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Native Community Resistance Mediates Plant Invasion Responses to Global Change Along Mediterranean Mountain Roads

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ABSTRACT

Aim: Climate warming, human modification and global connectivity are eroding the abiotic barriers (i.e., climatic filtering and low propagule pressure) that have traditionally limited the spread of non-native species in mountain ecosystems. Meanwhile, these global changes are also reshaping native plant communities, potentially weakening their biotic resistance to invasion. Yet, the role of native community resistance in mediating the upslope spread of non-native species remains largely overlooked, limiting our understanding of the indirect effects of global change on mountain plant invasions.

Location: Central Apennines Mountain range, Italy.

Methods: Following the Mountain Invasion Research Network (MIREN) protocol, we surveyed native and non-native vegetation close and far from roads at 60 sites along three mountain roads. Using current and historical climatic data and aerial images from the 1950s, we quantified climate and land-use changes. Dominant plant traits and functional diversity were used to capture the biotic resistance of native communities. We then applied structural equation modelling to investigate how native biotic resistance mediates the effect of global change drivers, that is, road disturbance and changes in land-use and climate, on the occurrence and cover of non-native species.

Results: We found that, beside climatic filtering, the biotic resistance of native communities is among the strongest drivers of non-native species occurrence and abundance. The changes in land-use occurred over the past 70 years indirectly influenced invasions by altering native community resistance. Agricultural abandonment at low- to middle elevations favoured short-statured native communities, offering low resistance. In contrast, forest expansion strengthened resistance through dominance of conservative native species.

Main Conclusion: Native community resistance, alongside climate and disturbance, is a key determinant of invasion patterns along elevational gradients in Mediterranean mountains. Despite global changes facilitating non-native plant upward shifts, native communities can mediate this spread and may still maintain a certain resistance to invasion.

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1 | Introduction

Mountains are characterized by unique biodiversity and provide crucial ecosystem services, including provisioning of food and water, carbon storage as well as space for recreational activities (Mengist et al. 2020; Schirpke et al. 2021). However, these environments are particularly sensitive to ongoing global changes, such as warming temperatures, shifting precipitation patterns and the modification of natural habitats by human activities (Alexander et al. 2016; Dainese et al. 2024; Lembrechts et al. 2016; Pauchard et al. 2009). Yet, until recently, mountain ecosystems had been generally considered to be relatively resistant to another big agent of global change, that is, the invasion of non-native plant species introduced by humans. This resistance is largely attributed to a combination of low propagule pressure of non-native species, a limited pool of non-natives adapted to the extreme climate of high elevations (i.e., climate filtering), little anthropogenic disturbance, and high resistance to invasion of native communities (Alexander et al. 2016; Milbau et al. 2013; Pauchard et al. 2009). However, climate warming and increased human modification have been reshaping native communities (Collins et al. 2022; Dainese et al. 2017; Geppert et al. 2021), thus potentially altering their resistance to invasion, while simultaneously creating more favourable conditions for the spread of non-native species in mountain areas (Cao Pinna et al. 2024; Petitpierre et al. 2016). Despite its theoretical importance, the role of native community resistance in mediating the effect of global change on plant invasion in mountain environments remains poorly explored (Alexander et al. 2015, 2018). As the annual rate of new non-native plant introductions continues to grow globally (Seebens et al. 2017, 2021), understanding how climate and land-use changes affect the resistance of native communities is crucial for anticipating and mitigating the spread on non-native species in these vulnerable mountain environments.

The ability of native communities to resist the establishment and expansion of new species explains why, under similar abiotic conditions and propagule availability, a non-native species may or may not successfully invade an ecosystem (Delavaux et al. 2023; Guo et al. 2024; Ibáñez et al. 2021; Richardson and Pyšek 2006). As a result, understanding which features make a community resistant to invasion and how global changes could potentially affect these characteristics is crucial for planning effective management strategies to counteract plant invasion (Roy et al. 2024). In this context, functional traits are increasingly being used as proxies for capturing the ability of native communities to withstand invasions in a wide range of ecosystems (Conti et al. 2018; Gallien and Carboni 2017) including mountains (McDougall et al. 2018). For example, native communities exhibiting traits related to high resource-use efficiency, strong competitive ability and rapid growth rates have been shown to resist invasion by limiting the resources accessible to the invaders (Emery and Gross 2007). Similarly, previous studies demonstrated that communities with greater functional diversity are more likely to exploit a wider range of resources (e.g., light, nutrients and water) and potentially leave fewer opportunities for invaders to establish (Delavaux et al. 2023; Elton 1958; Funk et al. 2008; Guo et al. 2024). Although some progress has been made in understanding the

mechanisms that allow native species to limit the establishment of non-natives, how ongoing global changes are influencing this biotic resistance, and in turn invasion success, remains poorly explored in mountain ecosystems (but see Barros et al. 2025).

Climate change, land-use modification, and native community resistance are interconnected forces shaping invasion dynamics (Pyšek et al. 2020). As an example, warming temperature can reduce climatic barriers and allow the expansion of non-native species toward higher elevations (Dainese et al. 2017; Delavaux et al. 2023; Pauchard et al. 2016). On the other hand, changes in land-use, such as urban or agricultural expansion, can increase propagule pressure and create new opportunities for non-native plant introduction that can profit from the new favourable conditions (Dainese et al. 2017; Pauchard and Alaback 2004; Rodewald and Arcese 2016). Still, changes in climate and land-use do not only influence plant invasion but can also reshape native communities. In particular, climate change has been shown to favour the expansion of thermophilus species from the lowlands (Gottfried et al. 2012; Lenoir et al. 2008; Steinbauer et al. 2022) while some changes in land-use, for example, the conversion of natural habitat to semi-natural ones, will likely facilitate native ruderal species as an effect of increased disturbance (Tasser and Tappeiner 2002). As a result, these two drivers of global change do not only influence plant invasions directly, but may also weaken the biotic resistance of native communities, thereby potentially opening new niches for non-native species (Lembrechts et al. 2017; Pauchard et al. 2016; Petitpierre et al. 2016), or increase biotic resistance instead (Bjorkman et al. 2018). Despite the large body of research that has investigated the effects of climate warming and land-use change on plant invasion in mountain ecosystems (Dainese et al. 2017; Geppert et al. 2021; Pauchard et al. 2009, 2016; Pauchard and Alaback 2004), the role of native community resistance in mediating the effects of these global change drivers, and thereby shaping their indirect effects on plant invasions, have been rarely investigated (Alexander et al. 2016).

Mountain roads serve as key corridors for the dispersal of non-native plants along elevation gradients, acting as reservoirs of propagules from nearby lowland and warmer regions (Lembrechts et al. 2017b; McDougall et al. 2018; Pauchard and Alaback 2004). Additionally, roadsides, often subject to active management practices such as vegetation clearing, provide an opportunity to compare the invasion resistance of disturbed roadside vegetation with undisturbed native plant communities further from the road. As such, mountain roads represent an excellent model system for studying the distribution and abundance of non-native species and their potential for invading high-elevation habitats in the current era of global change. In this study, we aimed to disentangle the complex set of direct and indirect drivers influencing plant invasion along elevation gradients in Mediterranean mountain ecosystems, focusing on the role played by native community resistance in mediating the effects of global changes on plant invasion. Specifically, (i) we first examined which among road disturbance, climate change, land-use change, and native community resistance is the most influential direct driver of non-native species occurrence and abundance; (ii) then, we explored whether global change drivers

indirectly influence plant invasion by altering the resistance of native plant communities.

