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# Unveiling the hypotheses of endemic richness: A study case in the Southwestern Alps

Maria Guerrina<sup>a,1</sup>, Davide Dagnino<sup>a,2</sup>, Luigi Minuto<sup>a,3</sup>, Frédéric Médail<sup>b,4</sup>,  
Gabriele Casazza<sup>a,\*,5</sup>

<sup>a</sup> Università di Genova, Dipartimento di Scienze della terra, Ambiente e Vita, Corso Europa 26, Genova I-16132, Italy

<sup>b</sup> Institut méditerranéen de biodiversité et d'écologie marine et continentale (IMBE), Aix Marseille Univ., Avignon Université, CNRS, IRD, Technopôle de l'Arbois-Méditerranée, BP 80, 13545 Aix-en-Provence Cedex 4, France

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## ABSTRACT

Areas where range-restricted species are concentrated are of importance for conservation. However, most of the studies aim at identifying areas rich in endemics for conservation planning, while few studies aim at understanding the causal factors of endemic richness. Here, our goal is to identify the determinants of endemic richness within a centre of endemism, the Southwestern European Alps, by testing four non-mutually exclusive hypotheses that have been proposed to explain patterns of endemic richness. In particular, we examined to what extent temporal and spatial climatic stability and environmental heterogeneity are related to endemic richness. Almost all hypotheses partially support the observed patterns of plant endemics richness within the SW Alps. In general, most of the relationships between environmental variables and endemic richness are statistically significant. However, the highest effect in explaining endemic richness is found for climate change velocity and standard deviation of slope, two factors affecting the possibility of species to disperse. This is in line with the idea that endemics are strongly limited by dispersal and not only by climate. Our results suggest that in regions where the effects of past climate changes were less dramatic endemic richness results from the interaction of species dispersal with regional and specific historical factors.

## 1. Introduction

Areas where range-restricted species are concentrated are of importance for conservation (Myers et al., 2000). In general, the number of endemics is strongly positively correlated with endangered species richness, and it is a key factor in defining the hotspots of biodiversity (Mittermeier et al., 1998; Myers et al., 2000). Several studies recognized past climate change as a key factor in both origin and maintenance of endemic richness over evolutionary time (e.g., Sandel et al., 2011; Feng et al., 2016). Indeed, past climate dynamics have affected both the diversification rates (Smyčka et al., 2017) and the survival of different lineages within restricted taxa (Médail and Diadema, 2009). However, it has been suggested that the distribution of endemic taxa in areas rich in

endemics may result not only from historical factors but also from ecological characteristics of the area such as geology, topography, isolation and current climate (Casazza et al., 2008; Noroozi et al., 2016; Tordoni et al., 2020). In the last years, the number of studies aimed at identifying areas rich in endemics for conservation planning has strongly increased, while there are still only few studies aiming at understanding the causal factors of endemic richness (Harrison and Noss, 2017).

Up to now, four hypotheses have been proposed to explain the relationship between climate and the remarkably high number of endemics in some areas (Zuloaga et al., 2019). First, under the climatic rarity hypothesis, we expect areas rich in endemics to have climates that are unusual in the region (Ohlemüller et al., 2008). Endemics may be

\* Corresponding author.

E-mail address: [gabriele.casazza@unige.it](mailto:gabriele.casazza@unige.it) (G. Casazza).

