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Wild edible plants in Italy: contributions to alpha- and beta-diversity across habitats and biogeographical regions

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Abstract

Background

Wild edible plants (WEPs) are identified through human use, yet their distribution in vegetation may also reflect ecological assembly processes. We examined whether WEPs exhibit distinctive diversity patterns across habitats and biogeographical regions in Italy. We combined the AlimurgITA inventory with vegetation-plot data from the European Vegetation Archive (20,314 plots retained after stratified resampling), comparing plot-level diversity, species accumulation at standardized sampling effort, and frequency-based beta-diversity components for WEPs, the most frequently documented quarter of WEPs, and other vascular plants.

Results

At 100 plots, vegetated man-made habitats accumulated approximately 381 WEP species, comparable to grasslands (379), despite markedly lower total plant richness (773 versus 1,086 species). Forest fringes and secondary scrub also supported high WEP richness, whereas aquatic, wetland, and sparsely vegetated habitats generally supported fewer WEPs. The proportional contribution of WEPs to local Shannon diversity was generally highest in the Continental region and lowest in the Alpine region. Compared with taxa not recorded as WEPs, WEP assemblages exhibited less species replacement and more between-habitat differentiation associated with species frequencies and compositional similarity. This contrast was especially evident among the most frequently documented WEPs and in the Alpine region.

Conclusions

The observed patterns are consistent with combined influences of environmental filtering, disturbance-associated habitat conditions, and regional species pools on the assembly of WEP-rich communities. The results highlight the potential importance of heterogeneous, human-influenced habitat mosaics for conserving plant diversity associated with traditional food uses.

Background

Wild edible plants (henceforth: WEPs) represent a substantial component of regional floras worldwide and have historically contributed to human diets across a wide range of biomes (Bacchetta et al., 2016; Shirsat et al., 2024). In Mediterranean and temperate regions, WEPs include hundreds of vascular plant species spanning diverse life forms, functional strategies, and habitat affinities (Couplan, 2009; Gori et al., 2026). Despite their long-standing relevance and their continued presence in natural and human-modified habitats, WEPs are rarely addressed as an ecological entity in their own right. Instead, they are most often considered through cultural, ethnobotanical, or nutritional perspectives (de Cortes Sánchez-

Mata & Tardío, 2016), while their role within plant communities and their contribution to biodiversity patterns remain largely unexplored.

In Italy, research on WEPs has expanded considerably over the last decades, producing a rich body of literature. The vast majority of studies focus on the compilation of floristic checklists and on ethnobotanical aspects such as culinary uses, harvested plant parts, periods of collection, preparation methods, and traditional criteria for species recognition (comprehensively reviewed by Di Marzio et al., 2025). These contributions have been fundamental for documenting traditional knowledge and safeguarding cultural heritage, and they have greatly improved our understanding of the edible potential of the Italian vascular flora. However, this literature is strongly biased toward descriptive inventories and use-oriented analyses, while little attention has been paid to the ecological context in which WEPs occur. As a consequence, WEPs are rarely framed within the conceptual and analytical tools of vegetation ecology and macroecology. While a few studies have quantified the richness, abundance, or compositional responses of edible wild plants to local habitat characteristics or management regimes, primarily within forest ecosystems and at regional scales (Duchesne & Wetzel, 2002; Granath & Strengbom, 2017; Pohjanmies et al., 2021), no study has explicitly investigated WEPs as a functional subset of plant communities across broad environmental gradients, nor assessed their contribution to patterns of biodiversity at multiple spatial scales. In particular, fundamental questions remain unanswered regarding how WEPs contribute to alpha diversity within vegetation plots, how they shape beta-diversity patterns across habitats and biogeographical regions, and whether their compositional variation is driven primarily by species turnover or by abundance gradients (Buhk et al., 2017). Similarly, it is still unclear to what extent habitat filtering, land-use intensity, and broad biogeographical constraints influence the distribution and frequency of WEPs compared to the overall plant species pool.

