitat at the bottom of isolated barrancos.

Average barranco depth ranged from 56m to 299m; average sampled depth ranged from 37m to 299m. Maximum depth ranged from 73m to 422m, and the HWR ranged from 1.84 to 2.54 (Table 1). We found a positive correlation between plot depth and elevation in barranco 1 ($r$=0.77, $P$= 0.001), 2 ($r$=0.58, $P$=0.39), 4 ($r$= 0.91, $P$<0.001) and 8 ($r$=0.89, $P$=0.001) (fig 3).

We did not find a significant increase in pAE, pMIE, or pSIE with increasing barranco depth (Table 2, fig 4). This was true for all depth measurements (average barranco depth, average sample depth, plot depth, and maximum depth), with one exception: pMIE increased significantly with plot depth (Table 2; slope=-0.27±0.11, $P$=0.018, $R^2$=0.055). Using plot depth in the models lowered the AIC values compared with models using alternative depth measurements.

We found a significant decrease in pAE and pMIE with elevation, while the decrease for pSIE was not significant (fig 5; see Table 2 for model outputs). When assessed individually with models, the relationship between pAE and elevation was significantly negative for barrancos 4 (slope=-0.007±0.003, $P$=0.012, $R^2$=0.44), 6 (slope=-0.004±0.002, $P$=0.045, $R^2$=0.69), and 7 (slope=-0.021±0.002, $P$<0.001, $R^2$=0.92). The remaining barrancos showed no significant relationship (fig 6). Species richness models showed a significant decrease in species richness with elevation but no significant relationship with depth (fig. 7). When barrancos were modelled separately, the negative relationship with elevation was significant for barrancos 2 (slope=-0.002±0.0004, $P$=0.002, $R^2$=0.59) and 6 (slope=-0.008±0.001, $P$=0.005, $R^2$=0.90).

We used binomial family errors for the pAE, pMIE, and pSIE generalized linear mixed-effects models because the response variables were proportions. As this accounts for the differences in species richness, the resulting $R^2$ values are extremely low due to the higher weighting of plots with high species richness. Using a linear mixed effects model with a Gaussian distribution produced higher $R^2$ values; we report these results in the supplementary Table S1).

## Discussion

On a global scale, archipelago endemics have been shown to increase with elevation (Steinbauer et al. 2016), but looking more closely at small-scale topographic variation may reveal more intricate patterns of endemism. We documented a decrease in the percent endemism with increasing elevation, a result that opposed our first prediction derived from previous studies. We also did not find an effect of barranco depth on percent endemism.

Using four different measures of barranco depth, at the plot level and the barranco level, we were unable to detect an effect of depth on percent endemism or species richness both within and between barrancos. It may be that such small-scale topography provides insufficient isolation or the isolation has not persisted long enough for speciation to occur within the barrancos, which could explain why there is just one barranco endemic. The relationship between barranco depth and elevation is strongly intertwined: barranco depth increases with elevation initially, as the barrancos carve into the mountain sides and then begins to decrease until the barrancos eventually disappear, merging and levelling out towards the sides of the caldera. Thus, the relationship between depth and elevation should be a unimodal one. Within our sample area, we capture the initial increase in depth with elevation and, although non-significant, we begin to see a decrease in depth in our most highly elevated barranco (barranco 6; fig 3). Detecting a relationship between percent endemism and depth is difficult as the variable is collinear with elevation. Although non-significant, depth shows weak positive relationships with endemism (fig 4). Future work could aim to tease apart these variables.

We find an increase in percent endemism (pAE and pMIE) with decreasing elevation. Higher habitat heterogeneity, through increased topographic complexity, may explain why we find this pattern, as the barrancos become more pronounced at lower elevations. The steep topography creates areas of light and shade, hot and cold, and dry and moist habitat, as well as extreme habitats like the steep, eroded barranco walls. High habitat heterogeneity and steep environmental gradients increase the number of niches, resulting in adaptation to diverse environmental conditions increasing the probability of speciation (Golestani et al. 2012, Stein et al. 2014, Huang et al. 2017). Furthermore, areas with high habitat heterogeneity are more likely to provide refuge for species during past climatic change, allowing species to persist (Fjeldså et al. 1999, Kallimanis et al. 2010, Harrison and Noss 2017). The northern part of La Palma is the oldest part of the island and may be a potential refuge for endemics that evolved under past environmental conditions.

