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Distribution of Plant Species and Dispersal Traits along Environmental Gradients in Central Mediterranean Summits

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Abstract: High-mountain ecosystems are spots of plant diversity in which species composition and traits depict a long evolutionary history of species adaptation to steep environmental gradients. We investigated the main trends in plant species composition and reproductive and dispersal traits (pollen vector, diaspore appendages, dispersal of diaspores and fruit type) in central Mediterranean summits in relation to environmental factors (altitude, aspect, debris cover and slope). Based on 114 plots, with floristic and environmental data collected in the year 2016 on alpine calcareous grasslands in the central Apennines, we explored how species composition varies in relation to environmental factors using CCA (canonical correspondence analysis). Then, we analyzed the relationships among species presence, the occurrence of reproductive and dispersal traits and environmental variables. We used for this analysis the fourth-corner model approach. Our results highlight a consistent response of floristic composition and of structural and ecological characteristics to environmental gradients, with elevation and debris cover being the most important ones. The environmental characteristics of the analyzed ecosystems (e.g., steep slopes and harsh environments) combined with the persistence of perennial plant species already present in each stand, the high precision of pollination and the prevalence of short-distance dissemination strategies should allow the calcareous endemic plant communities of the analyzed Mediterranean summits to be conserved at least for a mid-term period slowing down the expansion of the warm-adapted species, less adapted to the local environmental constraints.

Keywords: alpine vegetation; calcareous high mountains; fourth corner; plant traits; pollen and diaspore dispersal

1. Introduction

Mountain environments throughout the world host highly specialized flora and fauna [1]. In Europe, mountain habitats contain approximately 20% of the native flora [2], most of which are endemics and rare [3] and constitute hotspots of plant diversity [1,4,5]. Such diversity is in part due to the particular climatic conditions that rapidly vary over very short distances along altitudinal gradients. In addition, high topographic diversity results in great habitat diversity, which in turn promotes high levels of specialization and species richness. In the Mediterranean area, high-elevation habitats are represented by few isolated peaks hosting a high number of endemic and rare plants of

great biogeographic interest [3]. Such mountain environments [6–8], are particularly threatened by global warming because of their pronounced orographic discontinuity, which make them worryingly vulnerable to biodiversity loss [9].

In the mountains of the temperate biome, many species have shifted their upper distribution limit upslope in conjunction with recent climate change, leading to growing species richness values in mountain summits [10]. Simultaneously with the upward shift of species, a decline in cold-adapted species is occurring [11] mainly due to the sensitivity of cold adapted species to warmer temperatures [12,13] and to their weak competitive ability compared with species from lower altitudinal belts [14].

The ability of plants to respond to warmer conditions (i.e., by colonizing new areas or changing local abundance) depends on both the reproductive/dispersal traits of the species that support different colonization capacities and on the local ecological conditions, which act as filters of plant establishment, selecting those species for which the local conditions of the site are suitable [15]. This is particularly evident in mountain ecosystems, where reproduction and dispersal strategies play a key role in ensuring species persistence. High mountains can be considered cold deserts characterized by a scarcity of soils suitable for germination and a short vegetative period in which seeds can develop and disperse.

In the context of climate change, the identification of the plant traits of newly appearing or disappearing species can help to understand the ongoing selection processes, which are important for predicting future species assemblages [8,16–19]. Moreover, regarding the distribution pattern of reproductive traits, the pollination spectra could be processed in the same way for various areas, allowing the expression of the availability and effectiveness of the various pollination agents in relation to the climate and the fauna [20].

In this framework the effects of altitude and aspect on the composition and dispersal traits (pollen vector, diaspore morphology, dispersal of diaspores, fruit type) of vascular plant species can provide invaluable information about the adaptive value of plant characteristics during climate change [21]. Indeed, in high elevation ecosystems, as altitude increases, climatic conditions become more severe for plant growth due to lower mean temperatures, higher solar radiation, shorter vegetative periods, etc. [22]. These climatic constraints play a key role in the selection and evolution of plants [23,24]. Plant species show a series of characteristics (or traits) that enable them to live and reproduce in these extreme environments. For example, as altitude increases, some growth forms tend to be more abundant [17,25]. Concerning the dispersal traits, recent research has affirmed that the alpine flora tends to have a short-distance seed dispersal and it is likely to be threatened by a migration lag as the local climate undergoes rapid changes [11,21,26]. Reproductive strategies in particular tend to differentiate along altitudinal (and climatic) gradients [26,27]. In addition to altitude, small-scale topography and geomorphological processes (nivation niches, long lasting snow cover, slope instability etc.) also play an important role in creating a great variety of microhabitats that differ significantly in species composition over short spatial scales [28–30]. For example, the thermal regimes that affect plant growth differ among aspects, leading to high species richness in the southeastern exposition of north-temperate orobiome [22]. On the other hand, the microhabitat diversity may allow the cold-adapted species to maintain a refugium along valley slopes following local temperature gradients and within topographic/geomorphological traps [24]. There is a growing body of scientific literature that addresses the distribution of plant traits in alpine environments; still, most of these studies are focused on only a few environmental variables (e.g., [18]) or describe limited areas (e.g., [21,31]). In this context, analyzing the relationships between plant traits and the environment in other ranges would be very useful to gain a more global understanding of plant adaptations and a better awareness of the assembly rules and composition of plant communities [25]. In this context, the present study explores the main trends in plant species composition and reproductive and dispersal traits in central Mediterranean summits in relation to environmental factors. Specifically, we organized our analysis into two steps: we first explored how species composition varies in relation to environmental factors (altitude, aspect, debris cover and slope), and we then analyzed whether these patterns are mirrored in reproductive and dispersal plant traits (pollen vector, diaspore appendages, dispersal of diaspores

and fruit type). In this way, we should be able to formulate a hypothesis about the ability of species to maintain their position and/or colonize new areas under warmer conditions.

In relation to the environmental variability that characterizes Mediterranean mountain summits and specifically the central Apennines [32], we should expect a consistent response in floristic composition and plant traits (e.g., [22,28]). Moreover, as in most of the terrestrial ecosystems and specifically in stressful environments, reproductive traits should be particularly effective in ensuring that blossoms produce an abundance of fertile seeds with a minimum investment of energy, for instance, through highly precise pollination mechanisms [33]. Furthermore, in isolated mountain summits, diaspore traits should ensure that seeds remain inside suitable habitats [34] and allow them to avoid dispersing to lower altitudinal belts characterized by different unfavorable environmental conditions.

