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Elevation and Soil Properties Determine Community Composition, but Not Vascular Plant Richness in Tropical Andean Roadside

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Abstract: Roadsides are common ecosystems worldwide, with specific environmental characteristics and multiple effects on plant diversity. As such, they represent examples of highly dynamic anthropogenic ecosystems. Our objective was to assess patterns of vascular species diversity in response to elevation and soil characteristics on a roadside in the Andean mountains of Ecuador. The study area was located in the southern Ecuadorian Andes, at five elevations ± 400 m a.s.l. (2600, 2200, 1800, 1400 and 1000 m a.s.l.), where we recorded species richness and abundance in transects perpendicular to the road. The effects of elevation and soil characteristics on species abundance and richness were analyzed using generalized linear mixed models (GLMMs), while species composition was assessed with a non-metric multidimensional scaling analysis (NMDS) and its relationship to environmental variables. We used indicator species analyses (ISA) to identify which species significantly characterized specific elevation and soil factors from primary succession for restoration processes at the roadside. Although elevation and soil characteristics do not condition vascular species richness, the composition is more similar at elevations E1 and E2 (2600 m and 2200 m a.s.l.), differing from low elevations E4 and E5 (1400 m and 1000 m a.s.l.), which in turn are more similar to each other, while intermediate elevation E3 is similar to the highest and lowest elevations. Soil variables that limited plant communities were pH, bulk density (gr/cm^3), silt (%), and sand (%) contents. The indicator species showed a preference for specific environmental and soil condition requirements associated with the different microhabitats and, thus, can be suggested for potential use in roadside revegetation processes in tropical areas. These results can help decision-makers in the implementation of biodiversity conservation and roadside environmental restoration projects in areas of Andean mountain ecosystems which have been affected by the construction of road infrastructure.

Keywords: altitude; mountainous region; microhabitat; beta diversity; indicator species; edaphic characteristics

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1. Introduction

In recent decades, ecologists and environmental restoration practitioners have agreed that successful restoration requires a solid scientific foundation grounded in an understanding of ecological principles [1–3]. Therefore, understanding how species assemble, function, and interact with environmental and soil factors is necessary for the development of ecosystem restoration projects [4,5]. In addition, areas degraded by road infrastructure have become a matter of scientific concern [6,7], due to the advancement of road networks and the negative ecological impacts caused to the landscape, such as habitat fragmentation, soil erosion, edge effects, and alien species invasion [7–12]. Consequently, roadsides represent an ideal scenario for studying the influence of environmental filters on the composition of plant communities [13], and, at the same time, they represent a great challenge for ecological restoration and selection of the most appropriate species in road revegetation processes [14].

Studies on roadside colonization reveal that plant establishment in the early stages follows a process of primary succession, whereby the floristic composition is mainly shaped by the arrival of diaspores from nearby communities [15,16]. Once diaspores have reached exposed slopes, abiotic conditions represent the first limiting filter for plant recruitment [17,18]. Furthermore, elevational gradients in mountainous areas are often composed of a series of complex biotic and abiotic changes that affect species distribution [19], such as temperature decrease, which favors plant growth, and elevation, which acts as a filter for plant species richness and abundance [2,20–23]. At a general level, investigations of roadside plant richness have suggested various patterns in response to biotic and abiotic changes associated with altitude [2,24]. For example, previous research generally reports that richness decreases with elevation [1,25,26]. However, other studies indicate that species richness has a hump-shaped response to elevation, and that patterns are different for native and non-native species [3,27].

On the other hand, on a small scale, other species distribution patterns are associated with physical and chemical soil conditions, such as a lack of nutrients in coarse-textured soils, high stoniness [28], a lack of organic matter [29], and highly consolidated bedrock [30], all of which will influence a suitable substrate for the establishment of plant diversity [29]. Thus, it has been reported that soil moisture, organic matter content, bulk density, and pH, change significantly along roadsides, which affects the composition of the plant community [31–34]. However, the ecological functioning of roadside plant communities has been little studied [6,18]. Most of the investigations that describe the altitudinal distribution of roadside species have been carried out in temperate ecosystems [3,22,24,35,36], including limited studies in the Neotropical region [1,23–25].

Currently, only one study evaluated changes in plant diversity on roadside in northern Ecuador related to elevation; however, soil physicochemical properties were not included in this study to understand plant diversity and responses along an elevation gradient. Therefore, new studies that provide more data are required, since roadsides are anthropized ecosystems that contain unique environmental, topographical, and edaphic characteristics [27]. In this context, to obtain information on the effect of elevation and soil edaphic factors on the occurrence and distribution of vascular species along an altitude gradient that goes from 2600 m to 1000 m a.s.l. at roadside located in Andean Mountain biomes, our research determined the following: (1) the diversity of roadside vascular species; and (2) the effect of elevation and edaphic factors on the distribution of species at the roadside. The data from this study can be used to generate an ecological base that serves for the selection of species in different microsites generated by the altitudinal gradient and by the characteristics of the soil. Knowledge of these potentially beneficial processes can be used for road revegetation in Andean biomes.