2 | Material and Methods

2.1 | Study Area and Sampling Design

The study was conducted in the Central Apennines Mountain range of central Italy (Figure S1). The area is characterized by a Mediterranean and temperate climate, with a mean annual temperature ranging from 13°C at the low elevation sites to 4°C at high altitude sites, and mean annual precipitations varying from 610 to 840 mm along the elevational gradient (Cutini et al. 2021; Pesaresi et al. 2017).

In spring–summer 2022, vegetation was sampled following the MIREN road survey protocol (see Haider et al. 2022, 2026 for details about the protocol), which consists in a stratified sampling along mountain roads, so as to cover the main elevational gradient within the mountainous region. Specifically, the sampling was carried out along the road of three mountain sites, namely Mount Terminillo (coordinates at the mountain peak N 42.473958 E 13.066039; elevational range between 420 and 1915 m a.s.l.; Lazio region), mountain chain of Gran Sasso (N 42.442080 E 13.559249; 595–2125 m a.s.l.; Abruzzo region), and Mt. Maiella (N 42.149692 E 14.115330; 485–2065 m a.s.l.; Abruzzo region). These three roads were similarly paved. That is, asphalt-covered, including at the highest elevations, so road type did not vary across sites. Along each road, we established 20 sites evenly stratified by elevation at approximately 80 m elevation intervals, corresponding to a minimum horizontal distance of 237 m. In each site, we sampled vegetation in two 2 × 50 m plots: one plot located close and parallel to the roads (hereafter roadside plot), where vegetation is subject to high anthropogenic disturbance; and a second plot perpendicular to the road and distant 50 m from the roadside (hereafter interior plot), representing a vegetation type exposed to lower disturbance levels (Figure S1). In two sites, due to excessive slope, placing the internal plots was not possible. As a result, in total the dataset included 118 plots, 60 roadside plots and 58 interior plots. In each plot, we recorded the presence and relative cover in percentage of all vascular plants. Elevation was measured in the field with a multi-GNSS GPS. Plant species nomenclature followed the Word Flora Online (WFO 2024). Species were classified into natives and non-natives according to Bartolucci et al. (2024) and Galasso et al. (2018, 2024).

2.2 | Plant Traits

We used plant traits to represent the competitive ability and functional diversity of the native community in order to capture potential biotic resistance and the availability of open niches for invasion (Gallien and Carboni 2017). We gathered trait data from the plant trait platform TRY (Kattge et al. 2020). To characterize functional differences between species, we examined four morphological traits responsible for the first two axes of variation in the global spectrum of plant form and function (Díaz et al. 2016). Specifically, we considered two traits associated with plant size, namely plant

height (H; m) and seed mass (SM; mg), and two traits related to the leaf economic spectrum, namely specific leaf area (SLA; mm² mg^{−1}) and leaf nitrogen content (LN; mg g^{−1}). These traits reflect the diversity of plant strategies in resource acquisition and competitive ability. Plant size captures the ability to intercept light and dominate the canopy (Violle et al. 2009), while leaf traits are associated with resource use efficiency and relative growth rate (Díaz et al. 2016; Wright et al. 2004). Trait values obtained by TRY were averaged across individuals by species. In all plots, trait data covered at least 80% of total plot vegetation (Pakeman and Quedstedt 2007).

2.3 | Climate

To reconstruct current climate and climate change occurred over the last 70 years, for the central point between the roadside and interior plot of each site, we gathered monthly precipitation, minimum and maximum temperature data at 1 km resolution for the period between 1931 and 2018 from the CHELSAcruts database (Karger and Zimmermann 2018). We averaged these data to calculate the mean annual precipitation (MAP), mean annual temperature (MAT), winter precipitation and summer maximum temperature. These four climatic variables were selected because they capture the main temperature and precipitation gradients relevant to mountain ecosystems and have been shown to be strong predictors of species and ecosystem responses to climate (Barros et al. 2025). These variables were calculated for three different climatic periods, each covering a 30-year interval to account for inter-annual climatic variability (World Meteorological Organization 2017): T1, running from 1931 to 1960; T2, from 1961 to 1990; and T3, from 1991 to 2020, representing the current climatic period. Although the CHELSAcruts dataset does not include monthly data for the most recent year (2020), climate normals for the T3 period (1991–2020) can be considered reliable as they are based on at least 80% of the 30-year interval (World Meteorological Organization 2017). To increase spatial accuracy, we downscaled the CHELSAcruts climate variables to 30 m resolution using the R package KrigR (Zurell et al. 2021), incorporating digital surface model (DSM at 30 m resolution), slope, and aspect as covariates. While the resolution of the climatic data may not capture fine-scale microclimatic variability among nearby plots, it is appropriate for describing site-level macroclimatic gradients relevant to the analyses.

2.4 | Land-Use

To assess current land-use as well as land-use changes, we visually inspected aerial ortho-photographs with 1 m resolution to produce three land-cover maps of the study area for the years 1954 (T1), 1988–1989 (T2) and 2022 (T3). Land cover was manually photo-interpreted in QGIS environment (QGIS 3.34.11; <https://www.qgis.org>) within a circular buffer of 250 m radius around the central point of each site (i.e., 50 m far from the roadside, adjacent to the interior plot). Following the CORINE Land Cover classification, we identified 6 land-cover classes (see Table S1 for a full description): artificial surfaces (ART), roads (ROA), agricultural areas (AGR), afforestations (AFF), forests (FOR) and grasslands (GRA). We thus calculated the percentage

landscape (PLand) of each class within each buffer for the three periods, using the 'lsm_c_pland' R function (*landscapemetric*; Hesselbarth et al. 2018).

We validated the land cover map relative to the year 2022 (T3) using 200 ground control points collected by field campaigns from 2022 and 2024 and evenly distributed across land-use cover types and the study area. To assess the accuracy of visual inspection, confusion matrices were constructed, and the following performance metrics were calculated: overall accuracy and Cohen's Kappa statistics (Congalton and Green 2019). The overall accuracy was 98% and Cohen's $K=0.98$, indicating a good land cover map accuracy. Since the land cover maps of the years 1954 and 1989 were photo-interpreted using backward editing technique on the basis of the most recent map (2022), the accuracy of older land cover maps can also be considered satisfactory (Malavasi et al. 2013).

2.5 | Deriving Drivers of Invasion

2.5.1 | Native Community Resistance

To investigate native community resistance, we used the relative cover of native species (thus excluding non-natives) to calculate functional diversity (FD) and trait community weighted means (CWMs), which quantify respectively the availability of open niches to invasion and the dominant functional strategy adopted by native species to outcompete non-natives.

