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Effects of Grain Size on Plant Diversity Patterns in a Mediterranean Mountain

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ABSTRACT

Question: Spatial grain size and sampling design are crucial to assess plant diversity patterns, yet their effects on alpha, beta, and gamma diversity along elevational gradients remain poorly understood.

Location: We investigated these effects along an elevational gradient in the Central Apennines (Italy) ranging from 1100 to 2486 m a.s.l.

Methods: Plant presence–absence data were recorded from 83 randomly selected nested plots, each containing seven grain sizes ranging from 0.25 m × 0.25 m to 16 m × 16 m. Alpha, beta, and gamma diversity were calculated at both the nested plot and grain size levels and analyzed along the elevational gradient. Gamma was assessed within 100-m elevational bands by aggregating species occurrences across nested plots and grain sizes within each band. Beta diversity was calculated among all nested plots and grain sizes, as well as within elevational bands, using Sørensen dissimilarity.

Results: Our results revealed a significant effect of grain size on elevational diversity patterns. Alpha diversity exhibited a stronger pattern at larger grain size, with species richness decreasing along the elevational gradient. Gamma diversity mirrored alpha diversity trends, increasing with grain size but decreasing with elevation. Beta diversity did not change with elevation but decreased with grain size.

Conclusion: These results emphasize the strong influence of grain size on plant diversity patterns along elevation gradients, highlighting its importance in biodiversity assessments. The nested sampling approach used appears to be a promising tool for testing diversity patterns along elevational gradients, offering a robust framework for future ecological studies.

Lorenzo Ricci and Gonzalo Velasco Mones contributed equally to this study.

1 | Introduction

One of the most important challenges in ecology is understanding the spatial and temporal patterns of biodiversity (Lomolino 2001; MacArthur and Wilson 1963). As biodiversity is affected by multiple factors, it is difficult to find a simple explanation for spatial and temporal patterns of variation in diversity (Montalvo et al. 1993). In particular, plant diversity, a fundamental component of ecosystems, is shaped by environmental conditions, biotic interactions, and disturbances (Laliberté et al. 2014). Among others, the distribution of plant communities (i.e., where different plant species occur across the landscape) is significantly influenced by climate (Peters et al. 2019), topography (Moeslund et al. 2013), and edaphic characteristics (Ohdo and Takahashi 2020). Importantly, species composition, the identity and abundance of species in a community, can vary markedly along elevational gradients (Lomolino 2001). In fact, changes in elevation are associated with variations of environmental variables that act as filter for plants by selecting those species with more suitable characteristics for the specific condition of the site (Pellissier et al. 2010; Guisan and Rahbek 2011; Matteodo et al. 2013). When investigating diversity patterns (e.g., alpha, beta, and gamma diversity), it is crucial to consider both the spatial grain and spatial extent of sampling. Spatial grain refers to the size of the sampling unit of observation, whereas spatial extent describes the total area over which observations are made (Cushman et al. 2010; Turner and Gardner 2015). Scale, as a broader concept, encompasses both grain and extent and can also include their spatial arrangement (Turner and Gardner 2015).

At the landscape scale, which is the largest one, the overall species diversity (gamma diversity) is determined by species richness within sites (i.e., alpha diversity) together with the variability in species composition among local communities (beta diversity) (Whittaker 1960; Allan 1975). Essentially, all these diversity metrics are strongly influenced by geographic, environmental, and elevational distances between sites (Nekola and White 1999; Condit et al. 2002; Morlon et al. 2008). As the distance increases, the similarity in species composition tends to decrease (Qian et al. 1998; Nekola and White 1999). Decrease in similarity with increasing geographic distance between sites is known as the distance decay of similarity (Nekola and White 1999; Poulin 2003; Soininen et al. 2007; Morlon et al. 2008), and it is a quantitative expression in an ecological context of Tobler's "first law of geography," that is, that "everything is related to everything else, but near things are more related than distant things" (Tobler 1970). It is partly due to changes in environmental conditions between sites as well as to the dispersal rate of organisms (Garcillán and Ezcurra 2003; Wetzel et al. 2012). Distance decay patterns are both extent- and grain-dependent. This phenomenon is mainly due to the role of ecological constraints that strongly vary along different spatial extent and sampling areas (Girdler and Connor Barrie 2008; Baselga and Gómez-Rodríguez 2021; Martín-Devasa et al. 2022). At smaller spatial extents, species interactions and microhabitat preferences may play a dominant role in shaping community composition, whereas at broader extents, factors such as climate gradients and dispersal limitations become more influential in determining species distributions (Rahbek 2005; Freestone and Inouye 2006; Li et al. 2020).

The species–area relationship (SAR) is a well-established principle in ecology, stating that the number of species increases with the sampled area, often following a power law (Arrhenius 1921). This relationship is particularly relevant when considering how spatial grain influences observed biodiversity patterns, as larger sampling areas typically encompass more species (Puglielli and Pärtel 2023). In the context of elevational gradients, larger sampling units may capture a broader range of species, influencing the measurement of alpha, beta, and gamma diversity (Tello et al. 2015). Consequently, the elevational patterns of species diversity may also vary depending on the spatial grain used for sampling. In mountainous regions, there are significant changes in environmental conditions over short geographic distances (Körner 2021). These changes affect plant diversity patterns, thus making the elevation gradients particularly suitable for studying alpha, beta, and gamma diversity patterns when varying grain sizes (Körner 2000; Bhatta et al. 2018; Albert et al. 2010).