<sup>1</sup> 0000-0002-8318-7565

<sup>2</sup> 0000-0003-4889-4317

<sup>3</sup> 0000-0002-1582-3806

<sup>4</sup> 0000-0002-1429-6661

<sup>5</sup> 0000-0002-3334-8551

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adapted to climatic conditions that have been more widespread during the past and that nowadays persist in few areas where species are concentrated. This might be the case of species adapted to cold climate that had a distribution wider than today during past cold periods, while they contracted during warm periods (e.g., [Finocchiario et al., 2023](#)). Therefore, areas nowadays cooler than the surroundings may accommodate a high number of endemics (the so-called cryptic southern refugia; [Stewart et al., 2010](#)). Second, under the climate seasonality hypothesis ([Addo-Bediako et al., 2000](#)), we expect areas rich in endemics to have low intra-annual climatic variation. Endemics are expected to concentrate in localities where the climate seasonality is low because of high within-locality seasonal variation (i.e., temporal variation in each locality – [Janzen, 1967](#); [Quintero and Wiens, 2013](#)) resulting in a wide niche breadth, which is usually related to large range size ([Slatyer et al., 2013](#)). Third, under the climatic buffer hypothesis ([Jetz and Rahbek, 2002](#)), we expect areas rich in endemics to have high topographic heterogeneity resulting in a high array of local climatic conditions. In fact, the topographic heterogeneity could result in past and present geographic barriers increasing historical opportunities for allopatric speciation ([Jetz and Rahbek, 2002](#)). Moreover, the local topographic characteristics may decouple the local climatic conditions from the regional ones ([Dobrowski, 2011](#)), causing large climatic differences within a short distance. Endemics, which usually are poorly dispersed ([Lowry and Lester, 2006](#)), may have survived mainly in highly heterogeneous areas where they may have kept pace with climatic changes by shifting over short distance ([Patsiou et al., 2014](#); [Casazza et al., 2016](#)). Fourth, under the long-term climate stability hypothesis ([Dynesius and Jansson, 2000](#); [Jansson and Dynesius, 2002](#)), we expect areas rich in endemics to have been climatically stable over time. Because endemics are usually characterized by narrow niche breadth ([Dullinger et al., 2012](#)), low colonization ability ([Lavergne et al., 2004](#)), and intrinsic dispersal limitation ([Baselga et al., 2012](#)), they may have become extinct in areas where current climate is strongly different from the past one, while they may have been gathered in climatically stable areas (i.e., areas where current climate is similar to the past one).

Here, we aim at identifying the determinants of endemic richness of vascular plants within the major centre of endemism of the Alps, the Southwestern Alps ([Médail and Verlaque, 1997](#); [Casazza et al., 2008](#); [Fauquette et al., 2018](#)). In particular, we test each of the four hypotheses by examining to what extent temporal and spatial climatic stability and heterogeneity are related to endemic richness. A deeper understanding

of the processes that influence endemic richness may offer a sound framework for guiding proactive conservation strategies.

## 2. Methods

### 2.1. Study area, endemic distribution and richness

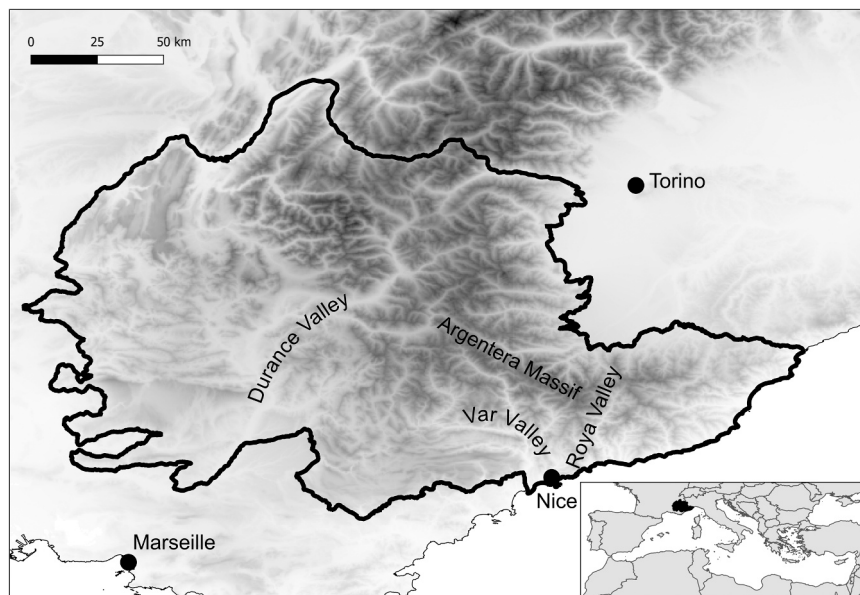
The Southwestern Alps (hereafter, SW Alps; [Fig. 1](#)) are located at the crossroad between the Mediterranean and the Alpine biogeographic region, and they constitute the richest area in endemic plant taxa in the Alps ([Aeschmann et al., 2011](#)). This richness is supposed to be the result of particular climatic conditions, habitat heterogeneity and biogeographical history ([Casazza et al., 2005, 2008](#); [Fauquette et al., 2018](#)).