For calculating FD, we first computed a multi-trait dissimilarity matrix between all native species using all collected traits ('gawdis' R function; de Bello et al. 2021). Then, we employed the functional distance matrix to calculate Rao quadratic entropy using the 'melodic' R function (de Bello et al. 2016). We separately calculated the native CWM of plant height, seed mass, SLA and LN using the 'functcomp' function (R package *FD*; Laliberté et al. 2014). We then conducted a principal component analysis (PCA, R package *vegan*; Oksanen et al. 2021) using all the CWM values to synthesize dominant native plant form and strategies within each community. The first two PCA axes (Figure 1D) were used as proxies of native community resistance. The first PCA axis (41% of the variance) distributes the native communities along a conservative-acquisitive strategy continuum, according to the 'slow-fast' leaf economic spectrum (Reich 2014; Wright et al. 2004), ranging from conservative species characterized by low SLA and LN (negative values) to acquisitive species with high SLA and LN (positive values). The second PCA axis (35% of the variance) separates native communities according to plant size, from communities dominated by short-statured species with small seeds (negative values) to those dominated by tall species with large seeds (positive values) (Díaz et al. 2016). Here we assume that (1) native communities dominated by species with traits associated with high competitive ability, including acquisitive resource-use strategies (high SLA and LN) and greater competitive effects for light and establishment (tall stature and large seed mass), should provide greater resistance to invasion; and (2) communities with higher FD should leave fewer ecological niches available for non-native species, thereby increasing biotic resistance.

2.5.2 | Climate and Land-Use Changes

We first assessed if climate and land use changes actually occurred over the past 70 years in the study area, in order to check if these could be tested as candidate drivers of invasion patterns. Short- and long-term changes in MAT, MAP, and the cover of each land-use classes were calculated, respectively, as the differences between T3 and T2 (Δ_{T3-T2} , short-term changes occurred over the last 30–40 years), and the delta between T3 and T1 (Δ_{T3-T1} , long-term changes occurred over the last 60–70 years). We thus obtained indices of change with negative and positive values indicating, respectively, a decrease or increase, while values equal to 0 indicate no changes. We then applied mixed-effect models ('lmer' function, lme4 package; Bates et al. 2014) to test if and how climate and land use changed over time. For climate changes, we used MAT and MAP as response variables and 'Time' as predictive categorical variable consisting of three levels, that is, T1, T2 and T3. To test for land-use changes, we used cover as response variable with 'Time', 'Land-use cover type', and their interaction as predictive variables. 'Land-use cover type' is a categorical variable consisting of six levels, that is, artificial surfaces (ART), roads (ROA), agricultural areas (AGR), afforestations (AFF), forests (FOR) and grasslands (GRA). All these models included the site nested in the mountain as random effects in order to account for the repeated measure over time and the variability between sites. Model residuals were visually inspected to ensure assumptions of homoscedasticity and normality (Zuur et al. 2009). MAT was log-transformed to meet model assumptions. Finally, Tukey's post hoc tests were used to assess the significance of temporal trends in climate and land-use. We then only considered significant changes as potential drivers of invasion in further analyses, that is, short-term changes (Δ_{T3-T2}) in MAT and MAP, and long-term changes (Δ_{T3-T1}) in the cover of agricultural area, forests, and grasslands (see Figure 1A,B).

To better describe and understand these long-term land-use changes, we built a transition matrix summarizing changes occurred in each cover type between T1 and T3 (Malavasi et al. 2018). To do so, we first converted vectorial layers of each cover type into a raster layer with a grain of 1 m for the three time periods. Then we built the transition matrices. Finally we showed these changes using a Chord-Diagram using the R function 'chordDiagram' (package *circlize*; Gu et al. 2024).

2.6 | Statistical Analysis

We used piecewise structural equation modelling (SEM, *piecewiseSEM* package; Lefcheck 2016) to investigate direct and indirect drivers of non-native species occurrence and abundance. Based on current knowledge about the drivers of plant invasion along elevation gradients, we outlined two meta-models (Figure S2; Table S2), one for non-native species occurrence and one for non-native species abundance, which involved all hypothesized causal paths linking road disturbance, native community resistance, current climate and land-use, temporal changes in climate and land-use with non-native species occurrence and abundance. Road disturbance, current climate and land-use, as well as temporal changes in climate and land-use are expected to directly influence non-native species occurrence

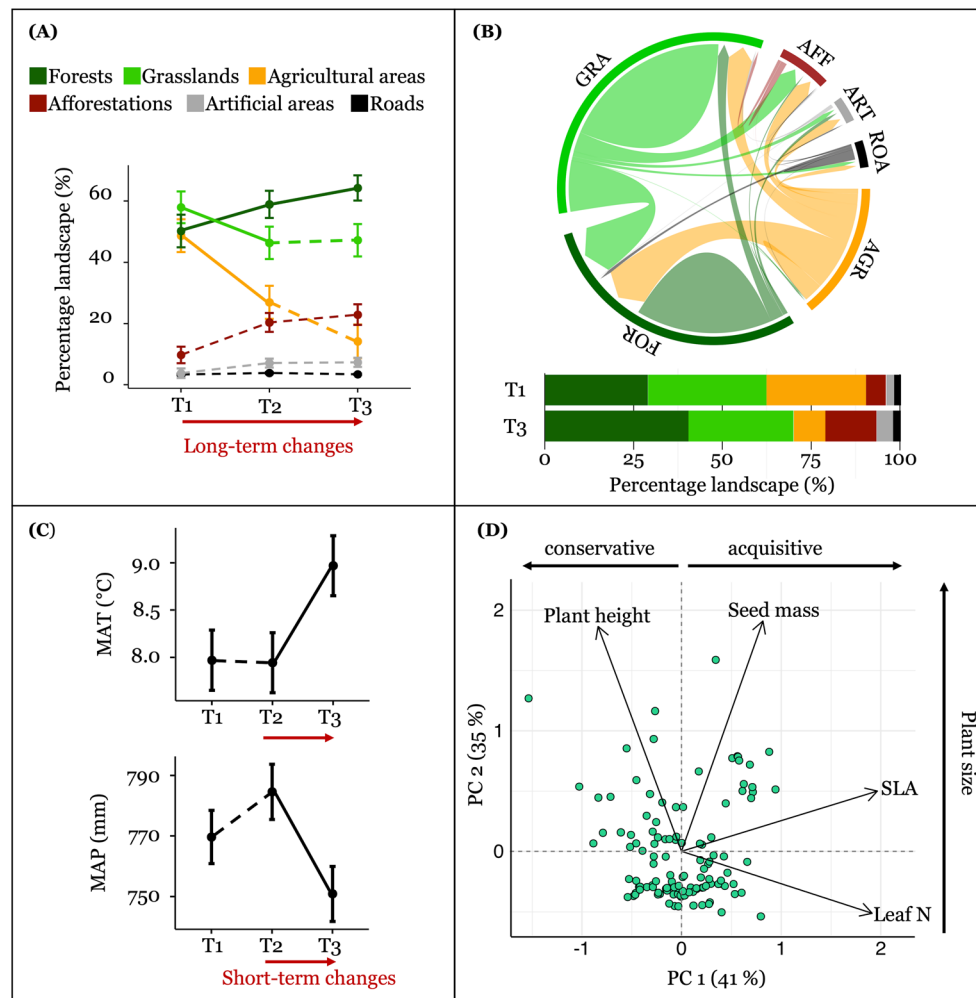


FIGURE 1 | Synthesis of land-use change (A and B), climate change (C), and the native community functional structure (D). (A) Changes in the percentage landscape covered by forests, grasslands, agricultural areas, afforestations, artificial areas, and roads occurred over the last 70 years, between 1954 (T1), 1988–1989 (T2) and 2022 (T3). Continuous lines refer to significant changes while dashed lines refer to non-significant ones. (B) Cord diagram and bar plot summarizing the changes in percentage of each land cover type between 1954 (T1) and 2022 (T3). In the chord diagram, the arrows represent the direction of change, while the width of the arrow represents the extent (%) of the transition. (C) Changes in mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) occurred between three 30-year climatic intervals: T1, running from 1931 to 1960; T2, from 1961 to 1990; and T3, from 1991 to 2020. Continuous lines refer to significant changes while dashed lines refer to non-significant ones. (D) Principal component analysis (PCA) of the community weighted means (CWMs) of specific plant height, seed mass, leaf area (SLA) and leaf nitrogen content. Each dot refers to a native plant community. The percentage of the total variance explained by each component is given in brackets. The PC1 ordinated the communities along a gradient of conservative-acquisitive dominant strategy while the PC2 separates communities according to plant size.