The identification of floristic gradients in response to environmental variability should offer sound bases for better interpretation of the effects of climate and land use change on high-mountain vegetation and should allow the responses of different species to changes in the extreme conditions of mountain summits to be understood [28].

2. Materials and Methods

2.1. Study Area

The study area is representative of Mediterranean high mountains [35] includes the widest high-mountain zone with alpine vegetation of the Apennines and comprises the higher sectors (from ~2400 to 2790 m a.s.l.) of Majella National Park (Figure 1). This area is characterized by a large limestone ridge that reaches 2793 m a.s.l. (Mt. Amaro) and lies along a north-south axis between the latitudes 42°00'14" N (Guado di Coccia) and 42°9'33" N (Majelletta). The highest part of the massif is characterized by a wide plateau summit, bordered by steep inclinations, incised by deep valleys [36]. We specifically analyzed the vegetation of the ridges (sensu [7]) characterized by *Silene acaulis* subsp. *acaulis* and *Viola magellensis* plant communities.

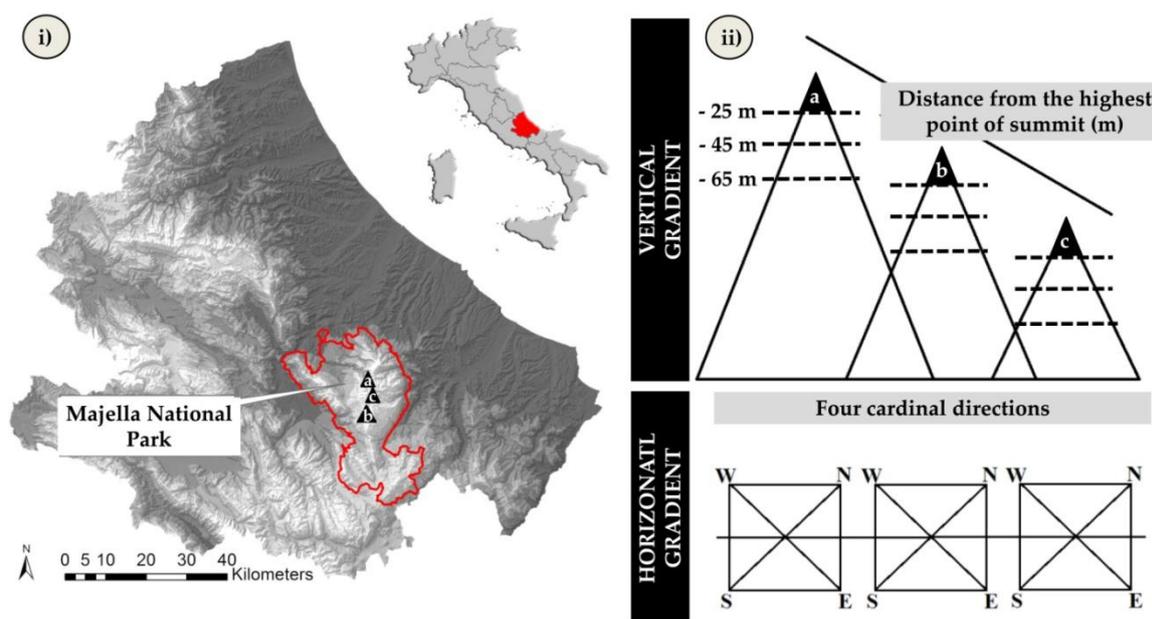


Figure 1. (i) Study area (triangles represent the analyzed mountain summits of the Majella massif: (a) Mt. Mammoccio, (b) Mt. Macellaro, (c) Mt. Femmina Morta). (ii) scheme representing the GLORIA multi-summit approach [36] followed for collecting data in the additional plots [37].

2.2. Data Collection

Floristic and environmental data were collected in 144 plots (1 m²) in summer 2015 on three mountain summits of the Majella massif (Mt. Femmina Morta, 2405 m a.s.l.; Mt. Macellaro, 2635 m a.s.l.; and Mt. Mammoccio, 2727 m a.s.l.). The sampling design followed the multi-summit approach of the GLORIA project [37]; see Figure 1, involving data collection in clusters of four grid plots located at 25, 45 and 65 m downslope of the highest point of each mountain summit and placed in each of the four cardinal directions. In short, we sampled the four cardinal directions of three summits at three distances from the summit point, for a total of 36 clusters of 4 plots, i.e., 144 plots. For each plot, we compiled a complete list of the vascular plant species and a set of environmental variables (elevation, slope, debris cover and aspect: northness and eastness).

Nomenclature of plant species conforms with Bartolucci et al. 2018 [38].

2.3. Plant Traits

To address our aims, relevant plant dispersal traits were selected and gathered from the literature. This approach was chosen because it would have been impossible to assess and measure all of the traits in the field, given the considerable number of plots and species. The traits represented the following main plant reproduction and dispersal functions: pollen vector, dispersal of diaspores, fruit type and diaspore appendages.

The data were collected from different sources, including databases (LEDA traitbase: A database of life-history traits of Northwest European flora and VIOLA: the VegetatIOn database of the central Apennines [39,40]) and the literature [27,41–45]. When possible, missing values were extrapolated from closely related species. Traits with many multiple states were simplified by grouping similar states together. The traits and states that were analyzed are listed in Table 1. For a complete list of species along with the relative families and dispersal traits see Table A1.

Table 1. Groups of traits considered along with references of sources and states.

Group of Traits	Traits—References	Trait States
Fruit type	Simplified from Landolt et al. [43]	Follicule Capsule Achene Legume Siliqua
Pollen vector	Simplified from Klotz et al. [46]; Aeschmann et al. [45]	Insect only Selfing Wind
Dispersal of diaspores	Simplified from Landolt et al. [43]	Zoochore Autochore Meteochore
Diaspore appendages	Klotz et al. [46]; Pignatti [41]	Awn (awn, hooks, calyx) Nude (no appendage) Pappus Wings (wings or fringes)

2.4. Data Analysis

To explore vegetation patterns in relation to environmental gradients (elevation, debris cover, slope, aspect: northness and eastness), we performed a direct gradient analysis using CCA (canonical correspondence analysis). First, we checked for correlation among environmental variables performing a Pearson correlation analysis. None of all variables exceeded the chosen 0.7 threshold (Figure A1), thus we retained them for subsequent analysis. We analyzed a matrix of 144 plots × 80 species, and we considered only the species with more than two presences. Monte Carlo tests (999 permutations)

of constrained ordination scores against environmental variables were performed to assess the significance of the correlations. CCA analysis was performed using the *vegan* package in R [47].