Accurate estimation of species diversity patterns implies decisions regarding both the selection of sampling sites and the choice of appropriate spatial grain sizes and shape (Kenkel et al. 1989; Stohlgren 2007; Bacaro et al. 2015). In biodiversity studies, the relationship between species diversity and spatial scale of observation remains a topic of debate. Although some suggest that species diversity is scale-independent (Gaston 2000; Ricklefs 2004; Bhatta et al. 2018; Sabatini et al. 2022), many others argue that scale dependence is a fundamental characteristic of biodiversity assessment. Spatial grain size, in particular, can significantly influence sampling effectiveness and the resulting diversity patterns (Albert et al. 2010; Güler et al. 2016). For example, Rahbek (2005) conducted a comprehensive synthesis of the effects of varying spatial grains across multiple studies, demonstrating that changes in grains profoundly influence species richness patterns and highlighting the critical role of scale in biodiversity studies. Furthermore, as highlighted by Keil and Chase (2019), diversity patterns are shaped by local environmental heterogeneity and regional species pools, underscoring the scale dependency of these patterns and the need for standardized, nested approaches to better isolate effects of different spatial scales on observed biodiversity patterns. Despite this, relatively few studies have explicitly focused on testing the effects of spatial grain size on plant diversity using standardized, nested sampling designs. While nested plots have indeed been widely employed in studies of the SAR (e.g., Meier and Hofer 2016; Borda-de-Água et al. 2025), most of this work has emphasized scaling patterns of richness rather than directly addressing how different spatial grain sizes influence diversity estimates across heterogeneous communities (but see Karger et al. 2011; Bhatta et al. 2018). Recent studies have shown that the variation in grains can lead to contrasting conclusions about both alpha and beta diversity (Dembicz et al. 2021; Sabatini et al. 2022), whereas factors such as plot shape and arrangement can also influence richness estimates (De Cáceres et al. 2012). These finding highlight a key knowledge gap: the need for a standardized, nested sampling design that allows for

the direct comparison of spatial grain size effects on observed biodiversity patterns. Such an approach enables a more robust understanding of the scale dependency of biodiversity patterns, particularly in environmentally heterogeneous systems like mountain landscapes (Körner 2021).

In this context, our study aimed to investigate how grain size influences observed plant diversity patterns along an elevational gradient in a Mediterranean mountain (Central Apennines, Italy), using a standardized nested sampling approach.

Specifically, we addressed the following questions:

i. How do alpha and gamma diversity change along elevation and grain size?

ii. How does beta diversity (i.e., community turnover in species composition) change along elevation and grain size?

iii. Is there a clear scale effect of spatial grain on the distance decay of similarity?

2 | Materials and Methods

2.1 | Study Area

The study area is located in the Mount Velino Nature Reserve, a limestone massif situated in the western sector of the Sirente Velino Regional Park (central Apennines, Italy) (Figure 1). It is characterized by a sub-Mediterranean climate with a drought period in summer and winter frost stress at the highest elevations (Petriccione 1993; Cutini et al. 2012, 2021). Along the elevational gradient, vegetation is shaped reflecting both edaphic conditions and land-use history. At lower and middle elevations (up to ~1600 m a.s.l.), secondary dry grasslands dominate, mostly derived from long-term grazing and mowing, and are characterized by a high floristic richness of hemicryptophytes (e.g., species of *Brachypodium* P. Beauv., *Carex* L., *Bromus* L. s.l., *Festuca* L., *Sesleria* Scop.), and chamaephytes such as *Anthyllis montana* L., *Globularia meridionalis* (Podp.) O. Schwarz, *Helianthemum* Mill. and *Teucrium* L., often interspersed with scattered phanerophytes like *Juniperus*