Furthermore, due to cold air pooling, the temperatures at barranco bottoms are cooler than normally expected at low elevations (Geiger et al. 2003, Dobrowski 2011); thus, high-elevation species are perhaps able to survive at lower elevations in barrancos. This may result in asymmetric dispersal down the barrancos but not up. Indeed, we did find that laurel forest species were present at lower elevations in the barrancos. Furthermore, barranco habitat may be important for dispersal between islands. The dispersal of high-elevation endemics is hindered by elevation-driven isolation, whereby species become more isolated at higher elevations due to the increasing remoteness from equivalent habitats (Steinbauer et al. 2016). The suitable habitat provided in these barrancos at low elevations may act as stepping-stones for endemics dispersing from high elevation zones on other islands, thereby lessening elevation-driven isolation in these environments. An alternative reason why we find more AEs at lower elevations in the barrancos might be due to the prevalence of this unique habitat. The barranco bed habitat is common in the Canary Islands but relatively rare beyond the archipelago. This may allow speciation to build up and persist through time.

In our sample area, we found that exotic species make up only 4% of species. Previous work on La Palma found the proportion of exotics (non-natives) to peak at an elevation of 500m, after which there is a strong decrease with increasing elevation (Steinbauer et al. 2017). As we sampled up to an elevation of 674m, the majority of our study area is located near the peak range for exotic species, indicating that exotics are largely excluded from the barrancos. As well as exotic plants, barrancos may also restrict the access of exotic herbivores to certain areas, particularly the steep barranco sides, which may act as refugia from exotic herbivores that preferentially feed on endemic plant species (Cubas et al. 2019).

The pattern we observed between endemism and elevation may not be representative of the entire elevation gradient as our plots only reach 674m a.s.l., whereas the highest elevations on La Palma are in excess of 2000m. Using elevational belts, Steinbauer et al. (2016, 2017) found an overall increase in the percentage of AEs with elevation on La Palma, but in a non-linear manner, with a slight dip in endemism at approximately 500m, consistent with our result. With regard to species richness, we find the same pattern: species richness decreases with elevation. This is not unexpected and may be due to the decrease in area with elevation. This follows similar patterns reported for many taxa of either a monotonic decrease or a humped-shaped relationship (Rahbek 1995).

Although we found no significant effect of barranco depth on percent endemism, we argue that the role barrancos play in the diversity and evolutionary dynamics of endemics species warrants further investigation within the Canary Islands and elsewhere, not least because of the relatively restricted elevation gradient we studied here and the co-linearity with elevation. Future work may also consider the different geological ages of barrancos, although in this study system age variation is unlikely due to their close proximity to each other. Barrancos appear to be rich in endemic species not only on La Palma but also on other islands in the Canaries, where the highest densities of endemics occur on steep slopes (Otto et al. 2016).On El Hierro, for example, endemics are primarily found on the rocky, steep sites made up of old bedrock (Von Gaisberg and Stierstorfer 2005). Considering the fact that the accessible area of the barrancos is very limited due to the extremely steep slopes and the rugged scarps forming waterfalls in times of run-off, the recorded number of species and endemics in these isolated barrancos is remarkable. Whether or not the depth of the barrancos plays a role in endemism, the presence of barrancos themselves may be important in offering a unique habitat for endemics and may explain why we see fluctuations in elevation–endemism gradients.

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## Author Contributions

All authors developed the central ideas. V.C, N.K, and C.L collected data in the field. V.C, R.F, A.C.A, and M.J.S analysed the data and prepared the manuscript. All authors provided comments on the final manuscript.

## Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb

**Table S1.** Model outputs from linear mixed effects models.

**Table S2.** Percentage of models that were significant  for elevation and depth after randomly sampling 6 plots from each valley 100 times.