To test the determinants of plant endemic richness, we selected 106 endemic (80 taxa) or sub-endemic (26 taxa) vascular plants of the SW Alps, representing, respectively, 66 % of the endemic and 65 % of the sub-endemic flora of this area. We selected taxa in which at least 75 % of the populations occur in the SW Alps, while we did not consider those taxa having nomenclatural problems or showing uncertainties in distributional data. Species occurrence data were obtained from regional databases (SILENE – CBNMed, Conservatoire botanique national méditerranéen, France and Li.Bi.Oss. – ARPAL, Agenzia regionale per la protezione dell’ambiente ligure, Italy) and literature sources ([Dagnino et al., 2020](#) and references therein). The final data set comprised 58,012 occurrences, ranging from 15 to 3172 occurrences per species. The taxa were scored as present or absent in each cell of a 5×5 km grid ([Table S1](#)).

We counted the number of endemic taxa present in each cell (ER, endemic richness). Additionally, we weighted the endemic species by the inverse of the number of cells in which each taxon occurs (WE, weighted endemic richness; [Linder, 2001](#)). The metrics were estimated in each cell of the grid.

### 2.2. Predictors of endemic richness

To test the four hypotheses explaining the current richness of endemics, we used 19 bioclimatic variables at about 1×1 km spatial resolution downloaded from CHELSA v.1.1.2 dataset ([Karger et al., 2017a; 2017b](#); [www.chelsa-climate.org](http://chelsa-climate.org)) for current (<http://chelsa-climate.org/downloads/>) and Last Glacial Maximum (LGM ~ 20 Kya; PMIP3; <http://chelsa-climate.org/last-glacial-maximum-climate/>). For the



**Fig. 1.** Location map of the SW Alps.

LGM, we used seven general atmospheric circulation models (GCMs): CCSM4, CNRM-CM5, FGOALS-g2, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P and MRI-CGCM3.

The Digital Elevation Model (DEM) used to calculate the topographic complexity indices was downloaded from the USGS Global Multi-Resolution Terrain Elevation Data 2010 ([https://topotools.cr.usgs.gov/gmted\\_viewer/viewer.htm](https://topotools.cr.usgs.gov/gmted_viewer/viewer.htm)), with a spatial resolution of 250 m. Bioclimatic variables were aggregated at 5×5 km resolution by averaging cell values to fit with the resolution of the endemism metrics. Then they were transformed to meet the assumption of normality and standardised by using the ‘bestNormalize’ package (Peterson and Cavanaugh, 2019) implemented in R (R Core Team, 2018). Eventually, we characterized the climatic space of the study area carrying out a principal component analysis (PCA) of the bioclimatic variables using the ‘ade4’ package (Dray and Dufour, 2007) implemented in R (R Core Team, 2018). To obtain past values for the two axes, the LGM variables were projected into the PCA space as passive variables.

To test the climatic rarity hypothesis (H1), we measured climatic rarity (CR) for each cell, according to Morueta-Holme et al., (2013), considering the average Euclidean distance in climatic space between each cell and all other cells within a 50 km radius. High values indicate rare climatic conditions with respect to the neighbouring cells.

To test the climate seasonality hypothesis (H2), we used temperature (TS) and precipitation (PS) seasonality.

To test the climatic buffer hypothesis (H3), we calculated topographic complexity using the DEM at 250 m resolution. For each 5×5 km cell we calculated: standard deviation of elevation (SE), elevation range (RE), standard deviation of slope (SS) and range slope (RS).