From an ecological perspective, 'wild edible' is a use-based designation, not a functional trait shared by all species in the group. Nevertheless, the representation of edible taxa within vegetation may reflect non-random community-assembly processes: many edible species are known to be generalists, disturbance-tolerant, or associated with open and semi-natural habitats (Falla et al. 2025), suggesting that abiotic filtering is expected to restrict their occurrence in environmentally demanding habitats, whereas recurrent disturbance, canopy opening and successional dynamics may create recruitment opportunities for species capable of exploiting heterogeneous or transient conditions (Nowak-Olejnik & Mocior, 2022). These processes can produce two distinguishable patterns: an increased representation of WEPs in particular habitat types, and changes in the frequencies of shared WEPs across habitats without complete species replacement (Mori et al., 2018). We therefore expect (i) disproportionate WEP richness in open, semi-natural and anthropogenic habitats compared with environmentally constrained systems; (ii) a greater role for between-habitat frequency differences than balanced species replacement in WEP beta diversity relative to other taxa; and (iii) regional modulation of these relationships by contrasting environmental conditions and species pools. Testing these hypotheses requires moving beyond local case studies and adopting a quantitative, large-scale approach grounded in vegetation-plot data.

The increasing availability of harmonized vegetation databases (Dengler et al., 2011; Chytrý et al., 2016) offers a unique opportunity to address these gaps. By integrating large-scale vegetation-plot datasets with comprehensive inventories of WEPs, it is now possible to investigate their macroecological patterns across entire regions and to explicitly quantify their contribution to plant diversity within and among habitats. Such an approach allows WEPs to be analysed not merely as culturally relevant species, but as an ecologically meaningful subset of the flora, embedded within the structure and dynamics of plant communities.

In this study, we combine a national-scale database of wild edible plant taxa with vegetation-plot data covering the full range of terrestrial habitat types in Italy. Our aim is to provide the first comprehensive assessment of the ecological role of WEPs within different vegetation types of Italy, explicitly addressing their contribution to biodiversity patterns across habitats and biogeographical regions. Specifically, we address the following research questions:

- How does WEPs species richness vary across habitat groups and habitat types, and how is it related to total plant species richness?
- What is the contribution of WEPs to alpha diversity within vegetation plots, and how does this contribution change across habitats and biogeographical regions?
- How do WEPs influence beta-diversity patterns across habitats, in terms of the relative importance of species turnover versus abundance gradients?
- Do WEPs exhibit distinct macroecological and compositional patterns compared to non-edible species, suggesting habitat filtering and ecological generalism as key drivers of their distribution?

Italy represents an ideal case study for investigating the macroecology of WEPs, as it encompasses strong latitudinal, elevational, and climatic gradients spanning Alpine, Continental, and Mediterranean biogeographical regions within a limited geographic extent. This environmental heterogeneity, combined with an exceptionally rich flora (Stinca et al., 2021) and a wide spectrum of natural, semi-natural, and anthropogenic habitats well represented in vegetation-plot databases (Agrillo et al., 2017), allows robust assessment of WEPs distribution patterns and their contribution to plant diversity across habitats and spatial scales.

Methods

Datasets

The list of WEPs of Italy was derived from the AlimurgITA database, a national inventory compiling vascular plant taxa recorded in over 300 publications about WEPs traditional uses at regional or subregional scale (Paura et al., 2021; Di Marzio et al., 2025). In this study, AlimurgITA was used exclusively to define the set of WEPs taxa, without considering attributes related to plant organs or modes of use. To explore potential differences between commonly used and less frequently cited edible species, we also identified a subset of “frequently reported WEPs”, defined as the top 25% of taxa

according to their frequency of citation in the AlimurgITA sources. This subset, grouping all the species with WEPs usage score below the 1st quartile, was obtained from the linear combination of normalized values of n. of citations and n. of administrative regions where a given WEPs is consumed. The top 25% WEPs were used to perform comparative analysis of distribution patterns between the total WEPs flora and the most commonly used WEPs.