2. Materials and Methods

2.1. Study Area

The study was carried out between November 2019 and June 2020 in the Andes of southern Ecuador, in the province of Zamora Chinchipe, on the Zamora-Loja road. The altitude gradient goes from 2600 m to 1000 m a.s.l. (Figure 1). The experimental area is characterized by similar slopes between concave and convex topography, which defines its floristic composition and forest structure [37]. Bioclimatic data for annual temperature (°C), and total annual precipitation (mm), were extracted from Worldclim ([38], Table 1).

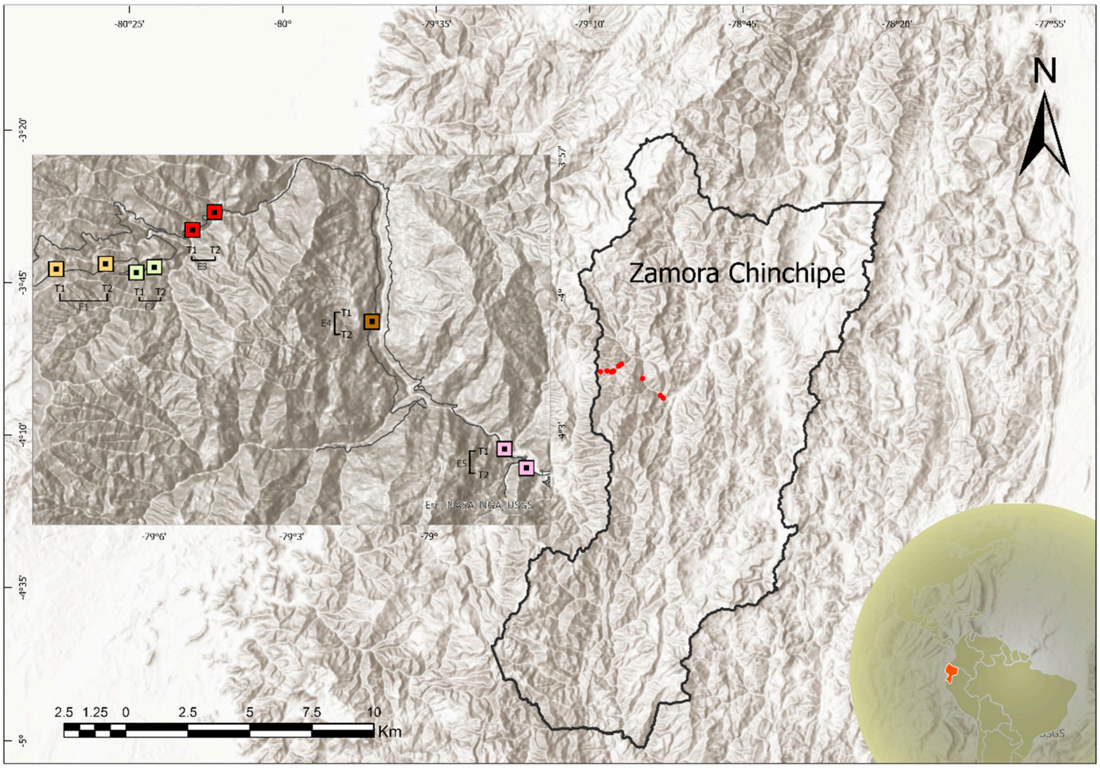

Figure 1. Study area in the southern Ecuadorian Andes, throughout the altitudinal gradient 2600 m to 1000 m a.s.l. on the Zamora-Loja road, covering the five elevations (E1–E5), with the location of two transects per elevation.

Table 1. Mean values of environmental variables for different elevation levels (E1–E5) and the type of ecosystems present in the study area.

Variable/Elevation	E1	E2	E3	E4	E5
Altitude (asl)	2.600	2.200	1.800	1.400	1.000
Temperature (°C)	14.2 ± 0.45	14.9 ± 0.00	17.3 ± 0.13	20.5 ± 0.00	23.0 ± 0.22
Precipitation (mm)	1 148.5 ± 19.50	1 101 ± 3.00	802 ± 0.00	1 027 ± 0.00	1 581 ± 65.00
Ecosystem	BSMN02	BSMN02	BSMN02	BSBN02	BSBN02

According to the Classification System of Terrestrial Ecosystems for Continental Ecuador [39], the vegetation is characterized ecologically as containing an evergreen montane forest at the Southeastern Cordillera of the Andes (BSMN02), and an evergreen low montane forest at the Southeastern Cordillera of the Andes (BSBN02). Selected roadsides are characterized by moderately steep slopes (20%–30%), that were measured with a clinometer (PM-5/360 PC Clinometer, Suunto, Finland).