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**Table 1.** Characteristics of each barranco in ascending order of percent endemism. Barranco ID corresponds to the barranco ID in Fig. 1. HWR = height to width ratio, SR = total species richness, which comprises: AE = archipelago endemics (further split into multi-island endemics [MIE] and single-island endemics [SIE]), NEN = non-endemic natives, Exo = exotics. Percent endemism was here calculated at the barranco level, as 100*AE/(AE+NEN).

| Barranco ID | No. of plots | Average barranco depth (m) | Average sample depth (m) | Maximum depth (m) | Elevation range sampled (m) | HWR | SR | AE | MIE | SIE | NEN | Exo | Percent endemism |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | 6 | 141 | 135 | 193 | 181 | 2.16 | 52 | 14 | 11 | 3 | 35 | 3 | 29 |
| 5 | 6 | 132 | 178 | 215 | 91 | 2.14 | 33 | 9 | 7 | 2 | 22 | 2 | 29 |
| 3 | 10 | 269 | 299 | 390 | 174 | 2.48 | 91 | 34 | 28 | 6 | 52 | 6 | 40 |
| 1 | 14 | 210 | 211 | 353 | 305 | 2.30 | 109 | 43 | 34 | 9 | 62 | 4 | 41 |
| 2 | 13 | 219 | 233 | 306 | 414 | 2.34 | 93 | 37 | 29 | 8 | 53 | 3 | 41 |
| 7 | 9 | 160 | 166 | 228 | 84 | 2.27 | 68 | 29 | 24 | 5 | 35 | 4 | 45 |
| 4 | 14 | 299 | 275 | 422 | 206 | 2.54 | 88 | 44 | 36 | 8 | 41 | 3 | 52 |

**Table 2.** Model outputs from generalised linear mixed effects models. Barranco was included as a random factor (intercept) in all models. pAE = percentage of archipelago endemics, pMIE = percentage of multi-island endemics, pSIE = percentage of single-island endemics, SR = species richness.

| **Model** | **Slope** | | | | **Intercept** | ***P*** | $R^2$ | **AIC** |
|---|---|---|---|---|---|---|---|---|
| | **Elevation** | ***P*** | **Depth** | ***P*** | | | | |
| pAE ~ elevation + average valley depth | -0.27±0.08 | <0.001*** | 0.11±0.09 | 0.216 | -0.46±0.07 | <0.001*** | 0.034 | 326.1 |
| pAE ~ elevation + average sample depth | -0.03±0.08 | <0.001*** | 0.01±0.09 | 0.898 | -0.46±0.08 | <0.001*** | 0.032 | 327.5 |
| pAE ~ elevation + plot depth | -0.17±0.28 | 0.550 | -0.25±0.23 | 0.243 | -0.50±0.22 | <0.022* | 0.064 | 265.6 |
| pAE ~ elevation + maximum depth | -0.28±0.07 | <0.001*** | 0.10±0.08 | 0.237 | -0.47±0.07 | <0.001*** | 0.034 | 326.2 |
| pMIE ~ elevation + average valley depth | -0.32-±0.09 | <0.001*** | 0.04±0.10 | 0.663 | -1.04±0.08 | <0.001*** | 0.040 | 302.0 |
| pMIE ~ elevation + average sample depth | -0.35±0.09 | <0.001*** | -0.04±0.11 | 0.694 | -1.03±0.09 | <0.001*** | 0.038 | 302.0 |
| pMIE ~ elevation + plot depth | -0.25±0.13 | 0.064 | -0.27±0.11 | 0.018* | -1.01±0.14 | <0.001*** | 0.055 | 244.6 |
| pMIE ~ elevation + maximum depth | -0.33±0.09 | <0.001*** | 0.03±0.10 | 0.754 | -1.04±0.09 | <0.001*** | 0.040 | 302.1 |
| pSIE ~ elevation + average valley depth | -0.03±0.12 | 0.813 | 0.17±0.16 | 0.275 | -2.03±0.14 | <0.001*** | 0.023 | 221.3 |
| pSIE ~ elevation + average sample depth | -0.04±0.12 | 0.710 | 0.12±0.16 | 0.436 | -2.03±0.14 | <0.001*** | 0.020 | 221.9 |
| pSIE ~ elevation + plot depth | -0.13±0.12 | 0.293 | 0.13±0.12 | 0.276 | -2.01±0.15 | <0.001*** | 0.024 | 184.0 |
| pSIE ~ elevation + maximum depth | -0.04±0.12 | 0.707 | 0.18±0.15 | 0.249 | -2.03±0.13 | <0.001*** | 0.023 | 221.1 |
| SR ~ elevation + average valley depth | -0.21±0.05 | <0.001*** | 0.03±0.10 | 0.768 | 2.87±0.09 | <0.001*** | 0.631 | 534.3 |
| SR ~ elevation + average sample depth | -0.21±0.05 | <0.001*** | 0.02±0.10 | 0.848 | 2.87±0.09 | <0.001*** | 0.628 | 534.3 |
| SR ~ elevation + plot depth | -0.25±0.06 | <0.001*** | 0.09±0.05 | 0.061 | 2.90±0.11 | <0.001*** | 0.704 | 447.6 |
| SR ~ elevation + maximum depth | -0.20±0.05 | <0.001*** | 0.08±0.09 | 0.812 | 2.88±0.09 | <0.001*** | 0.636 | 533.7 |