Then, we analyzed the relationship between species presence, traits occurrence and environmental variables using the fourth-corner model approach [48,49]. Briefly, we explored trait responses to environmental gradients by the simultaneous analysis of the information contained in three tables: L (species distribution across samples), R (environmental characteristics of samples), and Q (species traits) [50]. We adopted the model-based solution to the fourth-corner model in which generalized linear models (GLMs) are fitted for species presence (L) as a function of a matrix of traits (Q) and a matrix of environmental predictors (R) and their 2-way interactions [49,51]. The interactions between species traits and environmental variables are the fourth-corner terms that allow quantification of how the environmental response of species changes as traits change. We used the *traitglm* function in the *mvabund* R package [51] to fit such model. Generalized linear models were fit using a Lasso penalty [52], which automatically performs model selection by setting to zero any interaction coefficients that do not reduce the Bayesian Information Criterion (BIC). The statistical significance of the fourth-corner terms was assessed by an analysis of deviance using 999 re-samples [47]. We graphically represented the fourth-corner coefficients using the *levelplot* function from the *lattice* package in R [53].

3. Results

The CCA (Figure 2) highlights the presence of clear environmental gradients mainly due to altitude, slope and debris cover. The constrained explained variance is high at approximately 27%, which indicates that the abiotic factors significantly contributed in disentangling the vegetation composition pattern. The first two axes accounted for 72% of the constrained variance, with the first axis explaining 55% ($F = 0.530$, $p < 0.001$). The other axes were not significant. The first axis was mainly correlated with debris cover (biplot score = -0.82) and elevation (biplot score = -0.77). The second axis was mainly correlated with slope (biplot score = 0.96) and, to a lesser extent, with elevation (biplot score = -0.49) and eastness (biplot score = -0.33). In correspondence with the first axis, two groups of species that occupy sites with similar environmental characteristics were also evident. One group, on the left (negative scores on the first (CCA1) axis—Table 2), is composed of cryophilous species such as *Crepis pygmaea*, *Alyssum cuneifolium*, *Saxifraga exarata* subsp. *ampullacea*, *Veronica aphylla* and *Galium magellensis* that tend to occur at higher altitudes in areas rich in debris. A second group, on the right, encompasses thermophilic species such as *Poa molinerii*, *Saxifraga tridactylites*, *Polygala alpestris* subsp. *alpestris*, *Oxytropis campestris* and *Sempervivum arachnoideum* that occur at lower altitudes. In correspondence with the second axis, two groups of species were also evident. One group, in the upper sector (positive scores on the second (CCA2) axis—Table 2), is composed of species adapted to steep slopes, such as *Veronica aphylla* and *Euphrasia minima* subsp. *minima*. A second group, on the lower sector (negative scores in the second (CCA2) axis), encompasses species such as *Trifolium pratensis* subsp. *semipurpureum* and *Ranunculus brevifolius* that occur on moderate slopes.

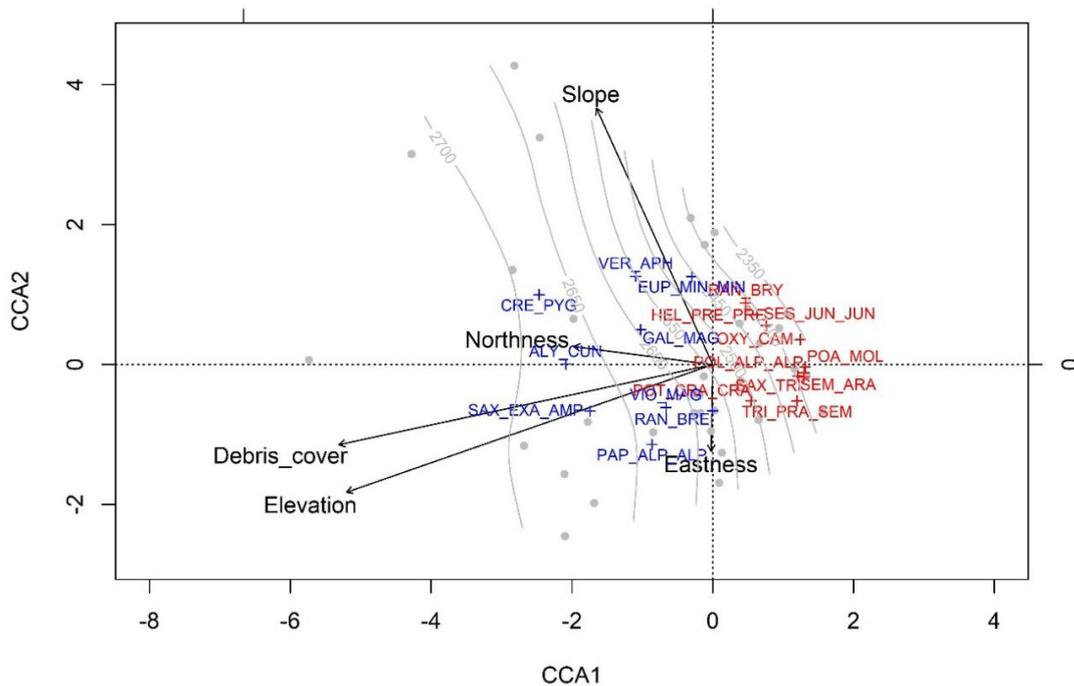


Figure 2. Biplot of the canonical correspondence analysis (CCA). Only the 20% of the species with the best fits are shown. Gray dots indicate the sites, isolines, site altitudes, and arrows the environmental variables. The species acronyms reported in two colors (blue: cryophilous; red: termophilic) are defined in Table 2.

Table 2. Species scores on the first two CCA axes. Only the 20% of the species with the best fits are shown. For each species, the complete name, the acronym and the pollination and dispersal traits are reported. pv = pollen vector, dd = dispersal of diaspores, ft = fruit type, sa = diaspore appendages. The species acronyms are reported in two colors, blue: cryophilous and red: termophilic.