Vegetation data (plot relevés, henceforth: plots) were extracted from the European Vegetation Archive (EVA, Chytrý et al., 2016) and redundant entries were removed, retaining one representative for plots featuring the same location, species composition, and cover values. Only plots sampled within the Italian territory and assigned to terrestrial habitats by the expert system EUNIS-Esy (Chytrý et al., 2020), based on the EUNIS habitat classification (Moss, 2008) were considered. For analytical purposes, habitats were aggregated into major habitat groups, corresponding to the Level 1 of the EUNIS classification hierarchy (e.g. forests, grasslands, shrublands, wetlands, coastal habitats, and anthropogenic or semi-natural habitats). Plots with incomplete taxonomic information or ambiguous habitat assignment at Level 2 of the EUNIS hierarchy were excluded. This hierarchical classification allowed the investigation of WEPs diversity patterns both at fine habitat resolution and across broader ecological gradients. Habitat nomenclature was standardized to the updated EUNIS nomenclature, especially for inland water habitats (Arts et al., 2022; Chytrý et al., 2024).

Taxonomic harmonization and data pre-processing

Taxonomic nomenclature in the vegetation plots was harmonized to the Euro + Med Checklist (Raab-Straube, 2006) using the SynBioSys Taxon Database (Schaminée et al., 2007) to ensure consistency between EVA and AlimurgITA. The taxonomic resolution was then set to the species level, synonyms and subspecies were merged, unresolved *taxa* were excluded, species complexes and critical taxonomic groups (such as *Alchemilla*, *Hieracium*, *Taraxacum*) have been grouped together following the Euro + Med treatment of aggregates, *taxa* identified only at genus level were retained only when the genus was unequivocally edible according to AlimurgITA.

Since vegetation layering was not relevant to our study, species cover values from different layers of the same relevé were combined following the probabilistic approach of Fischer (2015).

To reduce the unequal sampling effort across habitats and to optimize the spatial, biological and structural diversity resolution, vegetation plots were downscaled through a stratified heterogeneity-constrained random resampling procedure (HCR, Knollová et al., 2005; Lengyel et al., 2011). The dataset was stratified by 10×10 km grid cells and, within each EUNIS Level 2 habitat type, a maximum of 3 plots per grid cell were retained. The resampling procedure was repeated 5,000 times to ensure the robustness of diversity estimates. HCR was not applied to those habitats accounting for fewer than 108 relevés after duplicate removal (‘U7’, ‘U6’, ‘S6’, ‘S4’, ‘R6’, ‘Q1’, ‘P2’, ‘N2’ for more details see Table 2 in Appendix 1). All subsequent analyses were based on the resampled dataset.

Data processing

Species richness was quantified for three species pools: (i) all vascular plant species, (ii) WEPs species, and (iii) the subset of frequently reported WEPs (top 25%). To assess differences in richness patterns while accounting for sampling effort, species accumulation curves were computed for each habitat type up to a threshold of 100 plots. These curves were generated using Kindt's exact formula, which calculates the expected mean species richness, and confidence intervals were derived from repeated randomizations of the *specaccum* function from the R package vegan (Oksanen et al., 2005).

Alpha-diversity was quantified at the plot level using species richness and Shannon diversity indices. To assess the contribution of WEPs to local plant diversity, we calculated the proportional contribution of WEPs to total alpha-diversity within each plot as the ratio between the Shannon diversity of WEPs and the Shannon diversity of the total species pool:

$$H_{WEPs} = \frac{\sum_{j=1}^{W} p_j \, ln(p_j)}{\sum_{i=1}^{S} p_i \, ln(p_i)}$$

where *p* represents the relative cover of a species, *W* is the number of WEPs species, and *S* is the total species richness. The index values range from 0 to 1, where 1 indicates that alpha-diversity is entirely driven by WEPs species, while 0 indicates that no WEPs species are present. Comparisons were performed across habitat groups and biogeographical regions to evaluate how the relative importance of WEPs varies along broad ecological gradients.

To explore the role of WEPs in beta-diversity patterns, we calculated beta-diversity components using the decomposition method for abundance data (Podani & Shmera, 2011).

We first selected habitats from different biogeographical regions with more than 33 plots resulting from the stratified HCR procedure. To control for uneven sampling effort, we standardized the data by resampling plots, stratified by habitat and biogeographic region to obtain a fixed sample size of 100 plots per group, applying replacement only to strata with less plots than the fixed size. Species frequencies were calculated as the sum of presences within these stratified plots. This procedure was repeated 1,000 times, and the average frequency for each species was calculated across iterations. Rare species (mean frequency < 0.5) were removed.