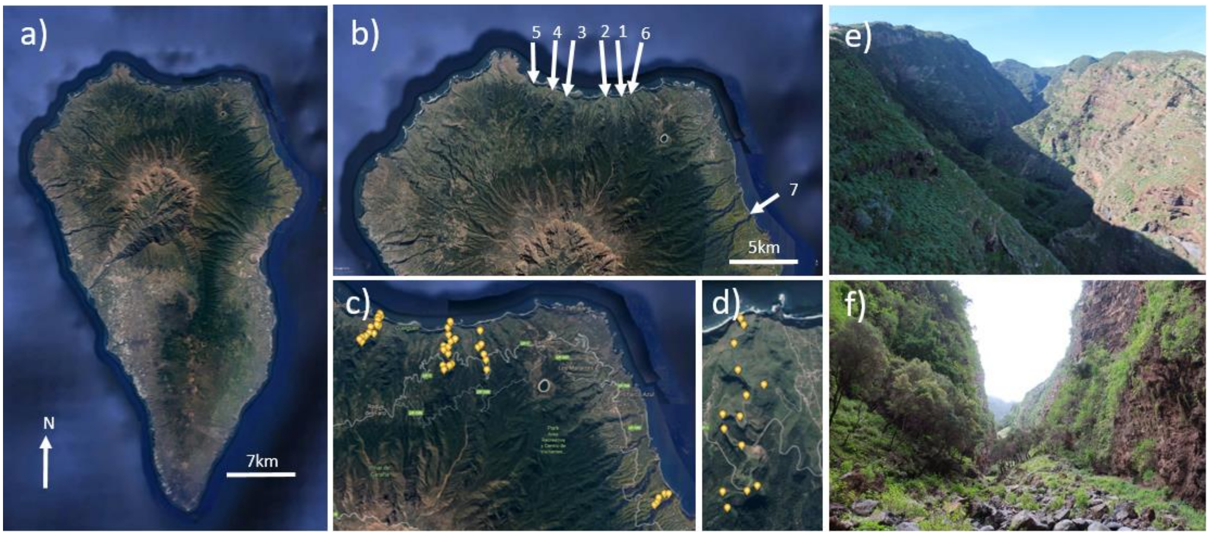

**Figure 1.** Maps of La Palma and the study area. a) Map of La Palma Island. b) View of the northern part of the island with the location of the barrancos labelled with their ID. Plot locations are shown for some of the barrancos in c). As an example, the plot spacing in barranco 2 is shown in d). Orientation (north) is the same in all panels. Images obtained from Google Earth Pro v 7.3.1.4507 (14/12/2015) 28°42’48.18”N, 17°54’20.81”W. Images of two different barrancos are shown in e) and f). Photo credit: Vanessa Cutts and Caroline Löwer.