Species	Acronym	CCA1	CCA2	pv	dd	ft	sa
<i>Crepis pygmaea</i>	CRE_PYG	−2.47	0.97	self	meteochores	achene	pappus
<i>Alyssum cuneifolium</i>	ALY_CUN	−2.08	0	insect	autochores	siliqua	wings
<i>Saxifraga exarata</i> subsp. <i>ampullacea</i>	SAX_EXA_AMP	−1.77	−0.65	self	autochores	capsule	nude
<i>Veronica aphylla</i>	VER_APH	−1.1	1.26	insect	meteochores	achene	pappus
<i>Galium magellensis</i>	GAL_MAG	−1	0.5	wind	zoochores	achene	nude
<i>Papaver alpinum</i> subsp. <i>alpinum</i>	PAP_ALP_ALP	−0.84	−1.13	insect	meteochores	capsule	nude
<i>Viola magellensis</i>	VIO_MAG	−0.64	−0.62	insect	autochores	capsule	nude
<i>Euphrasia minima</i> subsp. <i>minima</i>	EUP_MIN_MIN	−0.31	1.26	self	autochores	capsule	nude
<i>Ranunculus brevifolius</i>	RAN_BRE	0	−0.65	insect	meteochores	achene	awn
<i>Ranunculus breynianus</i>	RAN_BRY	0.48	0.89	insect	meteochores	achene	awn
<i>Potentilla crantzii</i> subsp. <i>crantzii</i>	POT_CRA_CRA	0.55	−0.51	insect	autochores	achene	awn
<i>Sesleria juncifolia</i> subsp. <i>juncifolia</i>	SES_JUN_JUN	0.63	0.72	wind	meteochores	achene	awn
<i>Helictochloa praetutiana</i> subsp. <i>praetutiana</i>	HEL_PRE_PRE	0.76	0.58	wind	meteochores	achene	awn
<i>Trifolium pratensis</i> subsp. <i>semipurpureum</i>	TRI_PRA_SEM	1.17	−0.49	insect	zoochores	legume	nude
<i>Sempervivum arachnoideum</i>	SEM_ARA	1.19	−0.15	insect	autochores	follicle	nude
<i>Oxytropis campestris</i>	OXY_CAM	1.23	0.36	insect	autochores	legume	nude
<i>Polygala alpestris</i> subsp. <i>alpestris</i>	POL_ALP_ALP	1.28	−0.1	insect	meteochores	capsule	awn
<i>Saxifraga tridactylites</i>	SAX_TRI	1.28	−0.17	self	autochores	capsule	nude
<i>Poa molinerii</i>	POA_MOL	1.3	−0.02	wind	meteochores	achene	awn

Concerning the different strategies of pollination, we observed a clear dominance of entomophilous species, with 67% of the analyzed flora pollinated by insects (Table 3). Moreover, entomophilous species are present in 62% of the plots. On the other hand, ~20% of the species have a wind pollination dispersion strategy, and this trait is present in ~30% of the plots. Self-pollination occurs in few species, and this character is present but rare in the sampled plots (~9% of the plots).

Table 3. Abundance of the different traits in the analyzed flora and in the sampled plots. N: number of sampled species; N%: percentage of the sampled species; Plots: number of plots in which each trait is present; Plot%: percentage of plots in which each trait is present.

Group of Traits	Traits	N	N%	Plots	Plot%
Pollen vector	insect	39	67.24	359	62.76
	self	7	12.07	50	8.74
	wind	12	20.69	163	28.50
Dispersal of diaspores	meteochores	24	41.38	199	34.79
	autochores	28	48.28	309	54.02
	zoochores	6	10.34	64	11.19
Seed appendages	awn	12	20.69	105	18.36
	nude	35	60.34	384	67.13
	pappus	7	12.07	45	7.87
	wings	4	6.90	38	6.64
Fruit type	achene	27	46.55	250	43.71
	capsule	21	36.21	229	40.03
	follicle	2	3.45	15	2.62
	legume	5	8.62	42	7.34
	siliqua	3	5.17	36	6.29

Analyzing the dispersal of diaspores (Table 3), we found that autochory, which accounts for 48.28% of the analyzed flora, is the most widespread dispersal mode, followed by meteochores (41.38%). The zoochory dispersion mechanism plays a less important role in this environment, with only 10% of species being dispersed by animals.

Regarding the presence and characteristics of seed appendages (Table 3), ~60% of the species have nude seeds, and the other 40% have awns, a pappus or wings.

Concerning fruit types (Table 2), the species with achenes and capsules totaled 46.5% and 36.21% of the whole species set, respectively, whereas the other fruit types reached ~17%.

According with the fourth-corner analysis (Figure 3), the species traits explain a significant amount of the variation in species distribution along the environmental variables (deviance = 134.2, $p = 0.001$). Indeed, each plant trait presented a specific behavior, but a general trend could be observed with stronger correlations with altitude and slope, weak correlations with debris cover and very weak relationships with aspect (as shown by the coefficient values).

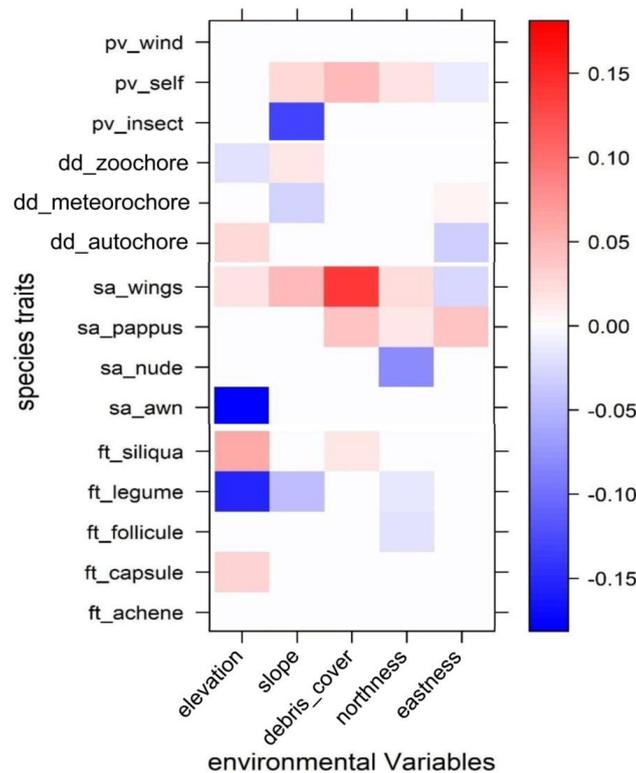


Figure 3. Results of the fourth-corner model. Traits are colored according to their fourth-corner coefficients: red indicates a significant positive trait-variable association, and blue indicates a significant negative trait-variable association. Color depth indicates the strength of the trait-variable association. pv: pollen vector, dd: dispersal of diaspores, sa: seed appendages, ft: fruit type.