and abundance but also indirectly, by altering the resistance of the native community to plant invasion (Lembrechts et al. 2017; Pauchard et al. 2016; Petitpierre et al. 2016), here expressed as native plant size, conservative-acquisitive plant strategy, and functional diversity. Finally, we also predicted a direct influence of native community resistance on non-native species occurrence and abundance.

For testing the factors directly driving the occurrence and abundance of non-native species along Mediterranean mountain roads, we fitted two separate generalized linear mixed-effect models ('glmer' R function, *lme4* package; Bates et al. 2014). Specifically, to model non-native species occurrence we used a logistic regression (binomial family) with presence/absence as response variable. To model non-native

species abundance, we restricted the analysis to plots where non-native plants were present. Abundance data were expressed as cover proportion and logit-transformed to meet model assumptions. We then fitted a linear mixed-effects model ('lmer' R function, *lme4* package; Bates et al. 2014). In both models, the explanatory variables were: road disturbance as binary variable (0 = interior plot and 1 = roadside plot), elevation, plant size (first PCA axis), conservative-acquisitive plant strategy (second PCA axis), functional diversity of native species, current MAT and MAP (during T3 interval), short-term changes (Δ_{T3-T2}) in MAT and MAP, current cover of each land-use cover type (at T3), and long-term changes (Δ_{T3-T1}) in the cover of agricultural areas, forests, and grasslands. Prior to model fitting, we checked for multicollinearity between predictors using the 'vifstep' R function (*usdm*

package; (Naimi 2012)) and excluded those with a Variance Inflation Factor (VIF) exceeding 3 (Zuur et al. 2009). The final set of predictive variables included: road disturbance, plant size, conservative-acquisitive plant strategy, functional diversity, current MAT, current MAP, short-term changes in MAT and MAP, current cover of agricultural areas, artificial areas, roads and grasslands, long-term changes in the cover of agricultural areas, grasslands, and forests. Note that elevation was excluded because, as expected, it was highly correlated with MAT ($r=0.99$, p -value <0.001). To complement the SEM analysis, we performed variance partitioning on the final models using the *variancePartition* R package (Hoffman and Schadt 2016) to quantify shared contributions of native community resistance, climate, and land-use and their temporal changes to the explained variance in non-native species occurrence and abundance. While SEMs allow the evaluation of direct and indirect relationships among predictors, variance partitioning provides a global decomposition of explained variance across predictor groups and quantifies the relative importance of each predictor as the percentage of the total variance explained by the model.

For testing how global change factors indirectly influence plant invasion via changes in the resistance of native communities, we fitted three separate linear mixed-effect models. Response variables were native plant size, conservative-acquisitive plant strategy, and functional diversity. Final predictors after checking for multicollinearity were: road disturbance, current MAT, current MAP, short-term changes in MAT and MAP, current cover of agricultural areas, artificial areas, roads, and grasslands, long-term changes in the cover of agricultural areas, grasslands, and forests. Considering all these relationships, each SEM consisted of four sub-models (listed in Table S2), all including mountain identity as random effect in order to account for the variability between mountains. To account for potential non-independence among plots within the same site, we estimated cluster-robust standard errors using site as clustering factor. Results were robust to the inclusion of cluster-robust standard errors accounting for within-site dependence (Table S3). SEM goodness-of-fit was evaluated through Fisher's C statistic. Alternative model structures were compared using Akaike Information Criterion (AIC), and among models equally supported ($\Delta AIC \leq 2$), the most parsimonious one was selected based on lower AIC values and Fisher's C p -values > 0.05 (Burnham and Anderson 2002; Richards 2005; Shipley 2013). Model assumptions were visually inspected. We finally computed indirect effects as the product of the standardized coefficients of the paths that form the indirect relationship (Gana and Broc 2019). To explore potential moderation effects beside mediation, we tested a reduced set of interaction terms focusing on the indirect pathways identified in the SEM, by including interactions between native biotic resistance metrics and the climatic and land-use predictors influencing them. These exploratory analyses did not reveal robust interaction effects (Table S4), further supporting the predominance of indirect (mediated) pathways in structuring invasion patterns.

All statistical analyses were conducted with R version 4.3.1 (R Core Team 2023).

3 | Results

3.1 | Non-Native Species

Across the surveyed plots, we found a total of 811 vascular plant species, ranging from 10 to 97 species per plot (mean = 43.63, SD = 16.81). Among these, 16 were classified as non-natives (Table S5; for more details see Santoianni et al. 2025). Within invaded plots, the number of non-native species ranged between 1 and 4 (mean = 1.77, SD = 0.9), while the non-native species cover ranged between 0.1% and 45.5% (mean = 5.43%, SD = 9.30).

3.2 | Changes in Climate and Land-Use

We found significant changes in both climate and land-use in this area over the past 70 years (Figure 1A–C; Table S6). However, changes in climate were more pronounced over the last 30 years (Figure 1C; Table S7), that is, between the climatic periods 1961–1990 (T2) and 1991–2020 (T3), while changes in land-use occurred earlier in time (Figure 1A; Table S8), starting from 1954 (T1). We thus considered only short-term changes for climate (Δ_{T3-T2}) and long-term changes for land-use (Δ_{T3-T1}) in further analyses. Between T2 and T3, MAT increased ($t=0.897^\circ\text{C}$, p -value <0.001) while MAP decreased ($t=-30.0\text{ mm}$, p -value <0.001). On the other hand, between 1954 (T1) and 2022 (T3), the study area experienced a decline in the cover of agricultural areas ($t=-34\%$, p -value <0.001) and grasslands ($t=-10\%$, p -value <0.048) that have been replaced by forests' expansion ($t=14\%$, p -value <0.017 , Figure 1B).