2.2. Design and Data Collection

Along the studied path, five zones with different elevations were considered, which were separated ± 400 m.a.s.l. from one zone to another (2600 m.a.s.l., 2200 m.a.s.l., 1800 m.a.s.l., 1400 m.a.s.l., 1000 m.a.s.l.). In each area, two replicas were considered, which in turn were located at ± 100 m.a.s.l. from each other (Figure 1). For each elevation (E1–E5), two 10 m^2 (2 m × 5 m) transects were established perpendicular to the road [40]. The length was measured from five linear meters from the edge of the road. Each transect was subdivided into 10 nested plots of one square meter, of which five nested plots were considered for sampling (2, 4, 6, 8 and 10). A total of 10 transects were installed, and 50 1 m^2 nested plots were sampled. The frequency and abundance of the species were quantified in each nested plot, using a 1 × 1 m^2 frequency grid (made of wood), divided into 0.10 × 0.10 cm^2 cells [41]. The native and non-native species were taxonomically identified in situ, and those that could not be identified were collected for comparison with the collections in the Herbarium of the Universidad Técnica Particular de Loja (HUTPL).

2.3. Soil Sampling and Laboratory Analytical Methods

To determine soil quality, samples were taken from each transect and the odd nested plots (1, 3, 5, 7 and 9) to avoid mechanical damage to the plants sampled in the even-numbered nested plots. Sampling for bulk density (BD) consisted of taking a sample from each odd plot at a depth of 0–5 cm by using standardized metallic cores (5.5 cm in diameter, 4 cm in height, 95 cm^3 in volume). Therefore, 10 individual samples were obtained for BD analysis at each elevation gradient, giving a total of 50 samples. Sampling for texture, pH, and macronutrient content consisted of using standardized metal cylinders (6 cm diameter, 10 cm height, 283 cm^3 volume) at a depth of 0–10 cm [42], obtaining five subsamples for each sampling site. The subsamples were mixed to obtain a composite sample, obtaining 2 samples for each altitudinal gradient and 10 composite samples in total.

In the laboratory, BD was first determined using the cylinder method, for which individual BD samples were oven-dried for 48 h at 105 °C [43]. Samples for the determination of texture, pH, and macronutrient contents were dried at room temperature for 72 h. Subsequently, all visible roots were removed, and the samples were sieved through a 2 mm mesh. Soil texture was determined using the Bouyoucos-hydrometer method [44], while the soil pH was measured with a pH meter using the standard method [44]. In addition, soil organic carbon (SOC) and soil organic matter (SOM) were determined using the Walkley and Black method [45], for which the sample was placed in an oven at 125 °C for 45 min, after oxidation in a solution of K2Cr2O7/H2SO4. Total nitrogen (TN) was determined by the Kjeldahl method, phosphorus content (mg/kg) by the modified Olsen method [46], and potassium content (cmol/kg) by atomic absorption spectrophotometry [47].

2.4. Data Analysis

Species richness was defined as specific richness at plot level. A rarefaction curve based on samples and a Chao 2 non-parametric richness estimator was used to determine the sampling effort at each elevation. To visualize changes in species richness, a box plot was performed.

The effects of altitude and soil variables on richness and abundance were analyzed separately using generalized mixed linear models (GLMMs) at plot level. In these models, altitude and soil physicochemical properties (PCA1 and PCA2) were used as predictors (fixed factors), whereas locality were included as random sources of variation. We assumed Poisson errors for the response variables with the log link function. Effects of random factors were tested using the Wald Z-statistic test, and GLMMs were fit using package "lme4" with the function "glmer" [48]. Following Bolker et al. [49], we used the Laplace approximation for likelihood estimates. For GLMMs, the minimal adequate model was selected based on Akaike's information criterion (AIC). Before GLMMs, a principal component analysis (PCA) was performed for the soil variables to avoid linearity effects. The residuals of the models were checked to verify that the assumptions of normality and homoscedasticity were met. Differences in plant community composition were observed by non-metric multidimensional scaling analysis (NMDS), using the Bray-Curtis distance and 999 Monte Carlo permutations. To analyze the effect of environmental variables (elevation, slope, and soil variables), a correlation between the two fitted axes and the environmental variables was performed with the "envfit" function. Finally, an indicator species analysis (ISA) [50] was carried out to determine the indicator species of primary succession in the restoration processes in the roadside. All statistical analyses were carried out using R software and functions in the package "vegan" [51].

3. Results

We recorded a total of 22 families represented by 44 genera and 54 native species, of which two were endemic (*Chusquea loxensis* and *Neurolepis laegaardii*) along the altitudinal gradient ranging from 2600 to 1000 m.a.s.l. The maximum species richness occurs in gradients E1 and E4 with 24 species each, followed by E2 and E5 with 21 and 20 species, respectively, and finally E3 with 18 species (Appendix A). Of the 22 families, the most diverse were as follows: Poaceae (15%) Orchidaceae (12%), Asteraceae (10%), Melastomataceae (8%), Lycopodiaceae (7%), and Ericaceae (7%). In contrast, the least diverse were as follows: Pteridaceae, Polygonaceae, and Polipodiaceae, with a representativeness of (2%). With regards to genera, 38 are represented by a single species, while the remaining 14% are represented by two species, namely, *Baccharis*, *Blechnum*, *Elleanthus*, *Gaultheria*, *Licopodium*, *Tibouchina*, and *Weimania*. The most abundant species throughout the altitudinal gradient of the study area were *Baccharis latifolia* (2%).