The fourth-corner analysis of pollination strategy (Figure 3) revealed that species pollinated by insects have a negative association with slope, while self-pollinated species tend to prefer environments characterized by north-facing, steep slopes with high debris cover. Concerning the dispersal of diaspores, the results do not show any significant trends; only slight preferences of autochorous species for higher altitudes and of zoochorous species for lower altitudes were observed. However, the fourth-corner model suggests that meteochorous species avoid steep slopes and prefer northern aspects (high value of northness).

Concerning the diaspores appendages (Figure 3), most of the species have nude diaspores (Table 2), and these species are widely distributed across the different environmental gradients with a weak negative relationship with northness. The species with winged seeds show a clear preference for extreme conditions and are positively correlated with altitude, slope, debris cover and a cold aspect (northness). In contrast, the species with awned seeds have a clear preference for lower elevations.

The distribution of fruit type is mainly related to the altitudinal gradient, with the species with siliques and capsules preferentially present at higher elevations and with legumes present at lower areas (Figure 3). There is also some evidence that legumes decrease at higher slopes and northness values.

4. Discussion

Our results revealed that differences in species composition and trait distributions are related to abiotic factors and that elevation and debris cover in particular seem to play the most important roles in determining such differences.

In particular, there was evidence of a pronounced change in species composition along the altitudinal gradient, with a clear assemblage of species adapted to harsh environmental conditions with

poor soils, high debris cover and low temperatures at higher elevations (e.g., *Alyssum cuneifolium*, *Viola magellensis*, *Galium magellensis*) and a group of species living in milder conditions in the lower sectors (*Oxytropis campestris*, *Sesleria juncifolia* subsp. *juncifolia*, *Helictochloa praetutiana* subsp. *praetutiana*). Our results correspond to a common trend in high mountains in which elevation is related to both decreasing temperatures and increasing rock and debris cover [28]. Indeed, in high-mountain environments, a slight increase in altitude often corresponds to a significant increase in stressful conditions [18,22].

On the other hand, in the central Apennines, as in other mountain systems [17,21,28,54–57], aspect plays a less-pronounced role than altitude does in explaining species and trait distribution patterns. Despite the subordinate role of aspect relative to elevation in shaping plant trait distributions [17,28,58,59], recent research has found that in a global change scenario, warmer aspects of alpine summits support higher numbers of colonization events and thus higher richness values [60]. In this context, aspect should play a key role in determining the pace of climate change-induced migration processes [22].

Regarding pollination, an entomophilous strategy is the most common one in the analyzed area. This strategy, quite common in terrestrial ecosystems, has the evolutionary advantage of high pollination precision [33] which ensures that the blossoms will produce many fertile seeds. In pollination ecology, ensuring pollen dispersal precision is crucial for the persistence of many species, and the evolution of pollination mechanisms in entomophilous blossoms is, on the whole, evolution towards an increasingly higher precision [61]. Indeed, in ecosystems characterized by sparse vegetation, the role of entomophilous pollination should be decisive in ensuring reproductive success. Even though some authors argue that the activity of insects in high mountains is limited [62,63], a study in the Alps demonstrated that the blossom visitation rates in high-mountain and foothill vegetation are comparable [64]. The other pollination strategies (e.g., wind and self-pollination) are less represented in the analyzed summits. Wind pollination is a good strategy in windy areas but has the drawback of requiring the production of high amounts of pollen to fertilize few blossoms. Such low fertilization precision should represent a further limit for small, isolated populations of anemophilous species that have no chance or reduced chances of cross-pollination [33]. On the other hand, even if self-pollination were an adequate functional behavior in environments in which pollen cannot easily reach mature blossoms, autogamy would still lead to negative genetic effects by increasing homozygosity and could promote the splitting off of microspecies [33].

Pollination traits (entomophily, anemophily, autogamy) heterogeneously vary across the different environmental gradients. For example, we found a negative relationship between the insect pollination strategy and steep slopes, and such a relationship should be related to the preference of insects for flat areas with less wind stress [65]. On the other hand, the self-pollination strategy tends to occur only in extreme environments (debris-rich, steep, north-exposed slopes) because, in such harsh conditions, self-pollination may be the only strategy allowing the species' persistence.

Concerning the fruit types, the dominance of achenes and capsules is evident, while the other fruit types (legume, follicle and siliqua) together only represent 15% of the total species. The distribution of fruit types is similar to the patterns observed by Pellissier et al. [25] the Alps, with achenes and capsules being dominant in the high mountains. As observed in the Alps, species with capsules and siliqua in the central Apennines also tend to prefer the higher sectors [25]. On the other hand, species with achenes are widely distributed along the entire altitudinal gradient. Matteodo et al. [17] observed an increase in species with achenes in the higher vegetation belts of the Alps and related the pattern to such species' good colonization ability. Similarly, the wide distribution of species with achenes in central Apennine summits is most likely related to their colonization ability, which could be considered a pre-adaptation to climate warming [17]. As observed by Pellissier et al. [25] in the Alps, also in the Apennines species with legume tend to only rarely occur at higher elevations.

In the analyzed summits the most common strategies for the dispersal of diaspores are meteochores and autochores, which together account for 90% of the total sampled flora. Meteochores species are

widely spread throughout the world but are especially prominent in open habitats as summits and high mountain slopes, steppes, prairies, garrigue, screes and deserts [66,67]. Seed dispersal is often regulated by climatic conditions, and specifically, the local meteorological variability significantly impacts seed dispersal distances [33]. In alpine habitats, the presence of strong winds [68] and perhaps the low mammal density should favor meteochores dispersion [25]. Moreover, the observed abundance of species with autonomous seed dispersal in high-altitude environments, has been previously found in other open habitats and arid environments where competition for space is absent [28,30,33]. Indeed, in alpine stressful habitats, most plants show low specialized dissemination mechanism that may be more related to phylogeny than to function [29]. Here selection pressure on dispersal mechanisms is mostly random because of various environmental constraints (e.g., difficulties in setting seeds, low chance of seedling or juvenile establishment and intense slope dynamics). On the other hand, the low seed-dispersal distance might favor germination and survival around the parent plants [69] which in turn may serve as an additional facilitating factor during the establishment of new individuals. As suggested by [24,70], the resource limitation at higher elevations in alpine debris slopes should affect changes on inter-specific interactions that shift from competition to facilitation mechanisms.