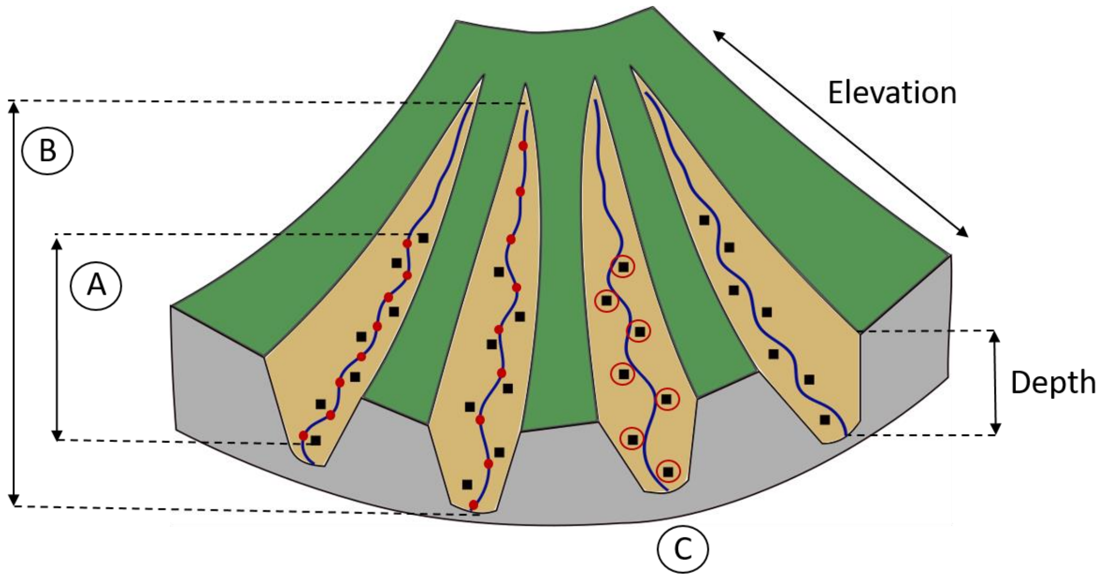

**Figure 2.** Schematic diagram depicting four barrancos situated on the flanks of the volcano. Black squares represent plots and the blue lines represent the floor of the barranco (which is now dry). Red dots and circles indicate where depth measurements were taken. Cases A-C illustrate the different depth measurements: A) average sample depth, where depth was measured at intervals between the first and last plot and an average taken, B) average barranco depth, where the depth was measured at intervals across the entire barranco and averaged, 3) plot depth, where the exact depth at each plot was considered. Maximum depth for each barranco was calculated as the maximum depth found from each of the other three depth measurements. The barranco on the right shows the elevation and depth gradients.