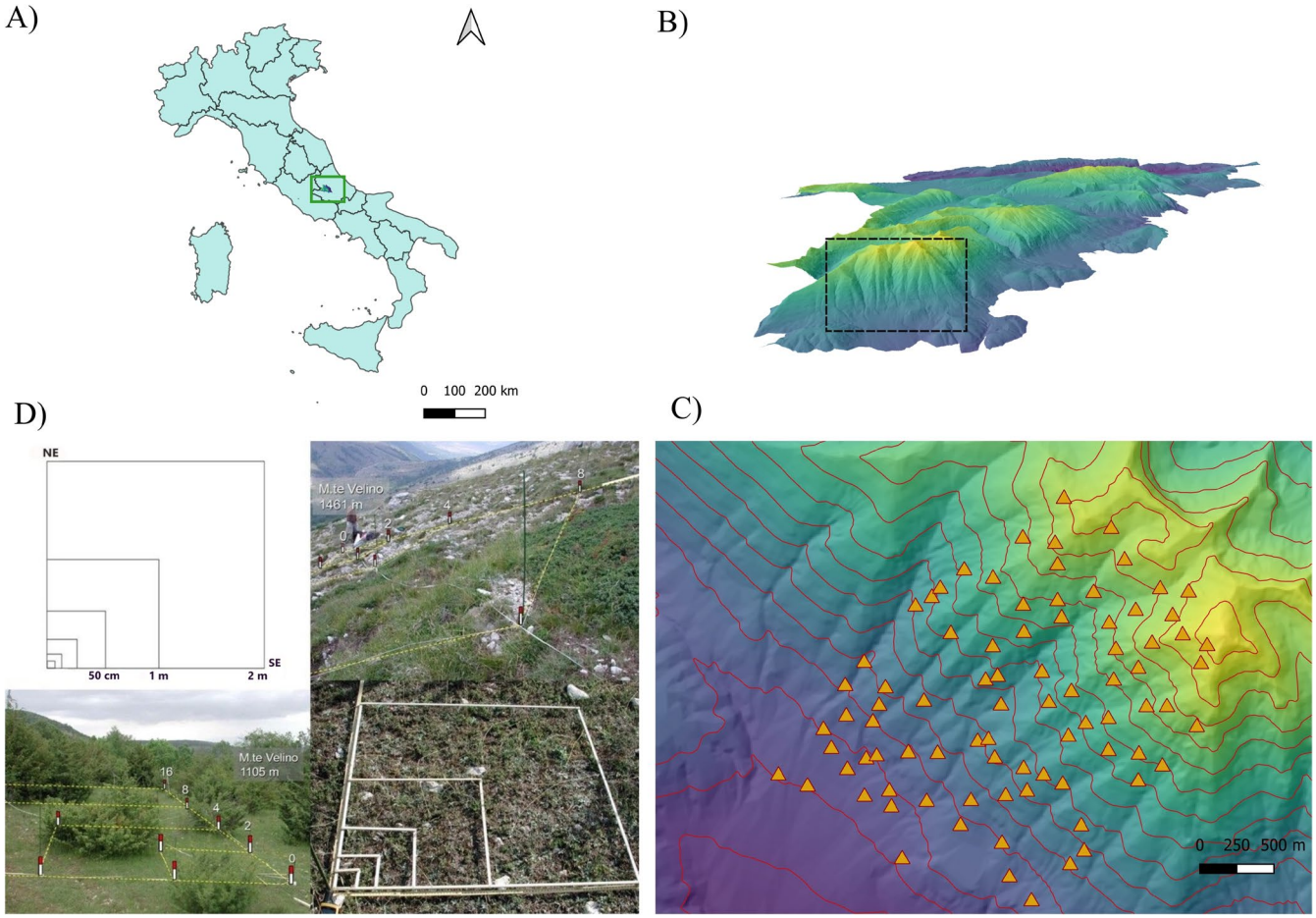

FIGURE 1 | (A) Map indicating the location of the study area within Italy. (B) 3D-rendered digital elevation model representing the entire Sirente Velino Regional Park, with a dashed box highlighting the Mount Velino Reserve area. (C) Zoomed-in view of the study area displaying the 83 sampled sites. The elevation gradient is represented by colors, ranging from dark blue at lower elevations to light yellow at higher elevations. (D) Nested sampling units used in the study. In the top left, a schematic representation of a nested plot shows how grain sizes increase by a factor of 4. The top right and bottom left panels depict the field implementation of the sampling design at different elevations, with yellow dashed lines indicating the sampling grid and markers labeling quadrat positions. The bottom right panel provides a close-up of the nested plot structure used for data collection. Note that the figure illustrates the full nested design established in the field; for the analyses presented in this study, only a subset of the surveyed grain sizes was selected.

communis L. subsp. *communis* and *J. oxycedrus* shrubs and patches of broadleaf forest regrowth (*Quercus cerris* L., *Q. pubescens* Willd., *Ostrya carpinifolia* Scop.) (Petriccione 1993; Theurillat et al. 2011; Bartolucci et al. 2019). Between 1600 and 2200 m a.s.l., there are fragments of mesothermophilous woodlands dominated by *Fagus sylvatica* L. Low-elevation grasslands gradually give way to subalpine dwarf heathlands, which are dominated by chamaephytes such as *Juniperus communis* subsp. *nana* Syme, and *Arctostaphylos uva-ursi* (L.) Spreng. These are often mixed with *Sesleria juncifolia* Suffren xerocryophilous grasslands and other plants adapted to frost and wind exposure, including *Astragalus sempervirens* L., *Edraianthus graminifolius* (L.) A. DC., *Saxifraga paniculata* Mill. and *Silene acaulis* (L.) Jacq. Above 2200 m a.s.l., vegetation becomes increasingly fragmented, with open primary grasslands dominated by stress-tolerant species (e.g., *Carex kitaibeliana* Bech., *Lomelosia graminifolia* (L.) Greuter & Burdet, *Sesleria juncifolia* Suffren), interspersed with bare limestone outcrops (Petriccione 1993; Theurillat et al. 2011; Bartolucci et al. 2019). In the uppermost zone, vegetation cover declines sharply and is progressively replaced by scree communities with pioneer species adapted to unstable substrates such as *Festuca dimorpha* Guss. This current vegetation mosaic has been strongly shaped by millennia of pastoral use, which maintained open habitats and prevented the upward expansion of forest. Only in recent decades, with the reduction of grazing, processes of shrub encroachment and forest recovery have become evident (Petriccione 1993; Theurillat et al. 2011). The area above 1800 m a.sl. is part of the Long-Term Ecological Research (LTER) Italy network, within the long-term monitoring macro-site "Apennine high ecosystems" (LTER_EU_IT_025) (Stanisci et al. 2021).

2.2 | Data Collection

Presence–absence data of plant species were collected during the period 2005–2006. The survey was conducted along an elevational transect 2-km wide ranging from 1100 to 2486 m a.s.l. (Theurillat et al. 2011). The elevational gradient was divided into 100-m elevational bands following the contour lines for a total of 13 bands (Figure 1 and Appendix S3).

Within each band, sampling sites were randomly selected. A sample site was defined as a fixed geographic location within an elevational band where vegetation was surveyed. As the area of each band can vary due to differences in slope, and the truncated upper part of the transect above 2300 m a.s.l., the number of sampling sites in each band was proportional to its spatial extent ensuring consistent sampling intensity along the transect. Due to the regular slope of the transect, the nine elevational bands from 1300 m to 2200 m a.s.l. were about 0.36–0.40 km^2 and contained a total of 84 sampling sites. However, only 83 sites were sampled as one site was not sampled in the 1100–1199 m elevational band. Within each band, sampling sites were placed at a minimum distance of 200 m to avoid spatial autocorrelation (Dormann et al. 2007; Legendre 1993). At each site, one nested plot was established according to a given scheme, which served as the fundamental unit for data collection and long-term monitoring. The base of the plot at the origin was oriented toward the southeast, while the orthogonal side was oriented toward the northeast (see Figure 1). This meant that the diagonal of the nested design always pointed east. A nested plot consisted of a hierarchical arrangement of 11 square subplots (representing spatial grain sizes), with increasing areas ranging from 1.5 cm × 1.5 cm, 3 cm × 3 cm, 6.25 cm × 6.25 cm, 12.5 cm × 12.5 cm, and so on up to 16 m × 16 m, that is, the grain size increased each time by a factor of 4 (from 0.000225 m^2 up to 1064 m^2). However, we did not use the first four grain sizes in our analysis that started with the 0.25 m × 0.25 m subplots. Following this sampling design, a total of 84 nested plots were established. In each subplot, the number of individuals was recorded for each species according to six classes following a geometric sequence (1, 2–5, 5–25, 26–125, 126–625, and ≥ 626 individuals). For the subplots 2 m × 2 m up to 16 m × 16 m, the cover of each species was also recorded according to a modified Braun-Blanquet scale (< 1%, 1%–5%, 5%–15%, 15%–25%, 25%–37.5%, 37.5%–50%, 50%–62.5%, 62.5%–75%, 75%–87.5%, and 87.5%–100%; Barkman et al. 1964). The data were recorded in 2006 and 2007. The data of the 2 m × 2 m subplot were stored in EVA-ReSurveyEurope (Knollová et al. 2024).