Zoochore which is a common strategy for the dispersal of diaspores at lower altitudes, in disturbed habitats and in grazed vegetation types [71], is present but rare in the analyzed summits. The modest presence of this strategy is most likely related to the scarcity of epizoochorous dispersion [71] at higher altitudes [72].

As regards diaspore morphology, most of the analyzed flora have nude seeds, a characteristic that strongly differentiates the analyzed summits from several terrestrial ecosystems in which the presence of diaspore appendages is very common [73]. Such results could be explained by the tendency of alpine vegetation to adopt local-scale dispersal strategies (e.g., [74]). Indeed, local dispersal ensures that seeds settle close to the mother plant and prevents the seeds from dispersing to unsuitable habitats on lower mountains or in the foothills [34,75]. Regardless, when considering the species with seed appendages, an elevation gradient emerges. Similar to what was observed in the Swiss Alps [25] species with winged seeds tend to preferentially occur at higher altitudes, while species with awns tend to be more frequent at lower altitudes. Such variation was also described by Navarro et al. [76], who affirmed that winged seeds tend to occur in the highly stressed environments of mountain summits because the presence of wings provides a sort of lift to diaspores that allows them to be transported by winds. Concerning the presence of seeds with awns, it is important to note that when such a seed lies on the ground, the orientation of the awns allows the seed to lie obliquely on the ground, which is the optimum position for seed burial. Seeds with a pappus are scarce but distributed along the entire gradient, with a slight preference for sites with high debris cover. The distance that a plumed diaspore can travel depends not only on wind velocity but also on air humidity. In a dry atmosphere, the hairs of the plumes often spread out, thereby facilitating abscission and increasing buoyancy. In general, the low air humidity in high altitude environments should therefore aid in the dispersal of plumed diaspores [21].

It is interesting to interpret our results and compare them with recent findings in the context of the effects of climate change on high-mountain ecosystems. For instance, Matteodo et al. [17] and Ninot et al. [31] hypothesized a decrease in species with nude seeds, and at the same time they postulated an increase in species with winged seeds and species with a pappus in mountain summits. At the same time, Wipf et al. [77], in a multitemporal vegetation analysis of the Alps, demonstrated an increase in species with awns, such as grasses. Because many species with awned seeds, mainly graminoids, are thermophilic and frequent at lower elevations (subalpine belt) [25], we should expect an upward shift of such species. Similar processes have been observed in the Alps by recent resampling analyses in which, in addition the expansion of thermophilic species, a role of warmer conditions in the colonization and dispersal processes was also postulated [17,21]. Anyway, in the analyzed Mediterranean summits, the long persistence of species and the presence of several taxa characterized by nude seeds with a short dissemination distance that feed the local seed bank [30] should ensure the

persistence of the alpine grasslands for a mid-term period. The persistence of species together with the observed process of species filling caused by the increase in abundance of the species already present in alpine and subalpine grasslands [19,78], suggest that the pattern of dispersal strategies of summit vegetation in central Apennines will change slightly in the next decades.

5. Conclusions

This study offers a preliminary picture of the composition of plant dispersal traits across environmental gradients on central Mediterranean high mountains. The study of central Apennines uncovered an important influence of elevation and debris cover gradients on floristic species composition patterns and structural and ecological characteristics of alpine plant communities. We observed a steep floristic gradient that should offer sound bases for better interpreting the effects of climate change on high-mountain vegetation and that should allow the response of different species to changes in the extreme conditions of mountain summits to be understood [28]. In this context, considering the altitudinal gradient as a surrogate for temperature, we should expect an increase over time in the more thermophilic species (e.g., *Oxytropis campestris*, *Sesleria juncifolia* subsp. *juncifolia*, *Helictochloa praetutiana* subsp. *praetutiana*) in response to the ongoing increase in temperatures and global warming processes. In a similar way, concerning the debris cover and soil development gradient, the ongoing rise in soil nutrients in alpine environments due to higher rates of organic degradation and nitrogen deposition [79] should promote the slow expansion more mesic species, such as *Oxytropis campestris*, *Poa molinerii*, and *Sempervivum arachnoideum*.

The observed relationships among altitudes and the analyzed traits highlight an important role of temperature in shaping the distribution of dispersal strategies in alpine calcareous grasslands. Moreover, the concurrent increase at higher elevations in the cover of calcareous debris seems to restrict the establishment and survival of plants on the upper summits to a few cold-adapted species that are able to live and grow on dry and poor soils. We also observed that several of the alpine and subalpine species occurring in the analyzed area have nude diaspores and a short-distance dissemination strategy, which provides support for the hypothesis of the evolutionary convergence of species under harsh and isolated ecosystems. Short range dispersal allows some seeds to leave the overcrowded maternal site, but still to remain within the neighborhood where the probability of site suitability may be higher than random. Short distance dispersal provides an efficient way of filling space. When a seed is established near its mother, the mother site will be refilled the next year and available space will be filled concentrically and solidly around the population founders [33]. To conclude, it is worth noting that the environmental characteristics of Apennines high-elevation summits (e.g., steep slopes and harsh environments) combined with the persistence of plant species already present in each stand, the high precision of pollination and the prevalence of short-distance dissemination strategies should allow the calcareous endemic plant communities at high elevations to persist for a mid-term period slowing down the expansion of the warm-adapted species, less adapted to the local environmental constraints that are expected to become more severe.

Author Contributions: For research articles with several authors, a short paragraph specifying their individual contributions must be provided. The following statements should be used “Conceptualization, M.D.M.; M.L.C., L.F., A.S.; Methodology, M.D.M.; M.L.C., L.F., V.D.C., L.D.M., A.R.F., A.S.; Software, M.D.M.; L.F., Validation, M.D.M.; M.L.C., L.F., V.D.C., L.D.M., A.R.F., A.S.; Formal Analysis, M.D.M.; M.L.C., L.F., A.S.; Investigation, M.D.M.; M.L.C., L.F., V.D.C., L.D.M., A.R.F., A.S.; Resources, V.D.C., L.D.M., A.R.F., A.S.; Data Curation, M.D.M.; L.F., V.D.C., L.D.M., A.R.F., A.S.; Writing-Original Draft Preparation, M.D.M.; M.L.C., L.F., V.D.C., L.D.M., A.R.F., A.S.; Writing-Review & Editing, M.D.M.; M.L.C., L.F., A.S.; Visualization, M.D.M.; M.L.C., L.F.; Supervision, A.R.F., A.S.; Project Administration, L.D.M., A.R.F., A.S.; Funding Acquisition, L.D.M., A.R.F., A.S.