To test the long-term climate stability hypothesis (H4), we used three different approaches. First, because most endemics have dispersal limitation (Baselga et al., 2012) and low colonization ability (Lavergne et al., 2004) and may have survived past climate change *in situ*, we assessed the climatic stability *in situ* (SI) as dissimilarity between the LGM and the present climate for each grid cell. We calculated the climatic dissimilarity as the Euclidean distance in PCA space between current and past climatic conditions under each GCM. Then, we quantified contemporary-past environmental dissimilarity for each grid cell as the average among GCM values. Moreover, to take into account of the possibility of migration, we quantified the regional climatic dissimilarity (CD) for each grid cell as the average among the Euclidean distances between the current climate space and past climate space for all cells within a 50-km buffer of each GCM. We also calculated the velocity of climate change (CV), that represents speed (distance/time) at which species have to migrate to remain under similar climatic conditions, using the approach developed by Hamann et al. (2015) and implemented in the R package ‘VoCC’ (García Molinos et al., 2019). For each PCA axis the climate threshold for matching analogous climates was set to 40 % of the range of values.

Pearson correlation was calculated and only predictors not highly correlated ( $r \leq |0.70|$ ) were retained for further analyses to avoid collinearity. Moreover, we also excluded the predictors that were correlated between different hypotheses to avoid confounding interpretation of results. For each hypothesis, at least one predictor was retained. The seven variables used in further analyses were: CR for climatic rarity hypothesis, PS and TS for climate seasonality hypothesis, RE and SS for climatic buffer hypothesis and, CV and SI for long-term climate stability hypothesis (see [Supplementary Material](#) for further details on correlation among the selected variables).

### 2.3. Statistical analyses

To explain the relationship between endemic richness and each predictor, we used the Spearman’s rank correlation coefficients. We first transformed the dependent variable to improve homoscedasticity and normality, and the independent variables to improve linearity. To

evaluate the importance of predictors we used the hierarchical partitioning because it assures that the contribution of a particular variable is neither enhanced nor masked through its correlation with other explanatory variables (Mac Nally, 2000). Hierarchical partitioning analysis was carried out by using the R package ‘hier.part’ (Walsh and Mac Nally, 2008). Then we used ordinary least squares (OLS) models to assess relationships between all predictor variables simultaneously and each of the endemic richness measures. Both species richness data and environmental variables may be spatially autocorrelated (i.e., adjacent pixels are more similar among themselves than expected by chance), affecting the efficiency of OLS estimates and inducing an overestimation of environmental variables with a low influence on the distribution of richness (Legendre, 1993). For this reason, we controlled for spatial autocorrelation using a spatial error simultaneous autoregressive model (SAR - Kissling and Carl, 2008) using a range of neighbourhood distances from 10 to 50 km. Spatial autocorrelation was tested by using the R package ‘spatialreg’ (Rigby and Stasinopoulos, 2005). As endemic richness is a count variable with excess of zeros due to both truly unoccupied habitat and imperfect detection, the relationship between predictors and endemic richness was also investigated using zero-inflated negative binomial regression model. To deal with the excess of zeros in the non-count variable EW, we used the beta inflated distribution regression model (Ospina and Ferrari, 2012) implemented in the R package ‘GAMLSS’ (Stasinopoulos and Rigby, 2007).

## 3. Results

The highest endemic richness (ER) values occurred mainly in the central-southern part of SW Alps, including both the upper part of Val Roya, which is calcareous, and the Argentera massif, which is siliceous (Fig. 1). As suggested by the high correlation value ( $\rho=0.79$ ,  $p \leq 0.001$ ), the highest weighted endemic richness (EW) values had a similar pattern, occurring mainly in the southern part of the main Alps ridge (Fig. 2A–B) and, in particular, in the upper part of the Roya Valley.