2.3 | Elevational Patterns of Alpha and Gamma Diversity

We calculated alpha diversity as the number of species observed (i.e., species richness) within each nested plot and each spatial grain. To determine gamma diversity within each 100-m elevational band, we quantified the total number of species occurring across all nested plots belonging to the elevational band. As the last elevational band (2400–2486 m) contained only a single nested plot, we excluded it from the gamma diversity analysis.

We assessed the influence of elevation on alpha and gamma diversity using two complementary approaches. In the first, we explicitly incorporated grain size, whereas in the second, we examined it separately through SAR scaling. Although these approaches address related questions, they provide distinct insights: The first clarifies the shape of the elevational trend, whereas the SAR analyses reveal how the strength of grain size–diversity relationships shifts along the gradient.

(1) Modeling diversity as count data. We performed polynomial linear regression using generalized linear models (GLMs) with negative binomial distribution (via the *MASS* package; Venables and Ripley 2002) to investigate the elevational patterns of alpha and gamma diversity. The negative binomial distribution was chosen over the Poisson distribution due to the presence of overdispersion (Ver Hoef and Boveng 2007). Our models contained linear, quadratic, and cubic terms of elevation to predict diversity, allowing us to identify whether the relationship exhibited zero, one, or two inflection points and thereby assessed its complexity. To evaluate whether the effect of elevation on diversity varied with spatial grains, we compared models with and without interactions with grain size and elevation. Grain size was log-transformed ($\log_2$) prior to modeling to improve model fit and interpretability.

Because diversity–elevation relationships are often nonlinear (e.g., monotonic declines, hump-shaped patterns, or more

complex responses), we explicitly considered polynomial models (linear, quadratic, cubic) to capture potential variation in their shape. Including these terms allowed us to test whether species richness and diversity components followed simple linear declines or instead exhibited more complex responses to elevation. The optimal model among linear, quadratic, and cubic alternatives was selected based on the Akaike information criterion (AIC) and the likelihood ratio test. Specifically, we prioritized models with higher Akaike weights. When models were nested, we conducted a likelihood ratio test to assess statistical improvement. In cases where models were not nested, we favored the most parsimonious model within two AIC units of the top-performing model (Burnham and Anderson 1998; Burnham et al. 2011). To further validate the results concerning the interaction between grain sizes and elevation, we also analyzed how the effect sizes of elevation on alpha diversity changed for each grain size ("local" models). In all models, we checked the spatial autocorrelation by calculating Moran's *I*, calculated with the *vegan* package (Oksanen 2015). Residual diagnostics and model validation were performed using the *DHARMA* package (Hartig 2016). Given the structure of our sampling approach, assessing collinearity among predictors was not necessary.

(2) Modeling diversity as the slope of the SAR. We derived the species–area relationship for each nested plot across all spatial grains (alpha diversity). For gamma diversity, we aggregated species richness across all nested plots within each 100-m elevational band. From these relationships, we extracted the z coefficient of the semi-logarithmic SA curve:

$$2^S = cA^z \Longrightarrow S = \log_2(c) + z \bullet \log_2(A)$$

where S is species richness, A is the area of the sampling unit, c is a constant related to overall species density, and z is the slope parameter describing the strength of the richness–area relationship. A higher z value indicates a stronger positive relationship between diversity and grain size. The use of base two logarithms was motivated by the separation of grain sizes in powers of two. Hence, we analyzed how z varied along the elevational gradient by choosing the best model based on AIC, comparing a linear (z ~ elevation), a logarithmic (z ~ log(elevation)), or a power-law (z ~ 1/elevation) relationship for both alpha and gamma diversity.

2.4 | Elevational Patterns of Beta Diversity

Beta diversity was quantified using the Sørensen dissimilarity index (or Sørensen distance) on the presence–absence data, which is widely used to assess differences in species composition when only incidence data are available (Baselga 2010). For each elevational band and spatial grain, we computed all pairwise dissimilarities among plots and then averaged them to obtain a single value of beta diversity for that combination. We then examined how beta diversity varied with elevation and spatial grain by correlating these values with elevation across 100-m elevational bands. All Sørensen dissimilarity computations were performed using the *proxy* package (Meyer and Buchta 2021), which allows the computation of distance matrices from custom distance functions. To investigate similarity decay with distance (based on latitude and longitude coordinates), we compared the Sørensen dissimilarity matrix with the geographic distance matrix among plots using Mantel tests. These correlations and their significance were computed using the *vegan* package (Legendre et al. 2015).

As a sensitivity analysis, we repeated the same procedures using Euclidean distances of species composition. Specifically, we calculated the mean Euclidean distance between vegetation matrices of nested plots at each spatial grain within each 100-m elevational band and then assessed their correlation with geographic distances (based on latitude and longitude coordinates) using Mantel tests. This allowed us to evaluate whether the patterns observed with Sørensen dissimilarity were robust to alternative dissimilarity measures. All the above analyses of alpha, beta, and gamma diversity and related figures were performed with R 4.4.2 (R Core Team 2024) and the packages *sf* (Pebesma 2018), *tidyverse* (Wickham et al. 2019), *DHARMa* (Hartig 2016), *MASS* (Venables and Ripley 2002), *vegan* (Oksanen 2015), and *qqplotr* (Almeida et al. 2018).

3 | Results

3.1 | Alpha and Gamma Diversity as Counts

When modeling species richness as a count, we found that there is a very marked effect of both grain size and elevation, with species richness decreasing along the elevational gradient. The likelihood ratio test discarded interactions between grain size and elevation as important predictors. All three polynomial terms (linear, quadratic, and cubic) had a significant effect with the following effect sizes: linear (-4.84 ± 0.62, $p < 0.001$), quadratic (0.83 ± 0.63, $p < 0.001$), and cubic (-1.16 ± 0.61, $p < 0.001$). Additionally, the logarithm of grain size had a significant positive effect (0.36 ± 0.01, $p < 0.001$). As a result, the diversity–elevation relationship followed a declining pattern as illustrated in Figure 2. The explained deviance of the model was 0.82. Moran's *I* on the residuals was -0.01 ($p = 0.98$), indicating negligible spatial autocorrelation and confirming the model's reliability.