3.3 | Most Important Drivers of Invasion

Through variance partitioning we identified the most important drivers influencing non-native species occurrence and abundance (Figure 2). Overall, both models demonstrated good explanatory power (R^2), explaining 65% of the variation in both non-native species occurrence and abundance. We found that non-native species occurrence was mainly driven by climate, with current MAT and MAP explaining 47% and 6% of the total variance, respectively, for a combined 53%. Road disturbance played a secondary role, explaining only 30% of the total variance. Native community resistance also contributed, although to a lesser extent, with plant size accounting for 10% and conservative-acquisitive strategy for 6%, together explaining 16% of the total variance. On the other hand, the abundance of non-native species was mainly influenced by native community resistance and climate. Plant size, conservative-acquisitive strategy, and functional diversity explained 14%, 4% and 10% of the variance, respectively, for a total of 28%, while current MAT and MAP explained 12% and 13% of variation, for a total of 25%. Temporal changes in climate and land-use, which accounted for none or very little of the variation in non-native species occurrence (only 1% of changes in agricultural areas), had a clearer effect on abundance. Specifically, short-term changes in MAT accounted for 11% of the variation, while long-term changes in surrounding land-use overall explained 19% of variation (12% due to changes in agricultural areas and 7% due to changes in forest cover). Finally, road disturbance

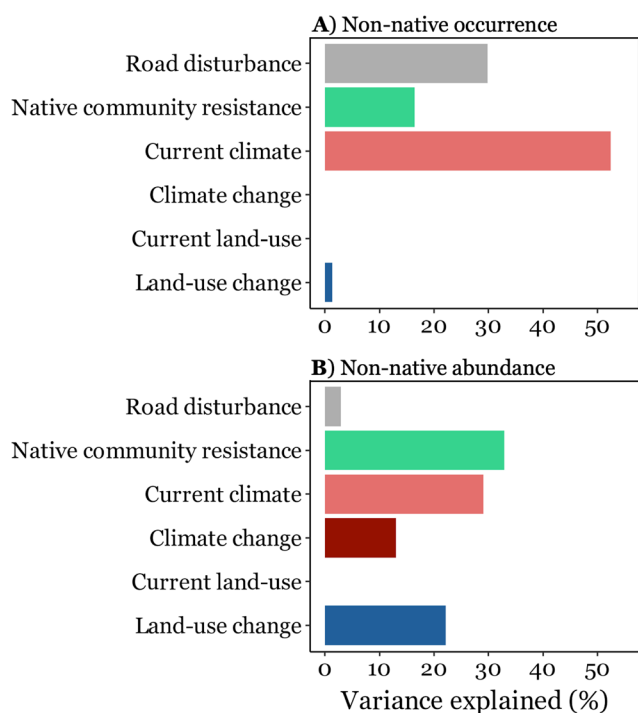


FIGURE 2 | Variance partitioning of the drivers of non-native species occurrence (A) and abundance (B). The relative importance is expressed as % of the total variance explained (model R^2) by each predictor in the models. Native community resistance (in green) refers to the summed effect of dominant plant size, conservative-acquisitive strategy, and functional diversity of the native communities. Current climate (in light red) is the summed effect current mean annual temperature (MAT) and precipitation (MAP), while climate change (in dark red) is the summed effect of short-term changes in MAT and MAP occurred over the last 40 years (Δ_{T3-T2}). Current land-use (in light blue) includes the effects of the percentage landscape (PLand) covered by agricultural areas, artificial areas, roads, and grasslands at T3, while land-use change (in dark blue) refers to the summed effects of long-term changes occurred in the surrounding landscape over the last 70 years (Δ_{T3-T1}) in the cover of agricultural areas, grasslands and forests.

had a negligible effect, explaining only 2% of variance in non-native species abundance.

3.4 | The Direct Effects of Global Change and Native Community Resistance on Plant Invasion

Both SEMs demonstrated a good fit to the data (SEM of non-native species occurrence Fischer's $C=49.06$, $df=50$, p -value=0.511; SEM of non-native species abundance Fischer's $C=28.71$, $df=34$, p -value=0.724; Figure 3) and identified the direct and indirect drivers of non-native species occurrence and abundance. Road disturbance had a positive direct effect on the occurrence of non-native species (Figure 4A) but no effect on their abundance (Figure 5A), indicating a higher probability of invasion in roadside-disturbed plots compared to interior-undisturbed plots, but similar abundance. Native plant size had a negative effect on non-native species occurrence (Figure 4B) while the native conservative-acquisitive strategy had a positive one (Figure 4C), denoting higher probability of invasion in

native communities dominated by short-statured plant species with an acquisitive resource strategy. We also found higher non-native species occurrence in sites with higher MAT (Figure 4D), while MAP had no effect (Figure 4E). On the other hand, the abundance of non-native species was similarly influenced by native community functional structure, with a negative effect of native plant size (Figure 5B) and a positive effect of native functional diversity (Figure 5D). Moreover, we found that non-native species were more abundant in sites with lower MAT (Figure 5E) and MAP (Figure 5F) as well as sites where MAT increased the most over the last 40 years (Figure 5G). Finally, non-native species abundance was higher in sites that over the last 70 years experienced in the surrounding landscape a contraction in the cover of agricultural areas (Figure 5I) and an expansion in forest cover (Figure 5H).

3.5 | The Indirect Effects of Global Change on Plant Invasion Mediated by Native Community Resistance

Through the SEM analysis, we showed that global change factors also indirectly affect non-native plants by altering the resistance of native communities to invasion (Figure 3). Global change drivers have indeed led to significant shifts in the native communities. Sites that experienced a decrease in agricultural cover were dominated by short-statured species with small seeds (Figure 3A), which in turn increase invasion probability (indirect effect = -0.05; Figure 3A). In contrast, forest expansion indirectly reduced invasion probability (indirect effect = -0.05; Figure 3A) by promoting the dominance of conservative species within native communities (Figure 3A), which are more resistant to invasion. Higher grassland cover in the surrounding landscape indirectly promoted non-native species occurrence (indirect effect=0.09; Figure 3A), as it was associated with smaller native plant size (Figure 3A), and thus with lower biotic resistance. Road disturbance favoured the dominance of acquisitive strategies (Figure 3A), thereby indirectly promoting non-native species occurrence (indirect effect=0.05; Figure 3A). By contrast, the abundance of non-native species was negatively influenced indirectly by both land-use and climate. Current agricultural cover increased native plant size (Figure 3B), which in turn decreased non-native species cover (indirect effect = -0.27; Figure 3B). Likewise, current MAP had a negative indirect effect on non-native species abundance (indirect effect = -0.19; Figure 3B) through its negative effect on native functional diversity (Figure 3B).

4 | Discussion

Native community resistance plays a central role in regulating the establishment and spread of non-native species across mountain ecosystems, yet how it mediates the effects of global change drivers is often overlooked. While human disturbance, climate and land-use changes are expected to facilitate plant invasion across mountain ecosystems (Alexander et al. 2016; Carboni, Calderon-Sanou, et al. 2018; Lembrechts et al. 2016; Pauchard et al. 2009, 2016), it remains unclear whether their effects are direct or are instead mediated by changes in the biotic resistance of native communities. This study addressed this question by