We then calculated the Bray-Curtis dissimilarity and its three additive components (replacement, abundance difference, and similarity, summing to 1) were stored as node pair attributes between habitats within the same biogeographical region. This workflow was applied to four subsets: the total species list, non-WEPs species, all WEPs species, and the top 25% WEPs. Network graphs were visualized using the NetworkX package in Python.

Network representations allowed direct comparison of compositional connectivity among habitats and facilitated the identification of habitats characterized by high species replacement versus those dominated by nestedness or abundance-driven gradients. To verify if the differences in species number

between non-WEPs and all WEPs subsets could influence the beta-diversity network results, the three additive components were recalculated once again 500 times for each stratum under the same stratified resampling procedure as before, but in this case for each resampling cycle the non-WEPs subset has been downsampled randomly to the same size of all WEP's (1010 species) and the total species list was also reassigned at each cycle as the sum of the random sampled non-WEPs list and all WEPs species. The results were plotted as SDR-Simplex graphs in R using ggtern (Appendix 2, Fig. 3).

Results

The initial dataset comprised approximately 85,000 plots representing over 300 EUNIS habitat types at Level 3 of the expert system classification. Application of the initial selection criteria reduced the dataset to 61,818 plots. Following HCR resampling, the final sample size decreased to 20,314 plots (Appendix 1, Table 1).

Alpha-diversity patterns

Across all habitats, WEPs richness increased with total species richness, but the relationship was not linear and varied substantially among habitat types. On average, WEPs accounted for a substantial proportion of local species diversity in anthropogenic habitats, grasslands, and forest edges, whereas their contribution was lowest in wetlands, aquatic habitats, and high-elevation or sparsely vegetated environments (Appendix 2, Fig. 1).

At the Level 1 of the EUNIS classification vegetated man-made habitats showed the highest accumulation values for both total and top 25% WEPs, followed by grasslands, shrublands, and forests. Water-related habitats and wetlands consistently displayed the lowest accumulation values (Fig. 1, Appendix 2, Fig. 2).

At the Level 2 of the EUNIS classification, the habitat types (Level 2) with the highest WEPs richness were V3 – Artificial grasslands and herb-dominated habitats (398.5 ± 17.6), Sa – Unclassified tall shrubland (331.0 ± 19.8), R1 – Dry grasslands (317.1 ± 15.0), T1 – Deciduous forests (294.9 ± 18.0), R5 – Woodland fringes and clearings (294.7 ± 15.7), S3 – Temperate and Mediterranean-montane scrub (290.1 ± 17.0), V1 – Arable gardens (285.5 ± 16.3), R2 – Mesic grasslands (284.1 ± 15.1), and T3 – Coniferous forests (273.1 ± 17.1). In contrast, habitats characterized by strong abiotic constraints, such as raised bogs, aquatic communities, and sparsely vegetated rocky habitats, exhibited consistently low WEPs richness (Appendix 1, Table 2).

The relative frequency of WEPs, expressed as the proportion of WEPs species relative to the total species pool, differed substantially among habitat groups (EUNIS Level 1). Vegetated man-made habitats exhibited the highest relative frequencies of WEPs, followed by forests, shrublands, and grasslands, whereas aquatic and wetland habitats showed markedly lower values (Appendix 2, Fig. 1).

At the EUNIS Level 2, several anthropogenic and semi-natural habitats showed WEPs relative frequencies exceeding 40% of the total species pool. Forest and shrubland habitats displayed intermediate but consistently high values, especially evergreen forests, riverine shrubs, maquis and unclassified tall shrubs, while grassland habitats showed greater variability depending on environmental conditions and management intensity. The relative frequency of the top 25% WEPs followed similar patterns but with reduced magnitude, indicating that a smaller subset of edible species accounts for a substantial proportion of WEPs occurrences across habitats.

Plots located in the Continental biogeographical region showed the highest mean contribution of WEPs to alpha diversity across most habitat groups. Mediterranean habitats displayed intermediate values with relatively low variability, particularly in forest and shrubland habitats. In contrast, Alpine habitats exhibited consistently lower WEPs contributions to alpha diversity, with particularly low values in wetlands and alpine grasslands, although some anthropogenic and freshwater-related habitats showed higher values but also great variability (Fig. 2). Interestingly, Alpine grasslands (R4) are among the richest habitats for non-WEPs species, displaying the highest overall frequencies for this group. By contrast, deciduous forests (T1) show higher overall WEPs frequency, with WEPs richness increasing from the Mediterranean to the Alpine region. Forest fringes (R5) constitute the richest habitat for WEPs in the Alpine region, whereas anthropogenic grasslands (V3) take this role in the Continental and Mediterranean regions.