When performing "local" models, our results confirmed the lack of interaction between grain size and elevations. The effect sizes of the regression remained nearly constant across grain sizes (see Appendix S4). However, the explained deviance increased logarithmically with grain size, from 0.09 to 0.56 (R^2 of logarithmic increase in explained deviance with grain size: 0.99; see Appendices S4, S5). This suggests that while the qualitative effect of elevation on alpha diversity is consistent across grain sizes, the ability to build a robust model with elevation as a predictor depends heavily on grain size, particularly when shifting from small to intermediate sizes. The results for gamma diversity followed a similar pattern (Figure 2). A third polynomial was necessary to capture the complexity of the diversity response along elevation, with the following effect: linear (-2.54 ± 0.28, $p < 0.001$), quadratic (0.28 ± 0.28, $p = 0.05$), and cubic (-0.8 ± 0.27, $p < 0.001$). Grain size had also a significant logarithmic effect (0.27 ± 0.02, $p < 0.001$). The model explained deviance was 0.94. Although a model with interactions between

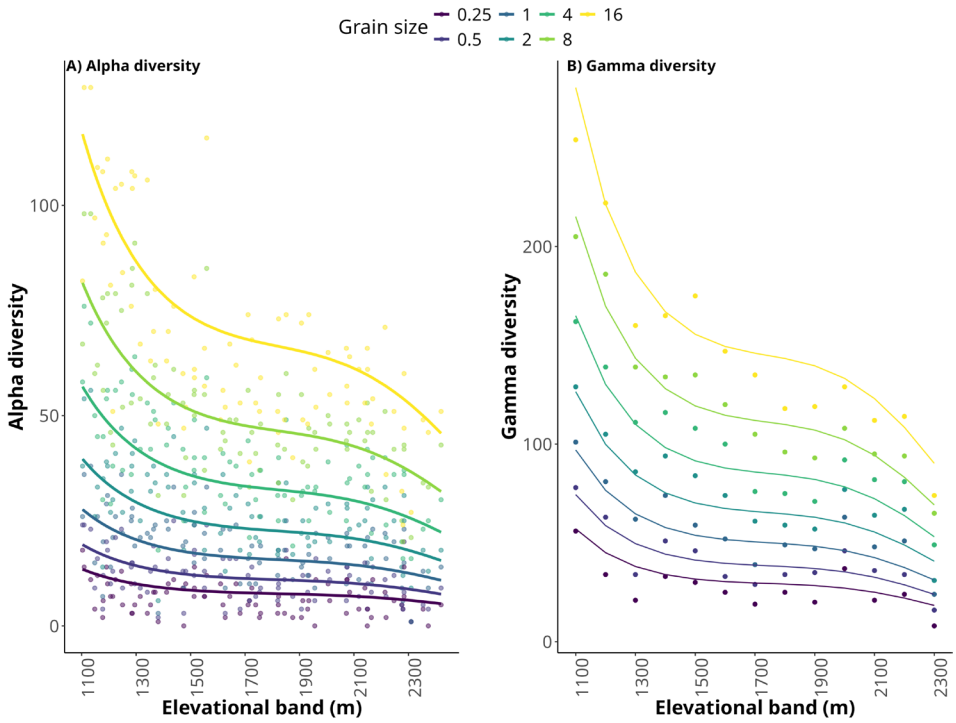

FIGURE 2 | Cubic relationship between species richness (alpha diversity) (A), gamma diversity (B), and the seven grain sizes (0.25 cm × 0.25 cm up to 16 m × 16 m) along elevation on Mount Velino, within 100-m elevational bands from 1100 m up to 2400 m a.s.l. The fitted lines represent the results of a negative binomial GLM, and dots observed diversity.

elevational band and grain size terms had a slightly higher Akaike weight than the model without interactions (0.56 vs. 0.44), the likelihood ratio test did not find the more complex model to be significantly better than the model without interaction ($p = 0.09$) (Appendix S6).

3.2 | Alpha and Gamma Diversity as SA Relationships

The logarithmic SA relationship was evident across all the elevational bands for both alpha and gamma diversity (Figure 3). The likelihood ratio test confirmed a significant interaction between grain size and elevational band in modeling these logarithmic SA relationships ($p < 0.001$ for both cases). Incorporating this interaction, the R^2 values of the SA relationships were 0.81 for alpha diversity and 0.91 for gamma diversity. In "local" models for each elevational band, the logarithmic coefficients of the SA relationship were all significant but exhibited a geometric decline across elevation. Specifically, the coefficients decreased from 15 to 6.5 for alpha diversity and from 32 to 11 for gamma diversity (R^2 for alpha diversity decay = 0.82; R^2 for gamma diversity decay = 0.94).

3.3 | Beta Diversity Along Elevational Gradient

Using the Sørensen dissimilarity index, we did not detect a clear decreasing relationship between beta diversity and elevation (Figure 4A) that was evident when using Euclidean distance (Appendix S7). Instead, the pattern across elevational bands was inconsistent and not statistically significant (Figure 4B). Nevertheless, a strong scale-dependent effect emerged: The dissimilarity index decreased with increasing grain size (Figure 4A). Importantly, this effect interacted with elevation such that the negative impact of larger plot size on beta diversity was stronger at high elevations than at low elevations (interaction $p = 0.02$). For comparison, results based on Euclidean distances (Appendix S7) showed a different pattern, where increasing grain size reinforces but does not change from a positive to a negative correlation between dissimilarity and elevation.

3.4 | Similarity Decay With Distance

The correlation between the distances of the floristic composition of the subplots and the increasing geographic distances ranged from 0.26 to 0.63 (Figure 5), all of them statistically significant, and the correlation increased with the logarithm of grain size (Figure 5 and Appendix S7). Given that geographic distance and elevation are strongly correlated (the first two axes of a PCoA on geographic distances explain 98% of elevation variation), the correlation between geographic distance and Sørensen dissimilarity shows the spatial turnover given mainly through elevation but clearly scaling with grain size (Appendix S8).