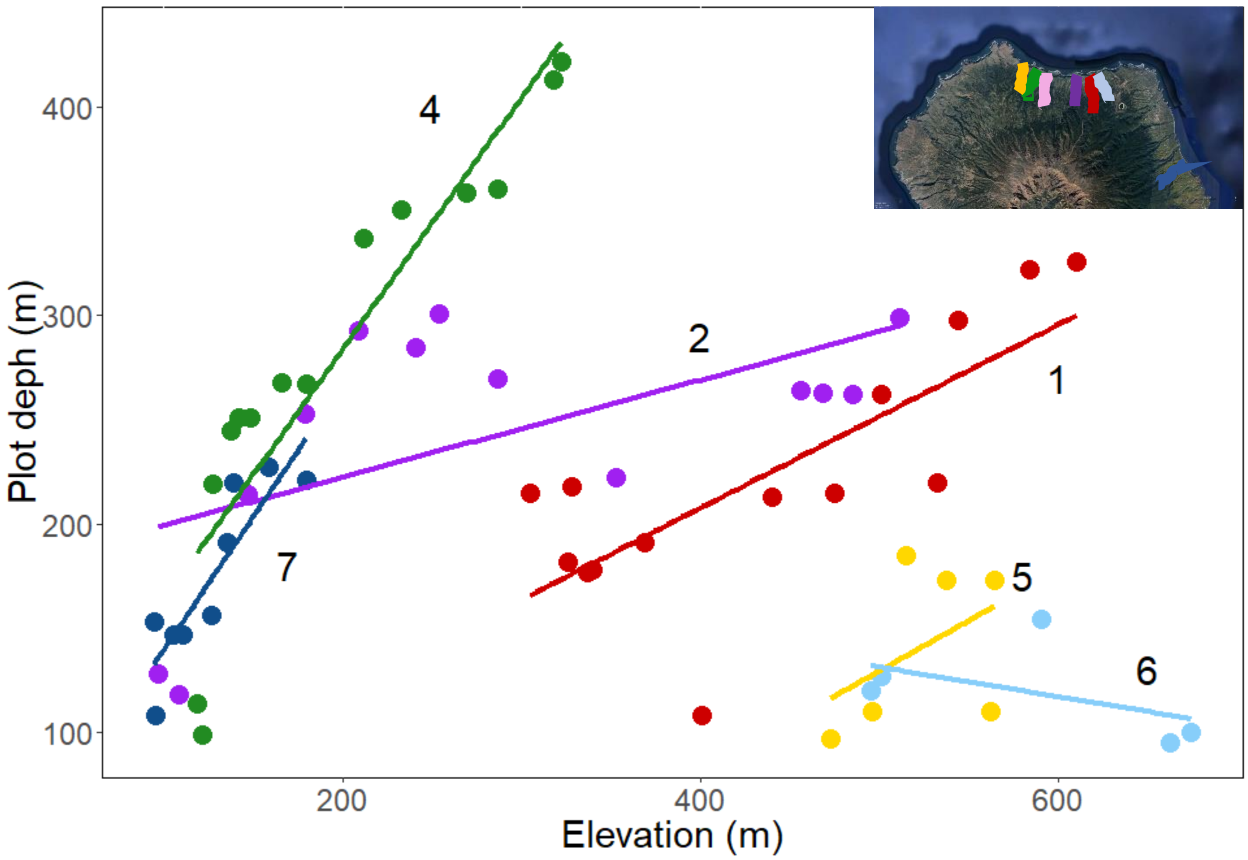

**Figure 3.** Significant positive correlations were found between plot depth and elevation for barranco 1 (*P*=0.001, *r*=0.77), 2 (*P*=0.039, *r*=0.58), 4 (*P*<0.001, *r*=0.91) and 8 (*P*=0.001, *r*=0.89). Each line is labelled with the corresponding barranco ID, which is synonymous with barranco ID in Table 1. Barranco 3 is not included in the scatter plot due to missing GPS points. The map in the top right corner show the location of the barrancos: colours match the correspond lines on the graph.