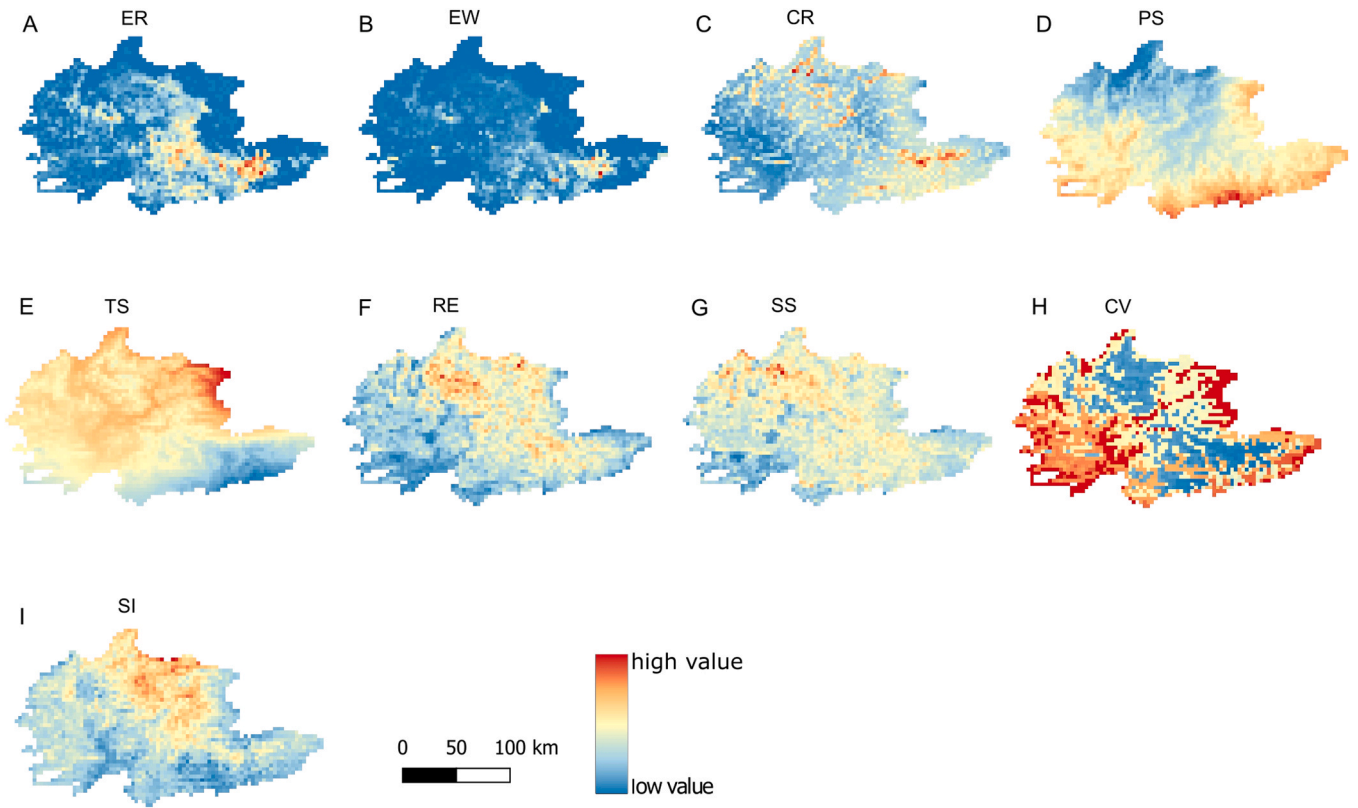
Rare climates occurred mainly in the southern and northern parts of the Alpine chain (Fig. 2C). High precipitation seasonality (PS) values occurred in the southern part, while high temperature seasonality (TS) values in the northern part of the study area (Fig. 2D–E). Highly topographically heterogeneous areas occurred mainly along the main mountain chain in the centre of the study area, even if they were rather scattered over the entire study area (Fig. 2F–G). The areas with highest dissimilarity between current and past climatic conditions occurred mainly in the northern part of the study area (Fig. 2H–I), even if these areas had low climate change velocity as well as some southern part of the study area.

According to these results, ER was moderately negatively correlated with climate change velocity (CV), weakly positively correlated with climatic rarity (CR), elevation range (RE), standard deviation of slope (SS) and weakly negatively correlated with TS (Table 1). Similarly, EW was weakly positively correlated with CR, moderately negatively correlated with TS and weakly negatively correlated CV (Table 1). The hierarchical partitioning analysis revealed that TS, SS and CV explained a high percentage of variance of ER and EW (Table 2). Moreover, RE explained roughly 10 % of EW variance only.