The species rarefaction curve and the non-parametric richness estimator indicated the highest estimated species richness occurring in gradients E4, with 36 species, followed by E2, with 32 species, E1, with 28 species, and E5 and E3, with 22 and 20 estimated species, respectively (Figure 2).

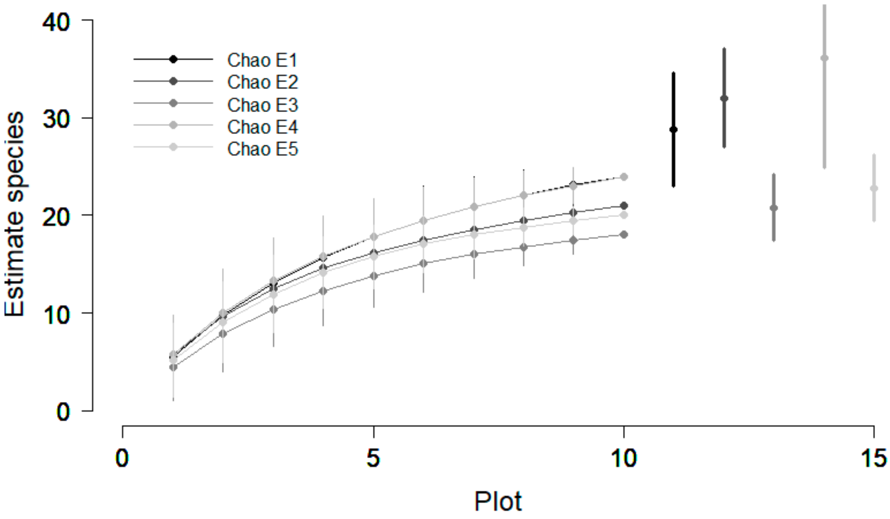

Figure 2. Rarefaction curves with 95% confidence intervals and a Chao 2 estimator (points on the right of the figure) for the five elevations.

3.1. Patterns of Richness and Abundance in Relation to Elevation and Edaphic Factors

Although richness did not show a distinct pattern with elevation, abundance showed a hump-shaped relationship with elevation (Figure 3). This hump shape may be due to edaphic factors, such as bulk density (E1: 1.43 g cm^{-3} and E2: 1.18 g cm^{-3}, respectively), sandy loam texture, and nitrogen content (E1: 0.7%), which were higher at higher elevations. On the other hand, sandy loam and clay loam textures (with higher sand content), and pH (E4: 5.3 and E5: 5.4, respectively), were higher at lower elevations (Figure 3, Appendix A). However, E3 is where bulk density is better (lower compaction; 0.9 g cm^{-3}) than at the other elevations.

This relationship was confirmed by GLMMs, where abundance had a maximum peak at middle elevations (E3 and E4), while for richness no significant effects of elevation and soil factors were detected (Figure 3, Appendices B and C).

3.2. Beta Diversity in Relation to Elevation and Edaphic Factors

The vascular plant composition of the higher elevations E1 and E2 (2600 and 2200 m a.s.l., respectively), clearly differed from the lower elevations E4 and E5 (1400 and 1000 m a.s.l., respectively), while the intermediate elevation E3 shares a similarity with the higher and lower elevations (Figure 4).

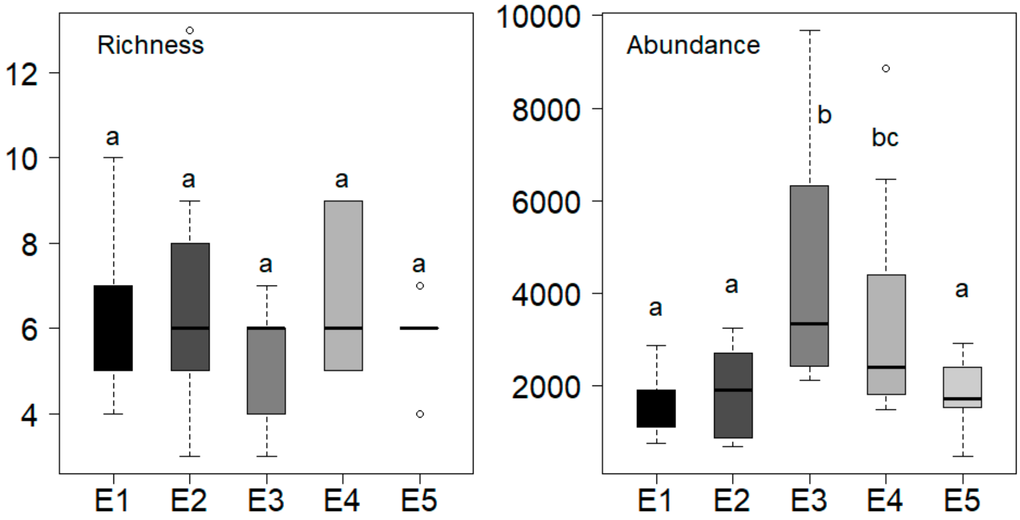

Figure 3. Box-plot of species richness at the five elevations throughout the altitudinal gradient of the study. Data is depicted through quartiles and different lowercase letters above the whiskers indicate significant differences altitudinal gradient (GLMMs $p < 0.05$).