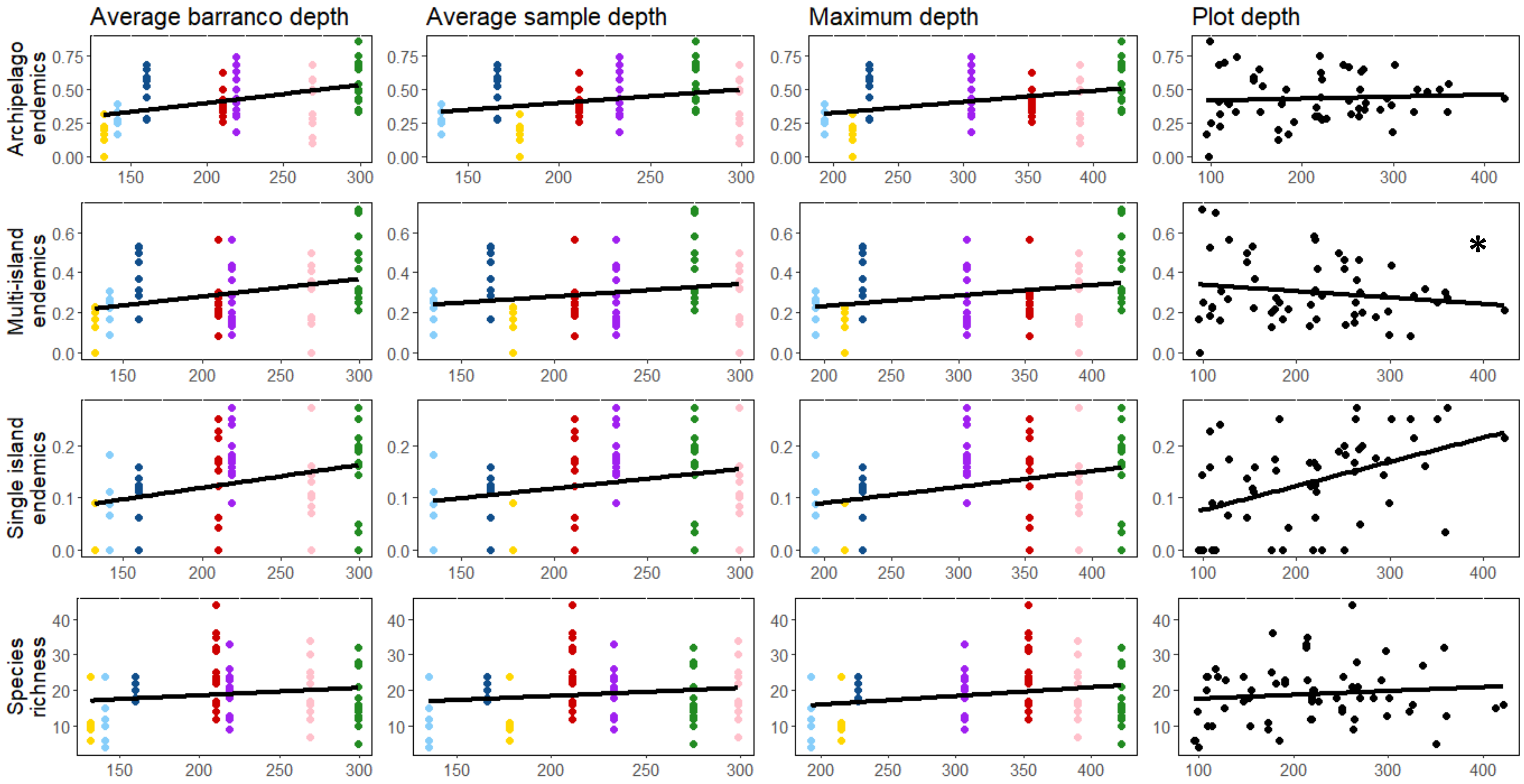

**Figure 4.** The observed relationships between percent endemism (AE, MIE, AIE) and all four depth metrics. The bottom row shows the relationship between species richness (SR) and depth. Relationships are not significant with the exception of MIE and plot depth (*P*= 0.055), denoted with *****. Points are coloured by barranco, which correspond to the colours in figure 3.

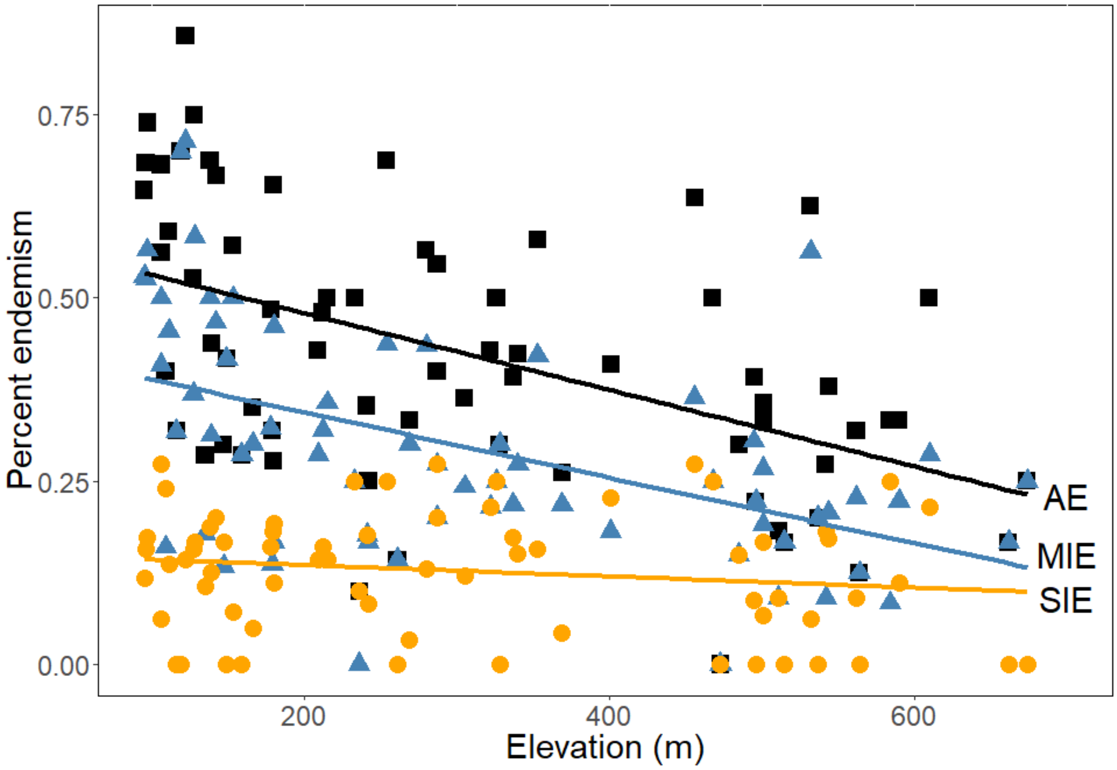

**Figure 5.** The observed relationships between percent endemism (AE, MIE, AIE) and elevation. Both AE and MIE show significant relationships with elevation (*P*<0.001), except when plot depth is included in the model. SIE shows no relationship with elevation. See Table 2 for model outputs.