In particular, both endemism metrics were negatively correlated with TS and CV, and positively correlated with SS and RE in most of the models (Table 3). The CR was positively related to EW, while the relationship with ER were contradictory and not significant. Relationships between PS and climatic stability *in situ* (SI) and both endemism metrics were not significant (Table 3).

## 4. Discussion

Our results suggest that all hypotheses, but climatic rarity hypothesis (H1), partially support the observed patterns of endemic plant richness in the SW Alps. In fact, most of the relationships are statistically



**Fig. 2.** Maps of the Southwestern Alps showing A) endemic richness (ER), B) weighted endemic richness (WE), C) climate rarity index (CR), D) temperature seasonality (TS), E) precipitation seasonality (PS), F) elevation range (RE), G) standard deviation of slope (SS), H) velocity of climate change (CV) and I) climatic stability (SI).

**Table 1**

Correlation between endemic richness metrics and all predictive variables based on Spearman's rank correlation coefficient. H1, climatic rarity hypothesis; H2, climate seasonality hypothesis; H3, climatic buffer hypothesis; H4, long-term climate stability hypothesis. ER, endemic richness; EW, weighted endemic richness; CR, climate rarity; TS, temperature seasonality; PS, precipitation seasonality; RE, elevation range; SS, standard deviation of slope; CD, climatic dissimilarity; SI, *in situ* climatic stability. \*\*\* $p \leq 0.001$ ; \*\* $p \leq 0.01$ ; \* $p \leq 0.05$ ; <sup>ns</sup> $p \geq 0.05$ .

	H 1 CR	H2 PS	H2 TS	H3 RE	H3 SS	H4 CV	H4 SI
ER	0.21***	0.07***	-0.36***	0.27***	0.26***	-0.47***	0.06***
EW	0.28***	0.19***	-0.42***	0.18***	0.18***	-0.33***	-0.05***

**Table 2**

Percentage of relative importance of the environmental variables on the variation in endemic richness (ER) and weighted endemic richness (EW). The total percentage of variance explained by the variables was reported (TotVar). H1, climatic rarity hypothesis; H2, climate seasonality hypothesis; H3, climatic buffer hypothesis; H4, long-term climate stability hypothesis. CR, climate rarity; PS, precipitation seasonality; TS, temperature seasonality; RE, elevation range; SS, standard deviation of slope; CV, climatic velocity; SI, climatic stability *in situ*.

Hypothesis	Variable	ER	EW
H1	CR	5.68	9.75
H2	PS	5.9	9.07
	TS	33.46	23.76
H3	RE	7.16	11.79
	SS	17.86	12.86
H4	CV	28.18	31.17
	SI	1.74	1.6
	TotVar	19.54	29.47

significant (Table 3) and the explained variance of the regression model ranges from weak to substantial (Table 3). The remaining unexplained variance suggests that other factors may play a role in determining endemic richness. For example, microrefugia, that is small areas where

conditions remain favourable for the persistence of populations, may occur at very small spatial scale (i.e., less than one hundred of square metres; Finocchiaro et al., 2023) not captured by our analyses. Furthermore, edaphic conditions, not considered in this study, may also influence the pattern of endemic richness. In fact, areas characterized by poor soils are expected to be particularly rich in endemics (Hopper, 2021) because harsh soils promote speciation (Kruckeberg, 1986). Another factor that may contribute to the unexplained variance is the species dispersal as it may influence the distribution pattern of different endemics (Essi et al., 2011; Zhang et al., 2009). Moreover, other factors such as competition (Casazza et al., 2005) and human impact (Lazarina et al., 2019) may affect distributional patterns of endemics.