4 | Discussion

Our study investigated how plant diversity patterns vary along an elevational gradient in the Central Apennines and how these patterns are influenced by spatial grain size. Using a nested

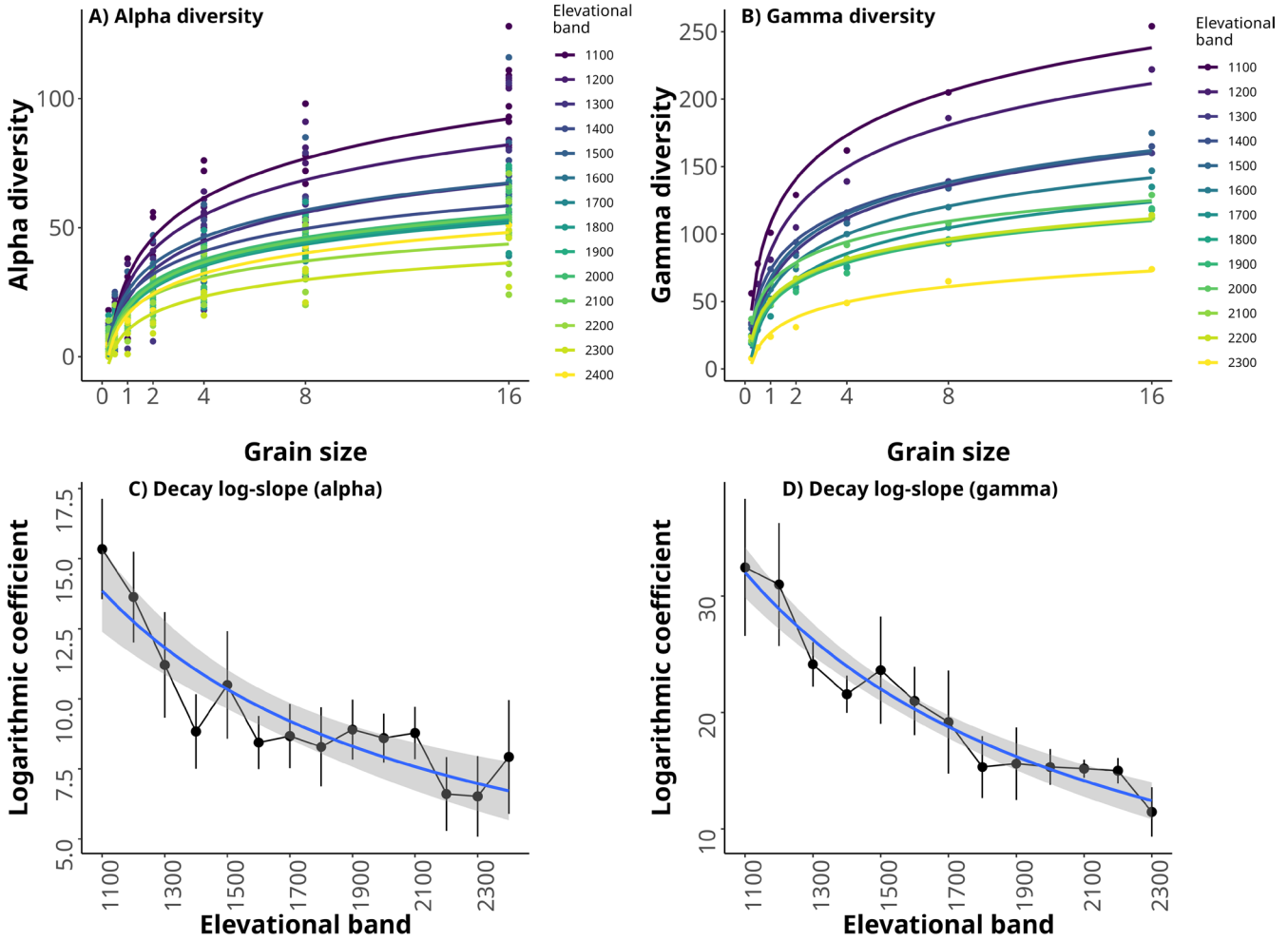

FIGURE 3 | Top: Species–area (SA) relationships in different elevational bands. SA relationship for (A) alpha diversity and (B) gamma diversity. Bottom: Decay with elevation of the coefficient of the SA relationship for (C) alpha diversity and (D) gamma diversity.

sampling design, we found that plant species diversity consistently declined with elevation, whereas spatial grain size strongly modulated the magnitude and structure of the diversity patterns.

Both alpha and gamma diversity declined monotonically with elevation, with no evidence of the hump-shaped pattern often described in global analyses of mountain gradients (Nogués-Bravo et al. 2008). Although hump-shaped trends are frequently described as the most common along an elevational species richness gradient, monotonic decreasing pattern is also frequently reported. The latter is particularly common in truncated gradients (Grytnes 2003; Grytnes and Beaman 2006; Grau et al. 2012), as observed in our study area, where species richness consistently declined monotonically along the elevational gradient. However, a truncated gradient hardly applies in our study area as only the upper elevational band is truncated, and the study area is very regular between 1300 and 2200 m a.s.l. This decline likely reflects not only the progressive intensification of environmental constraints along elevation, in particular temperature and the related growth period, but also precipitation, seasonality, soil, geological, topographical and geomorphological characteristics, and land use (Lomolino 2001; Vittoz et al. 2010). Thus, the absence of a hump-shaped pattern may not reflect the truncated upper part of the gradient.