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Appendix A

Table A1. Complete list of species along with the corresponding taxonomic family and the analyzed dispersal traits. **pv**: pollen vector, **dd**: dispersal of diaspores, **sa**: seed appendages, **ft**: fruit type.

Species Name	Taxonomic Family	pv	dd	ft	sa
<i>Achillea barrelieri</i> subsp. <i>barrelieri</i>	Asteraceae	insect	autochory	achene	wings
<i>Adonis distorta</i>	Ranunculaceae	insect	zoochory	achene	awn
<i>Alyssum cuneifolium</i>	Brassicaceae	insect	autochory	siliqua	wings
<i>Androsace villosa</i> subsp. <i>villosa</i>	Primulaceae	insect	autochory	capsule	nude
<i>Anthyllis montana</i> subsp. <i>montana</i>	Fabaceae	insect	meteochoy	legume	nude
<i>Anthyllis vulneraria</i> subsp. <i>pulchella</i>	Fabaceae	insect	meteochoy	legume	nude
<i>Arabis alpina</i> subsp. <i>caucasica</i>	Brassicaceae	insect	autochory	siliqua	nude
<i>Arenaria grandiflora</i> subsp. <i>grandiflora</i>	Caryophyllaceae	insect	autochory	capsule	nude
<i>Armeria gracilis</i>	Plumbaginaceae	insect	meteochoy	achene	wings
<i>Aster alpinus</i> subsp. <i>alpinus</i>	Asteraceae	insect	meteochoy	achene	wings
<i>Bellis perennis</i>	Asteraceae	insect	autochory	achene	nude
<i>Bistorta vivipara</i>	Polygonaceae	insect	autochory	achene	nude
<i>Bunium petraeum</i>	Apiaceae	insect	zoochory	achene	nude
<i>Campanula cochleariifolia</i>	Campanulaceae	insect	autochory	capsule	nude
<i>Campanula scheuchzeri</i> subsp. <i>scheuchzeri</i>	Campanulaceae	insect	autochory	capsule	nude
<i>Carduus chrysacanthus</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Carex humilis</i>	Cyperaceae	wind	meteochoy	achene	nude
<i>Carex kitaibeliana</i>	Cyperaceae	wind	zoochory	achene	nude
<i>Carex myosuroides</i>	Juncaceae	wind	meteochoy	achene	awn
<i>Carum heldreichii</i>	Apiaceae	insect	zoochory	achene	nude
<i>Cerastium thomasi</i>	Caryophyllaceae	wind	autochory	capsule	nude
<i>Cerastium tomentosum</i>	Caryophyllaceae	self	autochory	capsule	nude
<i>Clinopodium alpinum</i> subsp. <i>alpinum</i>	Lamiaceae	insect	zoochory	achene	nude
<i>Crepis aurea</i> subsp. <i>glabrescens</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Crepis magellensis</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Crepis pygmaea</i>	Asteraceae	self	meteochoy	achene	pappus
<i>Doronicum columnae</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Draba aizoides</i> subsp. <i>aizoides</i>	Brassicaceae	insect	autochory	siliqua	nude
<i>Edraianthus graminifolius</i> subsp. <i>graminifolius</i>	Campanulaceae	insect	autochory	capsule	nude
<i>Erigeron epiroticus</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Erysimum majellense</i>	Brassicaceae	insect	autochory	siliqua	nude
<i>Euphrasia minima</i> subsp. <i>minima</i>	Scrophulariaceae	self	autochory	capsule	nude
<i>Festuca violacea</i> subsp. <i>italica</i>	Poaceae	wind	meteochoy	achene	awn
<i>Galium magellense</i>	Rubiaceae	wind	zoochory	achene	nude
<i>Gentiana nivalis</i>	Gentianaceae	self	autochory	capsule	nude
<i>Gentiana orbicularis</i>	Gentianaceae	insect	autochory	capsule	nude
<i>Gentiana verna</i> subsp. <i>verna</i>	Gentianaceae	insect	autochory	capsule	nude
<i>Helianthemum oelandicum</i> subsp. <i>alpestre</i>	Cistaceae	insect	zoochory	capsule	nude
<i>Helictichloa praetutiana</i> subsp. <i>praetutiana</i>	Poaceae	wind	meteochoy	achene	awn
<i>Iberis saxatilis</i> subsp. <i>saxatilis</i>	Brassicaceae	insect	meteochoy	siliqua	nude
<i>Leontopodium nivale</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Leucanthemum tridactylites</i>	Asteraceae	insect	autochory	achene	nude
<i>Linaria alpina</i>	Scrophulariaceae	insect	autochory	capsule	nude
<i>Luzula spicata</i> subsp. <i>italica</i>	Juncaceae	wind	autochory	capsule	nude
<i>Myosotis graui</i>	Boraginaceae	insect	autochory	achene	nude
<i>Omalotheca diminuta</i>	Asteraceae	wind	meteochoy	achene	pappus
<i>Oreojuncus monanthos</i>	Cyperaceae	wind	zoochory	capsule	nude
<i>Oxytropis campestris</i>	Fabaceae	insect	autochory	legume	nude
<i>Papaver alpinum</i> subsp. <i>alpinum</i>	Caryophyllaceae	insect	meteochoy	capsule	nude
<i>Paronychia kapela</i> subsp. <i>kapela</i>	Papaveraceae	insect	autochory	achene	nude
<i>Pedicularis elegans</i>	Scrophulariaceae	insect	autochory	capsule	nude
<i>Phyteuma orbiculare</i>	Campanulaceae	insect	autochory	capsule	nude
<i>Pilosella lactucella</i>	Asteraceae	self	meteochoy	achene	pappus
<i>Plantago atrata</i> subsp. <i>atrata</i>	Plantaginaceae	wind	zoochory	capsule	nude
<i>Poa alpina</i> subsp. <i>alpina</i>	Poaceae	wind	meteochoy	achene	awn
<i>Poa molinerii</i>	Poaceae	wind	meteochoy	achene	awn
<i>Polygala alpestris</i> subsp. <i>alpestris</i>	Polygalaceae	insect	meteochoy	capsule	awn

Table A1. Cont.