According to our results, temperature seasonality (i.e., H2 - climate seasonality hypothesis), velocity of climate change (i.e., H4 - long-term climate stability hypothesis) and the standard deviation of slope (i.e., H3 - climatic buffer hypothesis) have the highest effect (Tables 1 and 2) in explaining endemic richness. Conversely, climatic rarity (i.e., H1), precipitation seasonality (i.e., H2), local climatic stability (i.e., H4) and range elevation (i.e., H3) weakly affect spatial patterns of endemics. In particular, areas of high endemic richness occur where both temperature seasonality and climate change velocity are low and where standard deviation of slope is high, respectively, in line with climate seasonality

**Table 3**

Parameter estimates for explanatory variables in regression models. ER, endemic richness; EW, weighted endemic richness; H1, climatic rarity hypothesis; H2, climate seasonality hypothesis; H3, climatic buffer hypothesis; H4, long-term climate stability hypothesis. CR, climate rarity; TS, temperature seasonality; PS, precipitation seasonality; SE, standard deviation of elevation; RE, elevation range; SS, standard deviation of slope; RS, range slope; SI, in situ climatic stability; CD, climatic dissimilarity; R2, explained variance; OLS, ordinary least squares models; SAR, spatial error simultaneous autoregressive model. \*\*\* $p \leq 0.001$ ; \*\* $p \leq 0.01$ ; \* $p \leq 0.05$ ; <sup>ns</sup> $p \geq 0.05$ .

	Variable	OLS model		SAR model		Zero-inflated model	
		ER	EW	ER	EW	ER	EW
	Intercept	-0.139***	-1.699***	-0.523 <sup>ns</sup>	-1.727***	1.376***	-2.882***
H1	CR	-0.206***	0.038***	0.026 <sup>ns</sup>	0.032*	-0.130***	0.077**
H2	PS	0.112***	0.107***	0.044 <sup>ns</sup>	-0.030 <sup>ns</sup>	0.072 <sup>ns</sup>	0.236***
	TS	-0.294***	-0.099***	-0.353***	-0.018 <sup>ns</sup>	-0.450***	-0.196***
H3	RE	0.023 <sup>ns</sup>	0.051**	0.132***	0.039*	0.262***	0.101**
	SS	0.282***	0.100***	0.154***	0.071***	0.175***	0.097***
H4	CV	-0.283***	-0.146***	-0.085*	-0.089***	-0.377***	-0.280***
	SI	-0.021 <sup>ns</sup>	-0.004 <sup>ns</sup>	0.066 <sup>ns</sup>	0.057***	0.112***	0.033 <sup>ns</sup>
	R2	0.19	0.29	0.52	0.49	0.33	0.21

hypothesis (H2), long-term stability hypothesis (H4) and climatic buffer hypothesis (H3).

We detected the same results in endemism and weighted endemic richness, which are highly correlated (Table 1), suggesting that the same processes have shaped the spatial pattern of endemic richness regardless of the rarity or range size of species. Nevertheless, contrary to the general expectation, weighted endemic richness is weakly correlated with climate rarity. Moreover, it is less related than endemic richness to topographic predictors and climate change velocity, two factors that may interact with the species dispersal of in determine distributional patterns of species. The weak relationship detected between weighted endemic richness and climatic rarity (i.e., H1) in the SW Alps does not support the general expectation that range-restricted species are concentrated where unusual climates (different from the dominant climate of the region) occur. This expectation is based on the idea that range-restricted species are interglacial relicts, that is species which were widespread during glacial periods and now have a narrow geographic distribution due to post-glacial contraction (Birks, 2008; Ohlemüller et al., 2008). Consequently, these species are expected to concentrate predominantly in areas where they have been able to survive the warm periods. However, several other processes may govern range size variation (Sheth et al., 2020). For example, the current narrow ranges of some plants endemic to the Alps may be due to a delayed recolonization of suitable sites from glacial refugia because of their dispersal limitations and narrow niche breadth (Svenning et al., 2008; Dullinger et al., 2012). This is corroborated by the weak correlation of weighted endemic richness with predictors related to dispersal possibility of the species, differently to that observed for the overall endemic richness. Furthermore, frequently neoendemics have small geographic ranges because they have not yet had time to fill their potential range (Lesica et al., 2006; Smyčka et al., 2023). In addition, the geography of speciation may also strongly affect range size (Skeels and Cardillo, 2019), as also suggested for several species endemic to the SW Alps (Casazza et al., 2016). For example, in *Primula* sect. *Auricula* the narrow range of the species likely results from speciation due to geographic isolation rather than from post-glacial contraction (Boucher et al., 2016; Casazza et al., 2013). Furthermore, as observed in the restricted-range tertiary relict species *Saxifraga florulenta*, the survival of relict species may benefit from the dynamics of microrefugia over time rather than from stable climatic conditions (Patsiou et al., 2014). These results suggest that in SW Alps, range-restricted species concentrate not where old climatic conditions persist over time but in glacial refugia where species survived glaciation, that is in the southern part of the main ridge of the Alps. In fact, in this area, we recorded high values of both weighted and non-weighted endemic richness.