Spatial grain size had a strong and consistent effect on alpha and gamma diversity (Figure 2). As expected, both alpha and gamma diversity increased with spatial grain size, in accordance with the SAR (Drakare et al. 2006). Importantly, however, we found that both slope and intercept of the SAR declined with elevation, suggesting that higher elevations support fewer species per unit area and that species accumulation with area occurs more slowly. Notably, this decline occurred most rapidly at the lower part of the elevational gradient between 1100 and 1400 m a.s.l. (Figure 2). One possible explanation is that low elevations host a high density of microhabitats and fine-scale heterogeneity, leading to high initial richness within small grains but a rapid saturation with increasing area, which reduces the SAR slope. In addition, past human activities at lower elevations (e.g., land use, disturbance, small-scale landscape heterogeneity) may have further contributed to this pattern by enhancing local compositional turnover (Cutini et al. 2012; Kemppinen et al. 2024). The decline is also stronger when the grain size increases.

The relationship between beta diversity (species turnover) and elevation was inconsistent. Across elevational bands, Sørensen dissimilarity did not reveal a clear monotonic decline with elevation, and correlations were generally weak and not statistically significant (Figure 4A). However, there is an interaction between

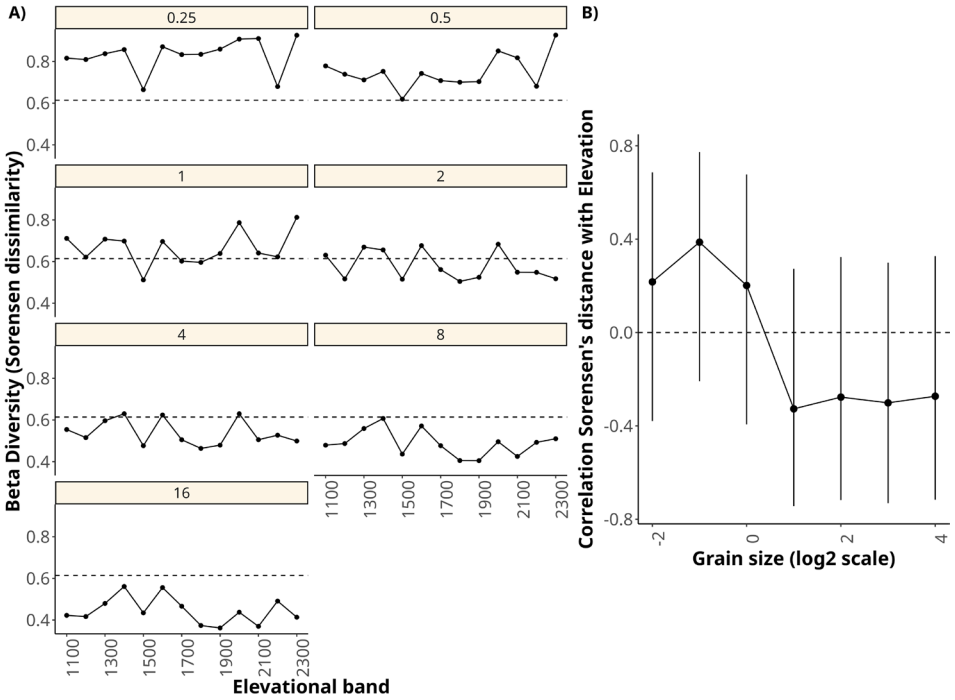

FIGURE 4 | (A) Relationship between Sørensen's dissimilarity and elevation for each 100-m elevational bands at different grain sizes (in squared meters; facet plot titles indicate subplot size). Points are the mean Sørensen dissimilarity, and the dashed horizontal line across the panels represents the mean Sørensen dissimilarity value for the whole dataset. (B) Correlation between Sørensen's distance and elevation across grain sizes; all of them are statistically nonsignificant but switch from a positive to a negative sign for grain sizes bigger than one square meter.

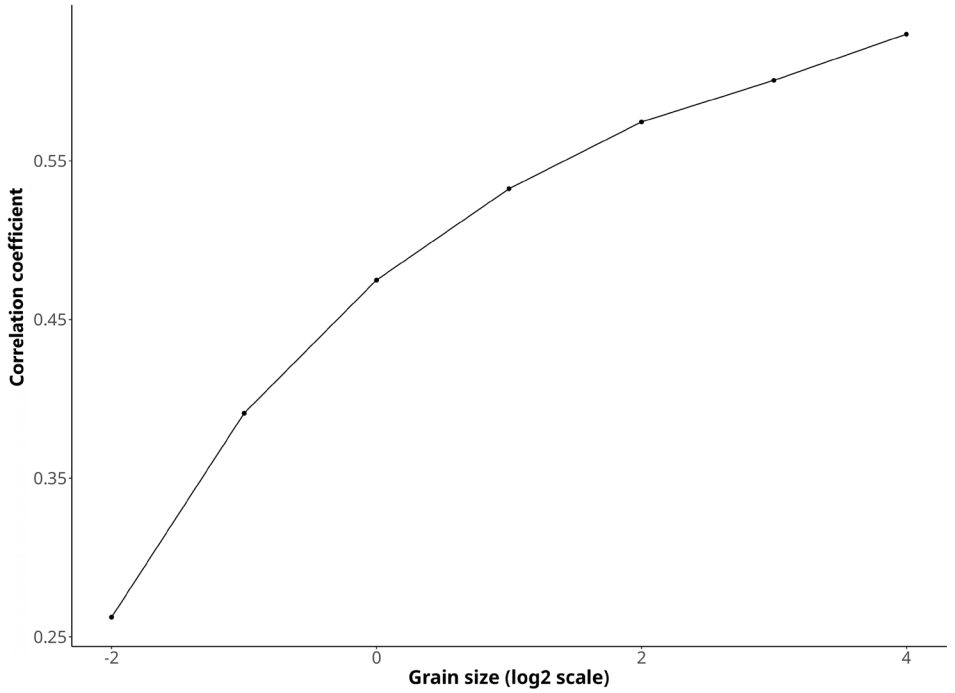

FIGURE 5 | The correlation between the pairwise Sørensen dissimilarity matrices of the species composition and the increase in geographic distance with grain size.

elevation and beta diversity, as spatial grain size strongly influenced it. We found that beta diversity consistently decreased with increasing grain size (Figure 4). This is because the fine spatial grain sizes reflected the stochastic species occupancy patterns, whereas the larger sizes reflected that fewer new species were encountered from the local pool at a given elevational band (Nekola and White 1999; Barton et al. 2013; Tan et al. 2017).