Species Name	Taxonomic Family	pv	dd	ft	sa
<i>Potentilla crantzii</i> subsp. <i>crantzii</i>	Rosaceae	insect	autochory	achene	awn
<i>Pulsatilla alpina</i> subsp. <i>alpina</i>	Ranunculaceae	insect	meteochoy	achene	awn
<i>Ranunculus brevifolius</i>	Ranunculaceae	insect	meteochoy	achene	awn
<i>Ranunculus breyninus</i>	Ranunculaceae	insect	meteochoy	achene	awn
<i>Sabulina verna</i> subsp. <i>verna</i>	Caryophyllaceae	wind	autochory	capsule	nude
<i>Salix retusa</i>	Salicaceae	wind	meteochoy	capsule	awn
<i>Saxifraga adscendens</i> subsp. <i>adscendens</i>	Saxifragaceae	self	autochory	capsule	nude
<i>Saxifraga exarata</i> subsp. <i>ampullacea</i>	Saxifragaceae	self	autochory	capsule	nude
<i>Saxifraga oppositifolia</i> subsp. <i>oppositifolia</i>	Saxifragaceae	self	autochory	capsule	nude
<i>Saxifraga paniculata</i>	Saxifragaceae	self	autochory	capsule	nude
<i>Saxifraga tridactylites</i>	Saxifragaceae	self	autochory	capsule	nude
<i>Scorzoneroides montana</i> subsp. <i>montana</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Sedum atratum</i>	Crassulaceae	insect	autochory	follicule	nude
<i>Sempervivum arachnoideum</i>	Crassulaceae	insect	autochory	follicule	nude
<i>Senecio squalidus</i> subsp. <i>squalidus</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Sesleria juncifolia</i> subsp. <i>juncifolia</i>	Poaceae	wind	meteochoy	achene	awn
<i>Silene acaulis</i> subsp. <i>acaulis</i>	Caryophyllaceae	insect	autochory	capsule	nude
<i>Taraxacum apenninum</i>	Asteraceae	insect	meteochoy	achene	pappus
<i>Thymus praecox</i> subsp. <i>polytrichus</i>	Lamiaceae	insect	autochory	legume	nude
<i>Trifolium pratense</i> subsp. <i>semipurpureum</i>	Fabaceae	insect	zoochory	legume	nude
<i>Trifolium thalii</i>	Fabaceae	insect	meteochoy	legume	nude
<i>Trinia dalechampii</i>	Apiaceae	insect	autochory	achene	nude
<i>Valeriana saliuunca</i>	Valerianaceae	insect	meteochoy	achene	pappus
<i>Veronica aphylla</i>	Scrophulariaceae	insect	autochory	capsule	nude
<i>Viola eugeniae</i> subsp. <i>eugeniae</i>	Violaceae	insect	zoochory	capsule	nude
<i>Viola magellensis</i>	Violaceae	insect	autochory	capsule	nude

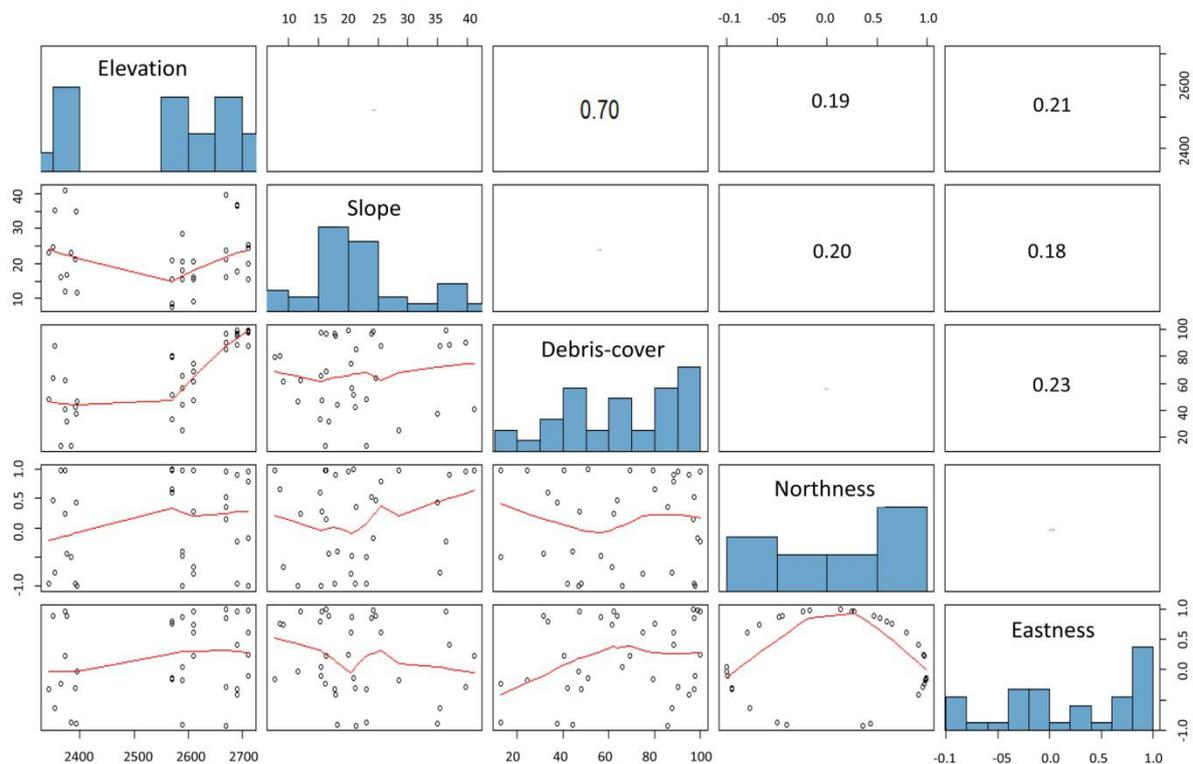


Figure A1. Pearson correlation matrix among environmental variables. None of the variables exceeded the chosen 0.7 threshold thus we retained all of them for subsequent analysis.

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