The higher effect of climate change velocity (i.e., H4) and standard deviation of slope (i.e., H3), two factors related to the dispersal possibility of species, compared to climatic rarity (i.e., H1) and local climate

stability (i.e., H4) in explaining endemic richness is in line with the idea that endemics' ranges are strongly limited by dispersal and not only by climate (Baselga et al., 2012). This result suggests that, within a centre of endemism, endemics are concentrated where they have been able to keep pace with past climate change. In the SW Alps, the high slope heterogeneity (i.e., H3) may have favoured the presence of suitable microhabitats facilitating short-distance migrations (i.e., low climate change velocity, H4), particularly in poor dispersers like several endemics (Dagnino et al., 2020; Essl et al., 2011; Patsiou et al., 2014; Quilichini and Debussche, 2000). In fact, it was suggested that this process played an important role in minimizing populations extinction in the SW Alps endemics, enabling them to survive the last glaciation in microrefugia close to current occurrences (Patsiou et al., 2014; Casazza et al., 2016). However, other endemics may disperse over long distances being dispersed by zoochory (e.g., *Prunus brigantina* and *Helictotrichon* spp.) or having efficient anemochory (e.g., *Ophrys* spp.). These efficient dispersers may have been able to keep pace with climate change by means of medium-distance dispersal and not only with short-distance dispersal, further favouring the correlation between endemic richness and low climate change velocity.

The importance of temperature seasonality (i.e., H2) in explaining endemic richness in SW Alps is in line with the idea that low seasonality may select for species with narrower thermal tolerances, and therefore with smaller geographical ranges (Addo-Bediako et al., 2000), as demonstrated for endemic birds (Sandel et al., 2011), moths (Grünig et al., 2017) and seed plants (Sandel et al., 2020). In plants, low values and temperature seasonality and high values of endemic richness are both found in the southern part of the SW Alps, where the mitigation capacity of the Mediterranean Sea keeps low the temperature variability. Moreover, in the SW Alps, one of the main glacial refugia in the Alps, the effect of the Mediterranean sea in addition to the high heterogeneity of the area (H3) assured favourable climatic conditions for species survival during the LGM and other past glacial events (Fauquette et al., 2018; Medail and Diadema, 2009).

Overall, no macroecological hypotheses fully account for species richness, suggesting that how environment affects species distribution is also a function of how far and how frequently species move (Chase et al., 2019; Hewitt et al., 2017). Taken together, our results suggest that the high heterogeneity of the area has resulted in a spatially heterogeneous effect of different factors affecting endemic richness throughout the area (i.e., temperature seasonality, velocity of climate change and topography). Our results suggest that a high richness of endemics results from the concomitance of several factors and are in line with previous findings according to which in the south-western Alps, weakly affected by past climate changes, the distribution of endemics has been influenced by both historical and ecological factors (Casazza et al., 2008).

## CRediT authorship contribution statement

**Gabriele Casazza:** Writing – original draft, Validation, Supervision, Formal analysis, Conceptualization. **Luigi Minuto:** Writing – review & editing, Validation. **Frédéric Médail:** Writing – review & editing, Validation. **Maria Guerrina:** Writing – review & editing, Visualization, Validation, Investigation. **Davide Dagnino:** Writing – review & editing, Validation, Investigation, Data curation.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

The authors do not have permission to share data.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ppees.2024.125792](https://doi.org/10.1016/j.ppees.2024.125792).

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