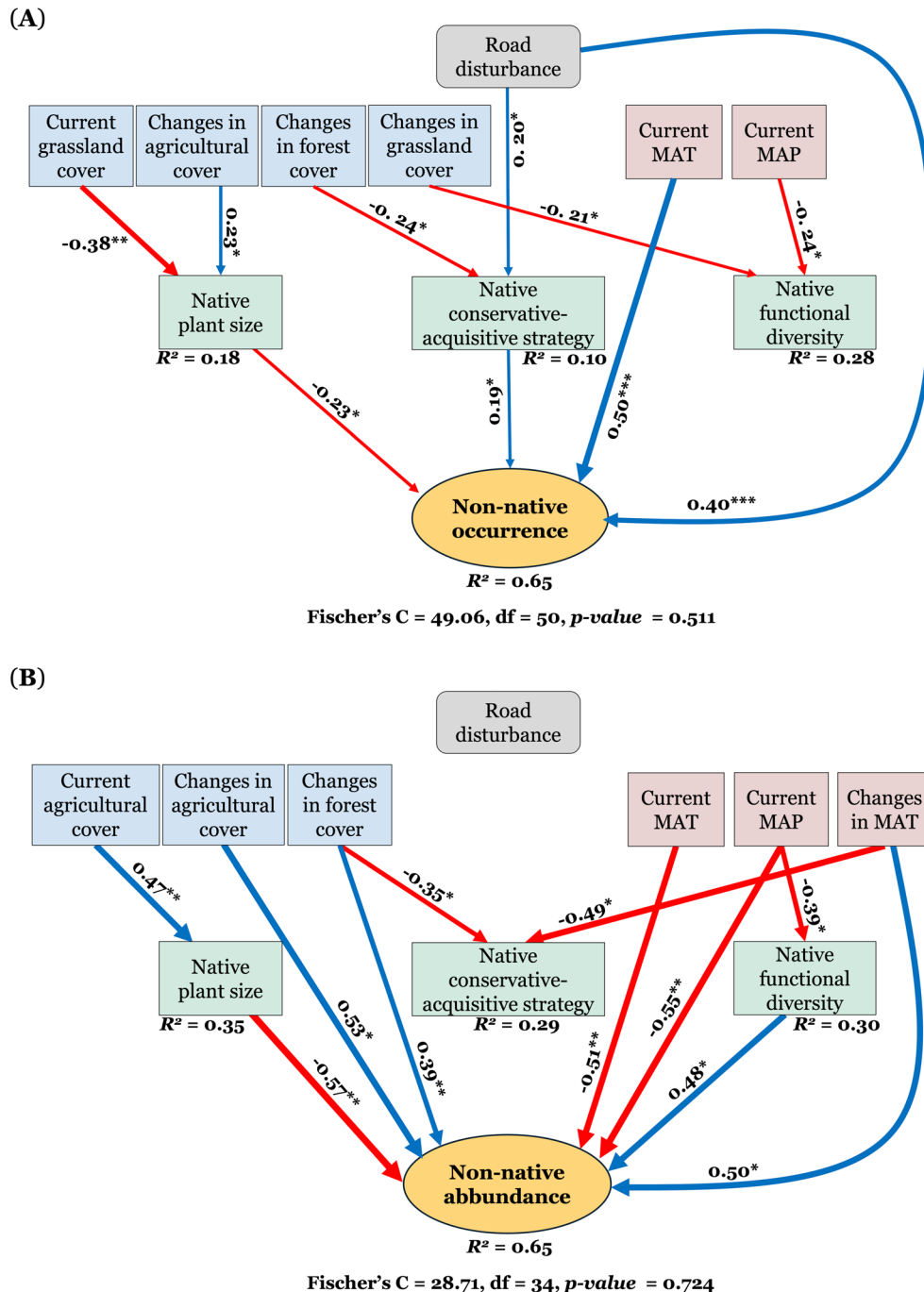


FIGURE 3 | Direct and indirect drivers of plant invasion. Structural equation model (SEM) illustrating the effects of road disturbance, native community resistance, current climate, land-use as well as changes in climate and land-use on non-native species occurrence and abundance and the interplay between these drivers. Red arrows refer to negative effects and blue arrows to positive ones. Arrow widths are proportional to standardized estimates, which are reported above each arrow together with significance levels indicated by asterisks (* $p\text{-value} < 0.05$; ** $p\text{-value} < 0.01$; *** $p\text{-value} < 0.001$). R^2 are reported next to the corresponding response variable. For road disturbance (binary variable comparing roadside vs. interior plots), standardized coefficients represent the standardized difference in non-native species occurrence or abundance between the two plot types and are not directly comparable to those of continuous predictors.

examining how global change drivers, such as human disturbance (here expressed by road disturbance), climate change and land-use changes, have affected the occurrence and abundance of non-native species in Mediterranean mountain ecosystems, both directly and indirectly through their impact on the functional structure and composition of the native communities.

Our results highlight that although climate filtering remains a key direct driver of plant invasion, the resistance of the native community is a decisive factor that mediates the distribution and abundance of non-native species along elevational gradients and their response to global changes. For example, the abandonment of agricultural lands has resulted in the development of

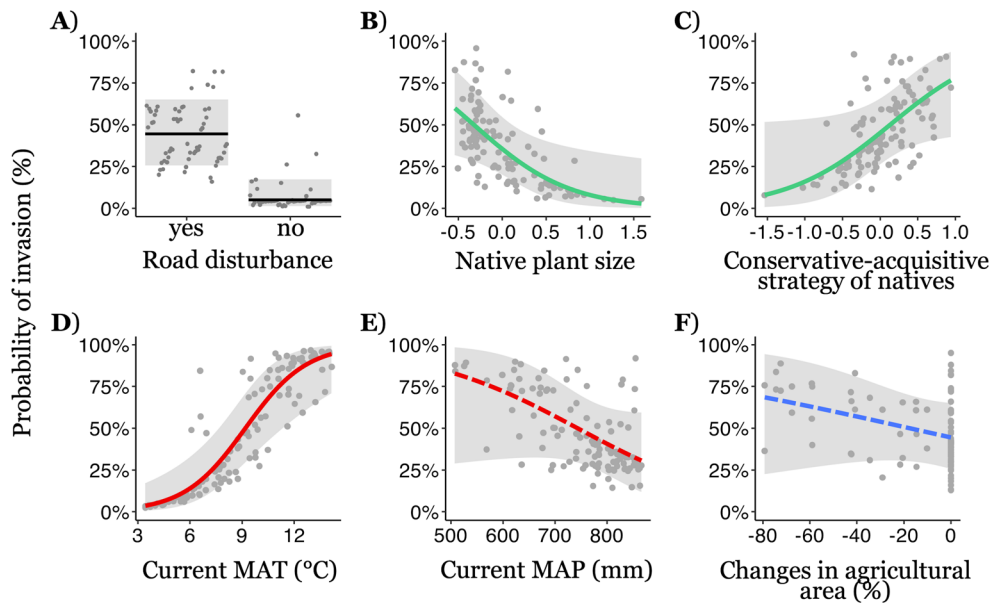


FIGURE 4 | Direct drivers of non-native species occurrence. The effects of road disturbance (A), native community resistance (B and C, in green), current climate (D and E, red), and changes in land-use (F, in blue) on non-native species occurrence, expressed as probability of invasion in percentage. The figure only shows final predictors retained after model selection of the generalized linear mixed-effect model testing the drivers of non-native species occurrence. Continuous regression lines refer to significant effects (p -value < 0.05), while dotted lines to marginal and non-significant effects (p -value > 0.05). shading areas associated with the lines represent the 95% confidence interval.