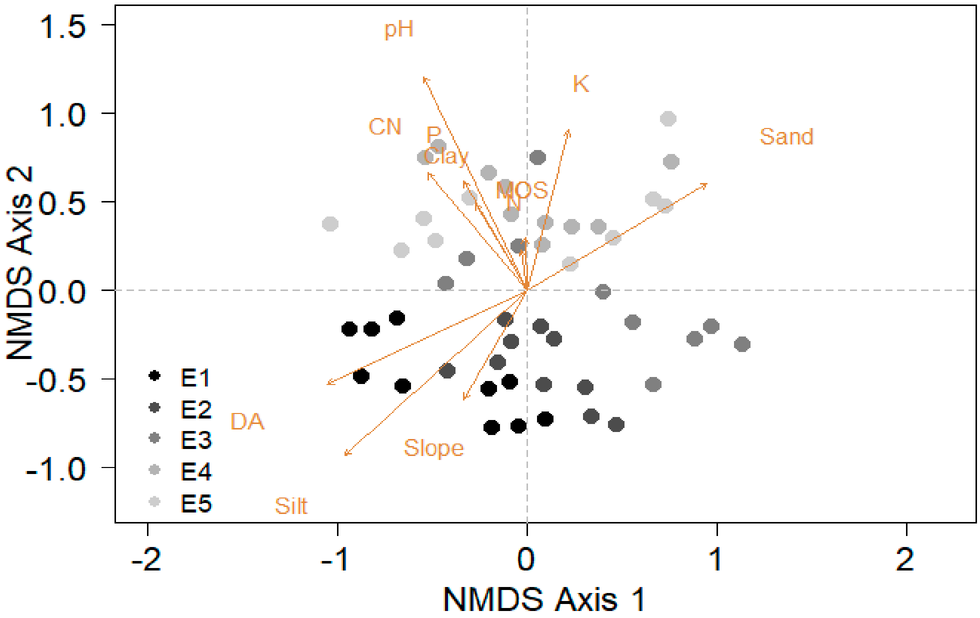

Figure 4. NMDS analysis of the influence of environmental variables on vascular plant composition at the five elevations of the study's altitudinal gradient (E1–E5).

A total of 49% of the variability in community composition is conditioned by elevation and soil variables, such as higher silt content, pH, and sand with 47%, 46%, and 37% respectively (Table 2). At higher elevations (E1 and E2), the higher silt content (sandy loam textures), bulk density, and slope are conditioning the composition of the communities, compared to the higher pH and sand content (sandy loam and sandy clay loam textures), which are determinant for the composition at lower elevations (E4 and E5, Table 2).

Table 2. NMDS ordination data by environmental factors and roadside vascular composition of the Loja-Zamora Road. The squared correlation coefficients (R^2) for axes 1 and 2, the p value and the contribution of each variable to the variability on each axis are shown.

	NMDS1	**NMDS2**	R^2	p **Value**
Slope	−0.48131	−0.87655	0.1309	0.035964
pH	−0.41188	0.91124	0.4681	0.000999
MOS	−0.0346	0.9994	0.0239	0.529471
N	−0.11675	0.99316	0.0141	0.675325
P	−0.47755	0.8786	0.1314	0.031968
K	0.23584	0.97179	0.2322	0.003996
C	−0.0346	0.9994	0.0239	0.529471
CN	−0.62129	0.78358	0.1907	0.007992
Bd	−0.89457	−0.44693	0.3712	0.000999
Sand	0.84395	0.53642	0.3382	0.000999
Silt	−0.71846	−0.69557	0.4796	0.000999
Clay	−0.48601	0.87395	0.0838	0.12987
Altitude			0.4919	0.000999
AltitudeG1	−0.4402	−0.4933		
AltitudeG2	0.0644	−0.4341		
AltitudeG3	0.3862	−0.0282		
AltitudeG4	0.012	0.5335		
AltitudeG5	−0.0224	0.4222		

3.3. Indicator Species

The indicator species analysis (ISA) determined a total of 20 species that are significantly more abundant and frequent in their respective microhabitats than the other plants, where species with an indicator value of >0.25% are considered as the best indicators (Table 3). At elevation E3, five indicator species were recorded, representing the highest number of indicator species among the five elevations, while for elevation E2, three indicator species were recorded, being the elevation with the fewest indicator species. At elevations, E1, E4, and E5, four species were recorded for each elevation (Table 3). However, these findings reflects the fact that two of these species, *Elleanthus aurantiacus* and *Baccharis genistelloides,* were found, at least occasionally, in all five microhabitats. Eight species were found in a single microhabitat. The other 10 were occasionally found in 2, 3, and up to 4 of the study elevations (Appendix D).

Table 3. Selected roadside vascular species as indicators across an altitudinal gradient in mountainous Andean ecosystems.