Beta-diversity patterns and network analysis

Network analyses revealed clear differences in the dominant drivers of compositional variation among species subsets. For the total species pool, beta-diversity was largely structured by species replacement, particularly in the Mediterranean and Continental regions. The non-WEPs subset showed similar but slightly stronger replacement-dominated patterns.

In contrast, beta-diversity patterns of WEPs were characterized by a pronounced increase in the relative importance of abundance difference and similarity, especially in the Alpine and Continental regions. This pattern was further accentuated when considering the subset of top 25% WEPs, for which abundance difference emerged as the dominant component of beta diversity across most habitats. Replacement-driven patterns persisted primarily among habitats belonging to different EUNIS Level 1 habitat groups, subjected to strong environmental constraints.

Network representations highlighted that habitats belonging to the same habitat group or linked by successional relationships tended to show higher compositional similarity for WEPs, whereas habitats differing strongly in structure or environmental conditions were connected mainly through replacement or gradient-dominated links.

The overall structure of beta-diversity patterns was broadly consistent across regions. In all biogeographical contexts, WEPs assemblages differed from non-WEPs assemblages by exhibiting reduced species turnover and increased abundance-driven differentiation and similarity among habitats.

This pattern was strongest in environmentally constrained regions, particularly in the Alpine context, where differences in WEPs composition among habitats were largely driven by uneven species frequencies and richness rather than by complete species replacement.

Regional specifics

In the Alpine region, abundance difference accounts for 56% of the dominant components for WEPs. Replacement acts as the main driver only for riverbeds/gravel shores (U7) and Alpine grasslands (R4). The highest WEPs richness is found in forest fringes (R5), deciduous forests (T1), and unclassified tall scrub (Sa), while arable crops (V1), and mesic grasslands (R2) host the highest overall WEPs frequencies. Rock- and water-related habitats occupy the external shell of the network due to low alpha-diversity and WEPs frequency.

In the Continental region, WEPs diversity shows higher turnover than in the Alpine region, suggesting more balanced compositional variations alongside a high dominance of intra-group similarity, accounting for 10% of dominant components. Anthropogenic grasslands (V3) and unclassified tall scrub (Sa) are the richest habitats, while deciduous forests (T1), mesic grasslands (R2), and arable crops (V1) display the highest overall WEPs frequencies.

In the Mediterranean region, the WEPs subset is characterized by a strong predominance of replacement, consistent with the balanced values found for overall WEPs frequency and richness. Anthropogenic grasslands (V3) clearly emerge as the richest and most diversified habitat for edible plants, while deciduous forests (T1) display the highest overall WEPs frequencies, mirroring trends in other regions.

The resampling procedure for species pool balancing between WEPs and not-WEPs coherently aligns with these findings as shown by the centroids position for each subset (Appendix 2, Fig. 3).

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Discussion

Our results demonstrate that wild edible plants are not randomly distributed within Italian vegetation. Instead, they constitute a distinct and ecologically structured subset of plant communities. Across habitat types and biogeographical regions, WEPs richness and frequency showed consistent departures from patterns expected solely on the basis of total species richness.

Environmental filtering and disturbance-associated mosaics

The contrast between vegetated man-made habitats and grasslands provides a useful starting point for interpreting community-assembly processes. At a standardized effort of 100 plots, these habitat groups accumulated similar numbers of WEP species (approximately 381 and 379, respectively), although grasslands accumulated many more vascular plant species overall (approximately 1,086 versus 773). WEP representation therefore cannot be explained by total accumulated richness alone. One plausible explanation is that open and recurrently disturbed habitats offer recruitment opportunities to a substantial subset of the Italian WEP flora, while habitat mosaics created by cultivation, abandonment, grazing and succession allow species with different ecological requirements to coexist at the landscape scale. Therefore, WEPs occurrence is shaped by a combination of ecological filtering and species traits that favour persistence in habitats with moderate disturbance, high resource availability, structural heterogeneity. Rather than reflecting cultural selection alone, the distribution of WEPs may be strongly constrained by fundamental ecological processes operating at the community level.