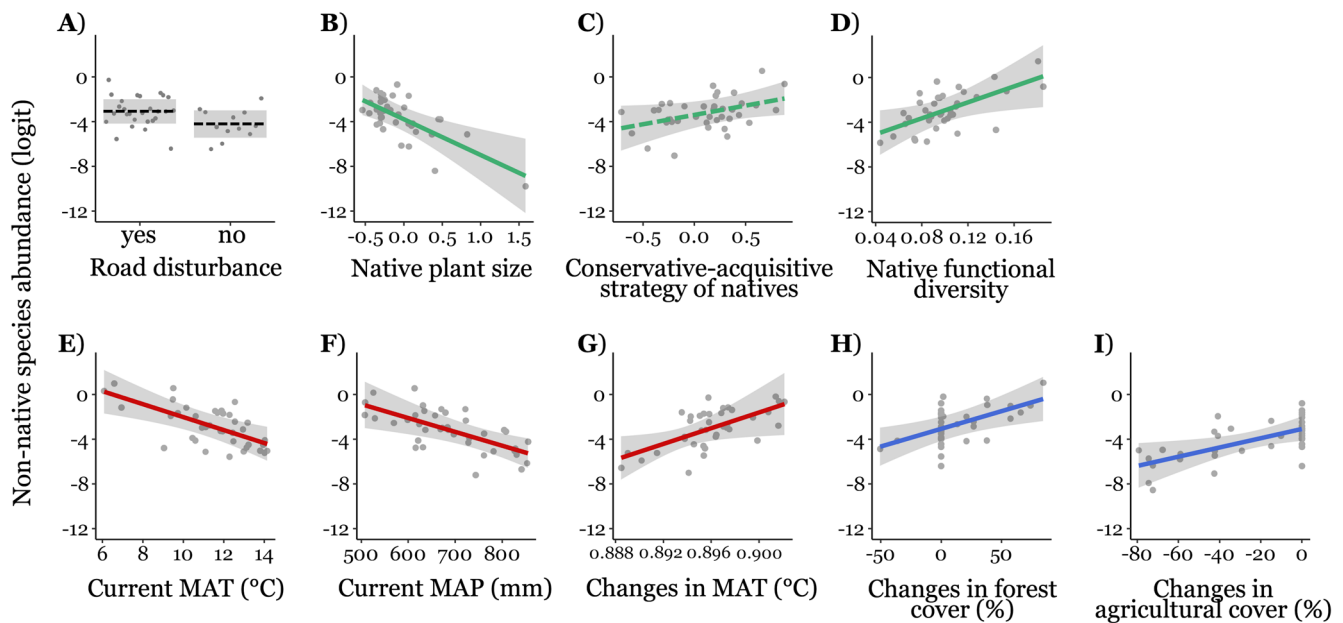


FIGURE 5 | Direct drivers of non-native species abundance. The effects of road disturbance (A), native community resistance (B–D, in green), current climate (E and F, red), and changes in climate (G, in red) and land-use (H and I, in blue) on non-native species abundance (logit). The figure only shows final predictors retained after model selection of the linear mixed-effect model testing the drivers of non-native species abundance. Continuous regression lines refer to significant effects (p -value < 0.05), while dotted lines to marginal and non-significant effects (p -value > 0.05). Shading areas associated with the lines represent the 95% confidence interval.

short-statured native plant communities that exert lower biotic resistance to non-native plant establishment; by contrast, the regeneration of forests on former agricultural lands has strengthened native community resistance through the dominance of conservative species. Overall, these findings demonstrate that

in Mediterranean mountain ecosystems, native communities continue to provide significant resistance to plant invasion despite ongoing global changes. This highlights the importance of maintaining and restoring native communities to mitigate future invasion risks.

4.1 | The Influence of Global Change Drivers and Biotic Resistance on Plant Invasion

High elevation plant communities are still considered to be less affected by plant invasion thanks to a combination of climate filtering, low propagule pressure, and limited human disturbance (Alexander et al. 2016; Dainese et al. 2024; Lembrechts et al. 2016; Pauchard et al. 2009). In support of this idea, mean annual temperature (MAT) emerged as the strongest driver of the presence of non-native species across the mountains of the Central Apennines, explaining 47% of variation in non-native species occurrence (Figure 2). This finding underscores the critical role of temperature as a limiting factor for non-native species establishment at higher elevations, where colder conditions and shorter growing seasons act as strong climatic filters (Delavaux et al. 2023; Hoch and Körner 2012; Sundqvist et al. 2013). Although most studies did not explicitly test the direct influence of temperature in driving non-native species patterns across mountain ranges, often using elevation as a proxy of temperature variation (Körner 2007), similar patterns of declining non-native species diversity with decreasing temperature have been consistently observed worldwide (Haider et al. 2018; Pauchard et al. 2009; Seipel et al. 2016). This is because non-native species, often originating from warmer regions (Cao Pinna et al. 2021), face significant challenges in surviving and reproducing in colder, high-altitude environments where metabolic processes and resource availability are constrained (Hoch and Körner 2012; Sundqvist et al. 2013). Nevertheless, the effect of climate on non-native species abundance was lower than on occurrence. While MAT and MAP together explained about half of the variation in non-native species occurrence, they accounted for only about a quarter of the variation in non-native species cover, slightly less than the variation explained by native community resistance (28%). This suggests that although climate remains a critical filter for determining whether non-native species can establish at higher elevations, their success in terms of dominance and spread within communities is more strongly mediated by biotic resistance. In other words, climate sets the stage for non-native species entry, but it is the composition and functional structure of native communities that largely determine their abundance once established. This pattern is consistent with theoretical and empirical evidence that competitive interactions and resource-use complementarity constrain the growth of non-native species (Cavieres 2021; Funk et al. 2008). Our results therefore highlight the need to consider not only abiotic filters but also the biotic context in predicting the outcomes of plant invasions under ongoing global change.

Alongside temperature, human disturbance, quantified with road disturbance, emerged as a critical driver of non-native plant occurrence but not of their abundance. Our findings revealed a greater probability of invasion in disturbed roadside plots compared to undisturbed ones located farther from roads. This pattern aligns with the well-documented role of roads as key vectors for invasion, facilitating both the dispersal of propagules and the creation of suitable conditions for establishment, such as altered soil microclimate and increased light availability (Haider et al. 2018; Lejeune et al. 2024; Lembrechts et al. 2017; McDougall et al. 2018). However, once established, the cover of non-native species did not differ significantly between roadside and more

distant plots. This suggests that while roads strongly influence the entry of non-native species into mountain ecosystems, their subsequent spread and dominance within communities depend more on local biotic interactions and resistance mechanisms than on disturbance per se. In other words, disturbance acts primarily as a gateway for invasion, whereas the degree of invasion success is mediated by the ecological characteristics of the receiving community (Christen and Matlack 2009; McDougall et al. 2018).

Linked to human disturbance, we also expected an influence of the cover of artificial structures and road networks in the surrounding on the presence and abundance of non-native species. Surprisingly, however, our analysis did not identify any significant effect of these variables. One possible explanation for this result is that, while artificial structures and road networks can serve as significant sources of propagule introduction and dispersal, their impact on invasion success may be limited to immediate surroundings and become more apparent only at finer spatial scales, where proximity to these features directly increases propagule pressure (Fuentes-Lillo et al. 2021). Another potential explanation involves a time lag in the response of non-native species to human modification of the landscape. While propagules may already be present, the establishment and spread of non-native plants can require time to overcome environmental barriers or take advantage of changes in native community composition (Carboni, Guéguen, et al. 2018). Such delays may obscure the current influence of artificial structures and road networks, even though their long-term role in facilitating invasions may still be significant (Essl et al. 2015). Our findings also show that the direct influence of land-use changes on non-native species was minimal. Nevertheless, their impact was exerted indirectly by altering the composition of native communities, thereby reshaping their biotic resistance to invasion (see below).