Zone	**Species**	**IndVal**	p**-Value**
Elevation 1	*Gaultheria vaccinioides* Wedd.	0.389	0.01
	Eriosorus aureonitens (Hook.) Copel.	0.3	0.032
	Maxillaria sp.	0.4	0.007
	Elleanthus aurantiacus Rchb.f	0.403	0.009
Elevation 2	*Bejaria resinosa* Mutis ex L. f.	0.407	0.025
	Cortaderia jubata (Lemoine) Stapf	0.441	0.005
	Digitaria ciliaris (Kents.) Koeler	0.595	0.001
Elevation 3	*Baccharis genistelloides* (Lam.) Pers.	0.59	0.015
	Carex lehmanniana Boott ex Walp.	0.3	0.025
	Sticherus bifidus (Willd.) Ching	0.419	0.006
	Lycopodium clavatun subsp. Contiguum	0.3	0.04
	Calamagrostis intermedia (J. Presl) Steud.	0.498	0.001
Elevation 4	*Lycopodiella andicola* B. Øllg.	0.5	0.002
	Lycopodium clavatum L.	0.298	0.029
	Axinaea sp.	0.4	0.005
	Neurolepis laegaardii L.G. Clark.	0.382	0.009

Table 3. *Cont.*

Zone	Species	IndVal	*p*-Value
Elevation 5	*Dennstaedtia mathewsii* (Hook.) C. Chr.	0.356	0.01
	Clidemia sp.	0.4	0.004
	Eleusine indica (L.) Gaertn.	0.27	0.038
	Melpomene moniliformis (Lag. ex Sw.)	0.31	0.028

4. Discussion

4.1. Patterns of Richness and Abundance in Relation to Elevation and Edaphic Factors

Our results indicated that species richness was not conditioned by elevation, although community composition was limited by elevation and edaphic factors at the roadside (e.g., pH, different texture types, silt, sand, and Bd content). Haider et al. [24] indicated that species richness presents a hump shape regarding elevation. However, in some areas there is no relationship between richness and elevation, as evidenced in our study. Disturbance and the presence of non-native species condition species richness related with elevation, as shown by Sandoya et al. [27] on roadsides in northern Ecuador.

The abundance of species pointed to a hump shape as a function of elevation, as has been documented for species richness in temperate and boreal zones (3, 24) as well as for tropical regions [27]. Thus, our results suggest that roadside in Andean Mountain biomes showed higher abundance at mid-elevation (e.g., 1800 m), highly correlated with abiotic changes (precipitation, temperature, soil, and topography). For example, *Baccharis genistelloides*, *Carex lehmanniana*, *Sticherus bifidus*, and *Calamagrostis intermedia* are more abundant in E3, where the bulk density is lower (0.9 g cm^{-3}) and, therefore, the soil is looser (less compacted), facilitating root growth. In this context, McGrath and Henry [52] and Jim [53] showed that the more compacted the soil is, the more moisture retention conditions are affected, limiting root growth [54] which shows that E3 has the best soil conditions for plant growth. Therefore, the pattern found in our study for abundance is consistent with other studies related with species richness that is higher at mid-elevations and decreases at higher elevations, where climate harshness increases and acts as an important filter [24,27,55].

4.2. Beta Diversity in Relation to Elevation and Edaphic Factors

Plant community composition was influenced by elevation and edaphic factors, as in the findings of several previous studies that have documented that elevation [25,26,56,57] and soil characteristics [16,55,58,59] are driving factors in the composition of roadside plant communities. In this context, our results are consistent with those reported by Karin and Mallik [60] and Arenas et al. [55] who point out that roadside soil characteristics influence different plant species communities. Furthermore, Solivers and Garcia [61] showed that at roadside, soil-plant interactions are more important than plant-plant interactions, so physical and chemical parameters are key in these anthropized ecosystems.

High gradient communities (e.g., *Gaultheria vaccinioides*, *Eriosorus aureonitens*, *Maxillaria* sp., and *Elleanthus aurantiacus*) were adapted to soil conditions with higher bulk density (higher compaction; 1.43 and 1.18 gr cm^{-3}, respectively, Appendix B), and in addition, as they grew in sandy loam textures (higher silt concentration, but with less sand concentration than the other contrasted gradients), erosive processes were greater, which explains why in E1 and E2 there is greater soil compaction. On the contrary, low gradient communities (e.g., *Lycopodiella andicola*, *Lycopodium clavatum* L., *Axinaea* sp., *Neurolepis laegaardii*, *Dennstaedtia mathewsii*, and *Melpomene moniliformis*) have adapted to sandy loam and sandy clay loam soil texture conditions (higher sand concentrations), which could lead to a relatively muted erosive process as demonstrated in other studies [56,62]. However, pH is a determining factor in the composition of roadside plants, as previous studies have shown [55,58,60]. Although the soil pH values found in our study are suboptimal (Appendix B), considering that values between 6.5 and 8.0 are required for adequate assimilation of macronutrients by plants [63], the pH values were higher in the lower gradients and, thus, the less compacted soil could facilitate the absorption of these nutrients, as reported by Schoonover [64]. In addition, the higher concentration of sand and a more favorable texture (sandy-loam and sandy-clay-loam textures in E4 and E5 respectively), allow for a higher concentration of K, which can determine different communities better than high gradients, where plant communities have adapted to more acidic pH conditions (low pH).