At smaller spatial grains, the relationship between beta diversity and elevation was positive but not statistically significant,

preventing firm conclusions (Figure 4A). However, the vegetation being more open at high elevation at Mount Velino, the fine grain sizes captured fewer species, leading to a higher turnover and a positive correlation with elevation. On the contrary, with a decrease in microhabitats, the larger grain sizes had a more similar species composition due to homogenization, leading to encountering even fewer new species, hence a lower turnover and a negative correlation with elevation.

Therefore, harsh climatic conditions act as strong ecological filters, promoting homogenization of community composition at coarser spatial grains (Kraft et al. 2011; Wang et al. 2012; Tello et al. 2015). At finer grains, by contrast, stochasticity and local environmental heterogeneity may buffer this filtering effect, resulting in greater variability among plots even under stressful conditions.

Furthermore, the distance decay in floristic composition across the entire study area, measured as the correlation between Sørensen dissimilarity and geographic distances, clearly increased with spatial grain (Figure 5). At fine spatial grains, turnover is largely stochastic and shows little relationship with either geographic distance or elevation. At larger spatial grains, however, plots capture a larger fraction of the local species pool. This increases the probability of including species restricted to elevational zones or rare species confined to specific habitats, thereby strengthening turnover with distance (Nekola and White 1999; Soininen et al. 2007).

Along the Velino massif, beta diversity was primarily influenced by elevation rather than geographic distance. The correlation between Sørensen dissimilarity and geographic distance within elevational bands was weak and inconsistent across spatial grains, indicating that geographic distance per se played a minor role. Instead, compositional turnover largely reflected elevational differences, consistent with the strong correlation between geographic and elevational distances in our sampling design.

The influence of elevation on beta diversity can be attributed to environmental conditions harshening at higher elevations (Gilbert and Lechowicz 2004; Nekola and White 1999). This effect is further explained by the replacement of plant communities along the elevation gradient (Nekola and White 1999), coupled with the filtering of species based on their physiological tolerance to climatic conditions (Ellenberg 1988; Körner 2021). These results additionally sustain the temperature-physiography hypothesis, which states that species richness along the elevational gradient is shaped by temperature and microhabitat diversity (Theurillat et al. 2003; Vittoz et al. 2010).

The nested sampling approach was essential to reveal how diversity patterns along the elevational gradient depend on spatial scale. For example, by comparing different spatial grains we observed that alpha and gamma diversity consistently declined with elevation, but the strength of this decline varied with sizes, being steepest at lower elevations where environmental heterogeneity is higher.

The method also showed that the SAR itself changes with elevation, with both the slope and intercept decreasing at higher altitudes, indicating weaker species accumulation. Furthermore, nested sampling allowed us to highlight contrasting patterns of beta diversity: while larger grains revealed a homogenization of communities at higher elevations, smaller grains reflected only stochastic patterns. Together, these insights clarify that spatial scale mediates the relative influence of environmental filtering and neutral processes along the gradient, something that would have been overlooked without a multi-scale design.

Moreover, this approach proved valuable in identifying species diversity patterns, thereby improving our capacity to analyze biodiversity patterns and inform conservation planning (Margules and Pressey 2000; Wilson et al. 2006; Arponen 2012).

5 | Conclusion

This study provides evidence that both spatial grain size and elevation influence patterns of plant diversity along an elevational gradient, although the strength of these effects varies among diversity components. For beta diversity, Sørensen dissimilarity did not reveal a consistent monotonic decline with elevation, but we detected a significant interaction between elevation and grain size: The reduction in species turnover with increasing grain size was more pronounced at high elevations than at low elevations. The mean Euclidean distance, included as a sensitivity test, showed stronger apparent declines with elevation and clearer distance–decay relationships, but these largely reflected the confounding effect of elevation on geographic distance. In parallel, we also observed general declines in species richness (alpha and gamma diversity) with increasing elevation and complex responses to elevation captured by polynomial terms, though these were not consistently significant. Grain size showed a clear positive effect on explanatory power, as model deviance explained increased logarithmically with grain size, especially from small to intermediate spatial grain. Patterns of beta diversity indicated a clear relationship with geographic distance, with strong correlations between geographic distance and elevation, suggesting that elevational variation is a key driver of community turnover.

Our nested analytical framework offers a structured way to disentangle the contributions of scale and environment to diversity patterns. However, future work should refine this approach by incorporating different life forms and strategies, as this would likely reveal additional insights into how plant functional strategies mediate diversity responses to elevation and scale.

Author Contributions

L.R., M.D.M., and G.V.M. conceived the research idea following a preliminary analysis of M.I. J.-P.T. conceived the sampling design for the long-term monitoring project. J.-P.T. and M.I. collected the data with the help of M.C. L.R. and G.V.M. performed the statistical analyses. L.R. and M.D.M. wrote the paper. All authors discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting the findings of this study were collected by the authors. Data from 2 m × 2 m plots have been archived to and are available through the European Vegetation Archive (EVA) under the dataset name "Central Apennines-Italy-MIUR 2005—GIVD: EU-IT-022." The data custodian is Jean-Paul Theurillat (jean-paul.theurillat@unige.ch). The complete dataset used in this study is provided as Supporting Information; species names were replaced with alphanumeric codes, as species identity was not required for the analyses. The code used to reproduce the analyses is openly available at: rxccx96/Effects-of-grain-size-on-plant-diversity-patterns-in-a-Mediterranean-mountain.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Presence/absence data supporting the findings of this study. Species identities are reported as alphanumeric codes. **Appendix S2:** Plot-level metadata, including geographic coordinates, elevation, and additional site characteristics. **Appendix S3:** Distribution of plots across elevational bands. **Appendix S4:** Effect of altitude on alpha diversity. **Appendix S5:** Deviance explained by elevation and grain size. **Appendix S6:** Likelihood ratio tests. **Appendix S7:** Correlation of beta diversity with elevation using Euclidean distance. **Appendix S8:** Relationship of geographic distances with elevation.