This interpretation is consistent with disturbance-associated filtering but is not a direct test of it, because EUNIS habitat classes do not quantify disturbance frequency, soil fertility, light availability or successional age.

Interpretation of frequency-based beta diversity

One of the most interesting outcomes of the present study is the contrasting beta-diversity structure of WEPs compared to non-edible species. While overall plant communities and non-WEPs subsets were primarily structured by species replacement, WEPs assemblages exhibited a marked shift toward abundance-difference and similarity-driven beta diversity. This pattern was especially pronounced for the subset of top 25% WEPs and in environmentally constrained regions, such as the Alps (Appendix 2, Fig. 3).

The increased dominance of replacement in the non-WEPs subset suggests high niche specialization and dispersal limitations, a view supported by the central role of Alpine grasslands for this group. Instead, the marked increase in abundance difference (or richness difference) in the case of WEPs, suggests that differences among habitats are driven less by complete species replacement and more by uneven changes in species frequencies and nestedness. This pattern is consistent with the hypothesis that many WEPs are ecological generalists with broad habitat tolerances, capable of occurring across multiple vegetation types but reaching high abundances only under favourable conditions. In this sense, WEPs appear to track gradients of resource availability and disturbance intensity rather than sharp habitat boundaries, in line with their scarcity in stress-dominated environments like aquatic habitats and cliffs.

The consistently high WEPs richness and frequency observed in anthropogenic and semi-natural habitats underlines the importance of habitat filtering associated with disturbance regimes and land-use intensity. These environments often combine open structure, nutrient availability, and repeated disturbance, conditions that favour fast-growing, competitive or ruderal species, many of which are represented among WEPs (Pasta et al. 2020; Falla et al. 2025).

It is interesting to note that the second richest habitat type for WEPs after the “anthropogenic grasslands” (V3, e.g. ruderal vegetation and roadsides) is “unclassified tall scrub” (Sa), i.e. sites dominated by tall shrubs that do not fit into specific natural scrubland definitions (Chytrý et al., 2020). These stands typically represent secondary vegetation characterized by an admixture of maquis, forest regeneration, and other scrub species, resulting from indirect human disturbances such as forest degradation and pastoralism in the Mediterranean Basin.

Conversely, habitats characterized by restrictive ecological conditions, such as cliffs, water bodies, and wetlands, showed low WEPs richness and limited contribution to diversity. This suggests that the ecological profile of Italian WEPs is skewed toward generalist and disturbance-tolerant species, occupying intermediate positions along stress–disturbance gradients, rather than strictly stress-tolerant or competitive species (Grime, 1977).

Region-specific processes

The Mediterranean region clearly outnumbers both the Continental and Alpine regions in total species richness (2818, 2240, and 2235, respectively) and in WEPs richness (837, 701, and 567, respectively). It exhibits a higher dominance of replacement relationships and lower richness difference across all species sets, reflecting the high ecological heterogeneity and climatic variability of Mediterranean landscapes that promote species turnover and niche diversification (Baselga, 2010; Blondel et al., 2010; Legendre, 2014). Conversely, the lower species richness and higher abundance difference observed in Alpine species sets can be attributed to the combined effects of climatic harshness, shorter growing seasons, and strong environmental filtering along elevation and temperature gradients, which limit the establishment and persistence of many generalist species. Although the Mediterranean region exhibits higher absolute richness, the Continental region shows slightly higher relative richness for WEPs species, which represent 31.3% of its total species pool (compared to 29.7% in the Mediterranean and 25.4% in the Alpine region). A similar trend is observed for the top 25% WEPs subset (9.4% Continental vs. 8.1% Alpine and 7.3% Mediterranean). The higher relative contribution of WEPs observed in the Continental region may reflect the convergence of favourable climatic conditions, land-use history and disturbance-related dynamics driven by the higher human density, compared to the Mediterranean and Alpine regions.