The indicator species (ISA) in our study were abundant and frequent in their respective microhabitats, e.g., for E1 and E2 species, such as *Gaultheria vaccinioides*, *Elleanthus aurantiacus*, *Bejaria resinosa*, and *Digitaria ciliaris*, were the better indicators, while for E4 and E5, *Lycopodium clavatum*, *Neurolepis laegaardii*, *Dennstaedtia mathewsii*, *Eleusine indica*, and *Melpomene moniliformis* have the highest indication values. Supporting our results, Karim and Mallik [60] note that species indicate their preference for particular sets of environmental and edaphic conditions associated with different roadside microhabitats. These results suggest that elevation and roadside soil properties in different microhabitats play an important role in determining plant community composition [34,55,58]. Although the functional traits of these species were not assessed in our study, they can be categorized as a potential for roadside revegetation processes in tropical areas.

Although there are commonalities with widely studied temperate regions, there are significant differences in how vascular species are structured as a function of environmental and edaphic variables in the highlands of the southern Andes of Ecuador. In this context, other factors not measured in this study, such as disturbance, adjacent vegetation patches, timing of intervention, roadside effect, and the presence of non-native species conditioning plant diversity should also be considered [24,27]. Further comprehensive studies prioritizing these approaches will make an important contribution to the development of guidelines for roadside revegetation.

5. Conclusions

Species composition on the roadside in mountainous areas of the southern Andes of Ecuador was limited by elevation and soil characteristics. Therefore, we found that community composition is a more sensitive indicator than species richness in the area of roadside studied. The indicator species with specific needs of altitude, bulk density, pH, amount of sand, and silt identified in our study (*Elleanthus aurantiacus*, *Digitaria ciliaris*, *Baccharis genistelloides*, *Lycopodiella andicola*, and *Dennstaedtia mathewsii*) can potentially be used in some roadside restoration programs implemented in tropical areas. On the other hand, it is essential to understand the interactions between elevation, physicochemical soil composition, and plant composition, as these factors are very useful in shaping the distribution of species. In this context, these results can help those responsible for generating policies and technical proposals for the design of biodiversity conservation projects and environmental restoration of roadside in areas of Andean Mountain ecosystems, which are highly intervened because of road infrastructure construction.

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Data Availability Statement: Data is contained within the article.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Description of soil variables in each altitudinal gradient (E1–E5). Mean values and standard deviation are given. SOM = soil organic matter; SOC = soil organic carbon; Bd = bulk density.

	E1	**E2**	**E3**	**E4**	**E5**
pH	4.82 ± 0.01	4.89 ± 0.1	4.8 ± 0.02	5.3 ± 0.01	5.4 ± 0.5
SOM (%)	1.3 ± 2.9	0.6 ± 0.7	1.2 ± 1.5	0.7 ± 0.7	1.4 ± 0.8
N (%)	0.7 ± 0.01	0.04 ± 0.04	0.06 ± 0.07	0.04 ± 0.04	0.07 ± 0.04
P (mg/kg)	3.5 ± 0.00	3.7 ± 0.28	3.5 ± 0.00	3.9 ± 0.56	3.5 ± 0.00
K (cmol/kg)	0.01 ± 0.00	0.01 ± 0.00	0.06 ± 0.00	0.02 ± 0.01	0.17 ± 0.00
SOC (%)	0.73 ± 0.04	0.38 ± 0.41	0.69 ± 0.88	0.42 ± 0.46	0.81 ± 0.49
C/N ratio	11.3 ± 0.49	9.4 ± 2.61	9.5 ± 3.53	11.5 ± 1.55	11.6 ± 0.00
Bd (gr cm^3)	1.43 ± 0.29	1.18 ± 0.35	0.90 ± 0.24	1.15 ± 0.30	1.17 ± 0.23
Sand (%)	60.6 ± 19.8	58.9 ± 8.0	62.6 ± 8.5	77.6 ± 1.4	65.6 ± 9.9
Silt (%)	22.0 ± 14.1	21.6 ± 2.3	20.0 ± 5.7	7.0 ± 4.2	10.0 ± 11.3
Clay (%)	17.4 ± 5.7	19.4 ± 5.7	17.4 ± 2.8	15.4 ± 2.8	24.4 ± 1.4
Textural class	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy clay loam

Appendix B

Table A2. Contribution of each soil variable to each axis of the principal component analysis. SOM = soil organic matter; Bd = bulk density.

	PC1	**PC2**
pH	0.0521	0.3578
SOM	−0.4725	−0.0172
N	−0.4725	−0.0487
P	0.3245	0.1257
K	−0.2017	0.2309
SOC	−0.4725	−0.0172
C/N	−0.3704	0.2317
Bd	−0.0737	−0.0503
Sand	0.0424	0.5875
Silt	0.0398	−0.6117
Clay	−0.1885	−0.1561

Appendix C

Table A3. GLMMs data with the relationship between altitudes (E1–E5), slope, and soil characteristics (represented as the two components of the PCA analyses PC1 and PC2, which bring together all soil characteristics) on roadside vascular species richness along an altitudinal gradient in mountainous Andean ecosystems.