Biotic resistance emerged as key determinant of plant invasion, by limiting the establishment and spread of non-native species (Elton 1958; Richardson and Pyšek 2006). We found stronger resistance in communities dominated by tall-statured species with large seeds and conservative leaf strategy. This likely reflects their higher competitive ability, particularly for light acquisition and during early establishment stages, which reduces opportunities for invaders. (Funk et al. 2008; Simpson et al. 2021; Suárez-Vidal et al. 2017; Violle et al. 2009; Westoby et al. 2002). Based on competitive exclusion and limiting similarity hypotheses (Daehler 2001; MacArthur and Levins 1967; Shea and Chesson 2002), we similarly expected acquisitive native species (e.g., with high SLA) to limit invasion by reducing niche availability (Kraft et al. 2015; Sheppard 2019). However, contrary to our expectations, our results instead support the preadaptation hypothesis in this case: as non-native plants are usually acquisitive, fast-growing species (Dawson et al. 2012; Heberling and Fridley 2013; Richardson and Pyšek 2006; Van Kleunen et al. 2010), they may preferentially invade communities with similar traits because they better align with the local resource conditions. Many studies have already demonstrated the strong influence of similarity between native and non-native species on invasion success in a wide range of environmental conditions (Carboni et al. 2013; Fan et al. 2023; Gallien et al. 2015; Le et al. 2024; Park et al. 2020) as well as the higher probability of non-native species to establish in native communities

with acquisitive leaf strategies (LaForgia et al. 2020; Lemoine et al. 2015; Li et al. 2022; Lodge et al. 2018). In other words, our results suggest that in mountain ecosystems conservative communities may be inherently less hospitable to fast-growing, acquisitive invaders that usually rely on high resource availability.

Functional diversity showed a different pattern, being positively related to non-native abundance but not occurrence. This suggests that native functional diversity does not necessarily prevent non-native species establishment, but may influence post-establishment spread. Higher functional diversity likely correlates with niche heterogeneity, allowing invaders to proliferate (Davies et al. 2005; Delavaux et al. 2023; Fridley et al. 2007; Guo et al. 2024).

4.2 | Biotic Resistance Mediates the Effect of Global Changes on Plant Invasion

As global changes are expected to reshuffle not only non-native species but also natives (Lembrechts et al. 2017; Pauchard et al. 2016; Petitpierre et al. 2016), this study aimed to examine how global changes indirectly influence plant invasion via effects on native community resistance. Our findings show that road disturbance and changes occurred in land-use and climate shaped the composition and structure of native communities and, in turn, invasion dynamics. In particular, we found that road disturbance increased the dominance of acquisitive, fast-growing species, which thrive in disturbed environments where competition for resources is reduced, and environmental conditions are more favourable to opportunistic growth strategies (Alvarez et al. 2025; Herben et al. 2018). These native plant communities offer favourable conditions for non-native plant establishment. Therefore, roads do not only favour invasion by acting as dispersal corridors and propagule reservoirs (Lembrechts et al. 2017), but also by changing native community composition.

Land-use changes occurred over the last 70 years in the study area have also indirectly influenced invasion dynamics by reshaping native plant community composition. In many European mountains, widespread agricultural abandonment and rural exodus since World War II has driven natural succession and forest recovery (Bracchetti et al. 2012; Lasanta et al. 2017; Sitzia et al. 2010), a pattern also observed in our study area (Evangelista et al. 2016; Frate et al. 2018; Malavasi et al. 2018). This transition has deeply transformed the vegetation structure by increasing conservative communities, with important implications for biotic resistance. Our findings show that forest expansion reduced the dominance of acquisitive species, making native communities less favourable to the establishment and expansion of non-native species. In line with our results, other studies already illustrated that mountain forests are still relatively resistant to invasion (Catford et al. 2012; Von Holle et al. 2003; Wagner et al. 2017). The dense canopy cover, understory, and thick litter layer of a forest could limit the ability of light-demanding, fast-growing invaders to succeed, thus creating physical barriers to invasion. Conversely, we also found that transitional or early successional stages following agricultural abandonment, such as meadows, remain more vulnerable to invasion, as their lower structural complexity and smaller plant stature create more opportunities for invaders. Our study thus

suggests that in Mediterranean mountain ecosystems, the gradual abandonment of agricultural lands and subsequent forest expansion are progressively enhancing native biotic resistance, whereas low- to middle elevations grasslands maintain a higher vulnerability to plant invasion. This is supported by the low representation of non-native trees in our dataset: only five were tree species, which predominantly invaded disturbed roadside plots rather than penetrating forest interiors (Santojanni et al. 2024, 2025). However, the most abundant non-native species in our study area was *Ailanthus altissima* (Mill.) S, an invasive tree species, raising important considerations. *Ailanthus altissima* has been recognized as a highly adaptable and aggressive invader, capable of exploiting disturbed habitats and encroaching into less disturbed forests (Kowarik and Säumel 2007; Marzalletti et al. 2025; Sladonja et al. 2015). Although native forests currently appear resistant, future changes in climatic or disturbance regimes could weaken this resistance and invasive species like *A. altissima* may seize the opportunity to expand further into forested habitats (Cao Pinna et al. 2024; Essl et al. 2012).

5 | Conclusion

This study demonstrates that plant invasion in Mediterranean mountain ecosystems is shaped not only by climate and human disturbance, but also by the resistance of native communities, which mediates the effects of global change on invasion dynamics. We found that climate and anthropogenic disturbance primarily control where non-native species can establish, while biotic interactions and native community functional structure largely determine invasion success after establishment. These findings highlight that predicting future plant invasions requires considering both ongoing global changes and biotic resistance, rather than treating them as independent processes. Conserving and restoring native communities that maintain high resistance to invasion should therefore be regarded as a key component of management strategies aimed at limiting the spread of non-native species under ongoing global change.

Author Contributions

M.C. and G.L.B. conceived and designed the study. All authors collected the data. G.L.B. and M.C. analysed and interpreted the data. G.L.B. wrote the first draft of the manuscript. All authors made significant contributions to the manuscript and approved it for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Santoianni et al. (2025) at <https://doi.org/10.3897/ved.139363>.

Peer Review

For transparency, the peer review documents associated with this article are available at <https://doi.org/10.1111/ddi.70264>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Detailed description of the land cover types

analysed with their relative attribution to the CORINE land cover classes. **Table S2:** Meta- and sub-models fitted in the SEM for testing the drivers of non-natives occurrence and non-natives abundance. **Table S3:** Model results using conventional and site-clustered standard errors. **Table S4:** Interacting effects between abiotic drivers and native community resistance on non-natives occurrence and non-natives abundance. **Table S5:** List of non-native species recorded in the study area. **Table S6:** Type III Analysis of Variance Table showing temporal changes in climate and land-use. **Table S7:** Temporal changes in mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm). **Table S8:** Temporal changes in percentage landscape (PLand, %) across land-use cover types. **Figure S1:** Study area and sampling design. **Figure S2:** SEM meta-model.