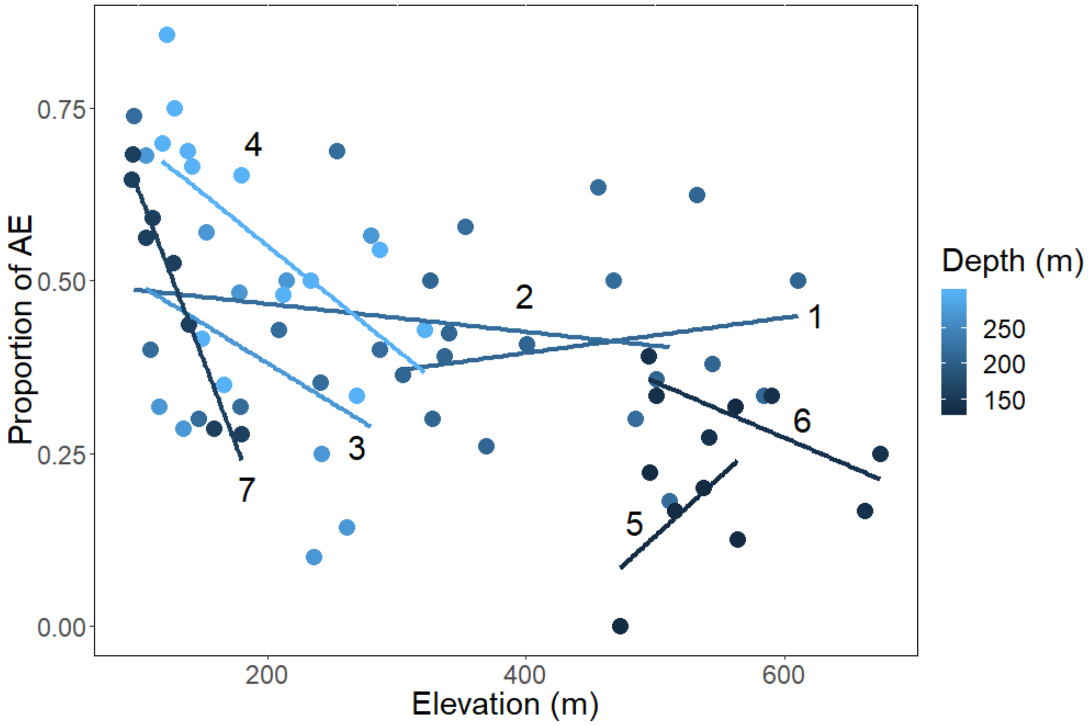

**Figure 6.** The relationship between pAE and elevation for each barranco. General linear models showed that pAE decreased significantly for barrancos 4 (slope=-0.007±0.003, $P$=0.012, $R^2$=0.44), 6 (slope=-0.004±0.002, $P$=0.045, $R^2$=0.69) and 7 (slope=-0.021±0.002, $P$<0.001, $R^2$=0.92). The relationship was not significant for the remaining barrancos. The colour scale reflects the change in average depth sampled between the barrancos, with lighter colours indicating deeper barrancos and darker colours indicating shallower barrancos. Although each barranco is situated on a different part of the elevational gradient, the general trend shows a decrease in pAE with elevation. Numbers indicate the barranco ID.

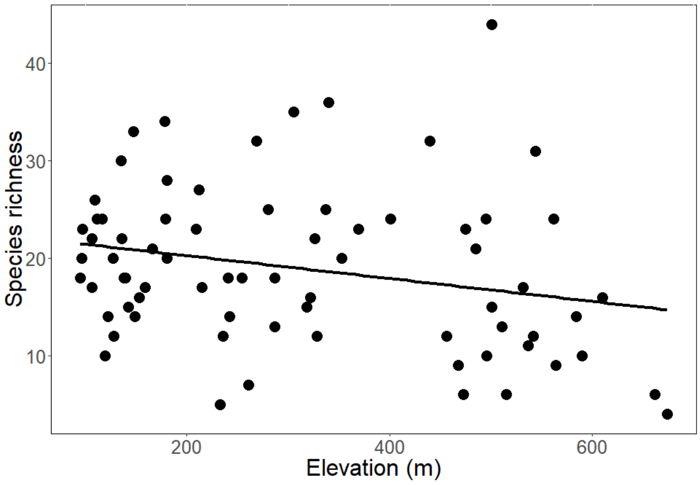

**Figure 7.** The relationship between species richness and elevation is a decreasing one (P<0.001).