Richness	**Estimate**	**Std Error**	**Z Value**	***p* Value**
AltitudeE1	1.768	0.153	11.571	0.467
AltitudeE2	0.131	0.185	0.711	0.477
AltitudeE3	−0.172	0.189	−0.907	0.364
AltitudeE4	0.281	0.283	0.993	0.321
AltitudeE5	0.021	0.241	0.086	0.931
PC1-soil	−0.030	0.034	−0.893	0.372
PC2-soil	−0.059	0.067	−0.879	0.380

Table A3. *Cont.*

Richness	Estimate	Std Error	Z Value	*p* Value
Abundance				
AltitudeE1	7.316	0.120	61.142	0.437
AltitudeE2	0.041	0.154	0.267	0.789
AltitudeE3	1.038	0.147	7.052	<0.0001
AltitudeE4	0.842	0.224	3.762	0.0001
AltitudeE5	0.331	0.190	1.744	0.081
PC1-soil	0.068	0.027	2.560	0.060
PC2-soil	−0.061	0.055	−1.123	0.261

Appendix D

Table A4. Families and number of species per elevation recorded.

	Elevations				
Family/Species	**E1**	**E2**	**E3**	**E4**	**E5**
Asteraceae					
Baccharis genistelloides (Lam.) Pers.	16	121	272	8	27
Baccharis latifolia (Ruiz & Pav.) Pers.		3	1		
Liabum sp.		1		5	
Sonchus oleraceus (L.) L.					5
Tessaria sp.		1			
Triplaris sp.		1			
Blechnaceae					
Blechnum binervatum (Poir.) C.V. Morton & Lellinger.		11			
Blechnum stipitatum A. Rojas.	25				
Bromeliaceae					
Guzmania sp.	4	14			
Pitcairnia cf pungens.	6	3			
Clethraceae					
Clethra finbriata Kunth	8				
Clethra revoluta (Ruiz & Pav.) Spreng.				2	
Cunoniaceae					
Weinmannia fagaroides Kunth				2	
Weinmannia glabra Lam.			2		
Cyperaceae					
Carex lehmanniana Boott ex Walp.			93		
Rhynchospora vulcani Boeckeler.	11	21			
Dennstaedtiaceae					
Dennstaedtia mathewsii (Hook.) C. Chr.					17
Pteridium sp. Gled. ex Scop.	28	58	28	9	
Dryopteridaceae					
Elaphoglossum sp. Schott ex J. Sm.	1				
Ericaceae					
Bejaria resinosa Mutis ex L. f.	4		33	6	4
Disterigma acuminatum (Kunth) Nied.	2				
Gaultheria erecta Vent.	32	47	18	8	11
Gaultheria vaccinioides Wedd.	40	16	11		5
Fabaceae					

Table A4. *Cont.*

	Elevations				
Family/Species	**E1**	**E2**	**E3**	**E4**	**E5**
Desmodium sp.					11
Medicago sp.					7
Gleicheniaceae					
Sticherus bifidus (Willd.) Ching			235	15	23
Gunneraceae					
Gunnera sp.				36	
Lycopodiaceae					
Lycopodiella andicola B. Øllg.				382	
Lycopodium clavatum L.				130	91
Lycopodium clavatun subsp. Contiguum			75		
Lycopodium jussiaei Desv. ex Poir.				6	
Melastomataceae					
Axinaea sp. Ruiz & Pav.				16	
Clidemia sp.					28
Miconia sp.					6
Tibouchina laxa (Desr.) Cogn.		5	8		
Tibouchina lepidota (Bonpl.) Baill.		67		21	18
Orchidaceae					
Elleanthus aurantiacus Rchb.f	148	12	1	9	4
Elleanthus sp.	8	23		5	
Maxillaria sp.	73				
Sobralia candida (Poepp. & Endl.) Rchb. f.			5	11	7
Phyllanthaceae					
Hyeronima sp.				5	
Piperaceae					
Piper sp.				5	2
Poaceae					
Axonopus scoparius H			69		
Calamagrostis intermedia (J. Presl) Steud.	1		168		
Chusquea loxensis L.G. Clacrk	18				
Cortaderia jubata (Lemoine) Stapf	17	67		15	5
Digitaria ciliaris (Kents.) Koeler	1	46			
Eleusine indica (L.) Gaertn.				33	82
Festuca subulifolia Benth.	12				
Neurolepis laegaardii L.G. Clark	1		38	60	51
Setaria parviflora (Poir.) Kerguélen			41		
Polygonaceae					
Muehlenbeckia tamnifolia (Kunth) Meisn.		20			
Polypodiaceae					
Melpomene moniliformis (Lag. ex Sw.) A.R. Sm. & R.C. Moran	146				174
Pteridaceae					
Eriosorus aureonitens (Hook.) Copel.	12				

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