Regional contrasts further suggest that the expression of these assembly patterns is context dependent. The relatively stronger replacement component in Mediterranean WEP assemblages is compatible with sharper habitat contrasts and a heterogeneous regional species pool, whereas the greater importance of frequency differences in Alpine assemblages may reflect a smaller shared pool surviving under stronger environmental constraints. These explanations remain provisional because the present analysis does not explicitly partition the effects of climate, habitat composition, spatial structure and land-use history. Importantly, the results therefore identify mechanisms worth testing rather than attributing observed differences to any single driver.

Limitations

Suggested replacement for the original limitations paragraph around lines 458–466.

Several limitations constrain mechanistic interpretation. The analysis is observational and based on vegetation plots representing a static snapshot; neither management intensity nor environmental variables were modelled as predictors, and repeated measurements of succession or disturbance were unavailable. WEPs are defined by recorded traditional uses rather than shared functional attributes, so ethnobotanical documentation and accessibility may influence group membership; conversely, taxa not listed in AlimurgITA should not automatically be described as biologically inedible. Likewise, the 'top 25%' group identifies taxa most frequently documented in ethnobotanical sources, not those most frequent in vegetation plots. Habitat-specific differences in sampling and species-pool composition may persist despite the stratified resampling procedures. Future work should test the proposed mechanisms using direct environmental and land-use covariates, functional traits, habitat-breadth metrics and temporal vegetation data.

Implications for biodiversity conservation and wild-food provisioning

Our findings have implications for biodiversity conservation and the management of landscapes supporting potential wild-food provisioning. The disproportionately high richness of wild edible plants in anthropogenic and semi-natural habitats suggests that their conservation cannot be confined to protected areas or ecosystems with minimal human influence. Instead, maintaining heterogeneous landscape mosaics, including grasslands, forest fringes, secondary shrublands, and ruderal vegetation, may contribute to safeguarding plant diversity associated with traditional food uses (Guadilla-Sáez et al. 2019; Falla et al. 2025).

This does not imply that disturbance should be promoted indiscriminately, but rather that conservation and land-use policies should recognize the ecological value of habitats shaped by long-standing human activities (Zerbe, 2022). Moreover, the prevalence of abundance-driven differences in WEP assemblages suggests that changes in habitat conditions may affect the local frequency of edible species even where overall species composition remains relatively stable. The observed differences among biogeographical regions further indicate that conservation priorities should be adapted to regional ecological contexts rather than based on uniform national prescriptions.

Integrating ethnobotanical inventories with vegetation-plot databases could therefore provide a valuable evidence base for identifying habitats of potential relevance to wild-food provisioning and incorporating this dimension into biodiversity monitoring, landscape planning, and ecosystem management. Nevertheless, the occurrence and richness of WEPs should not be equated with the actual delivery of provisioning ecosystem services, which also depends on resource availability, accessibility, cultural practices, and sustainable harvesting. Bridging this gap will require further research linking ecological patterns with traditional ecological knowledge, local management practices, and the sustainable use of wild plant resources.

Conclusions

Despite clear differences in absolute richness among biogeographical regions of Italy, the overall structure of WEPs diversity patterns was remarkably consistent. Across Alpine, Continental, and Mediterranean regions, WEPs showed a recurring pattern of differentiation from non-WEPs species in their beta-diversity structure, exhibiting reduced turnover and increased abundance-driven differentiation. This broad geographical coherence suggests that the ecological processes shaping WEPs assemblages operate similarly across broad climatic contexts, even though their expression is modulated by regional species pools and environmental constraints. The Mediterranean region, despite hosting the highest absolute species richness, did not show a corresponding increase in the relative contribution of WEPs, indicating that floristic richness alone does not translate into a higher prevalence of edible species within communities.

By locating WEP diversity within a community-assembly framework, our study identifies heterogeneous landscape mosaics as potentially important settings for conserving species associated with traditional food uses, without equating plant occurrence with realized provisioning services. Also, our results highlight the importance of environmental filtering and disturbance regimes in shaping WEPs distribution and frequency. Framing WEPs within a macroecological perspective opens new avenues for understanding their role in plant diversity patterns and provides a quantitative baseline for future ecological and conservation-oriented research.

Abbreviations

EVA
European Vegetation Archive
EUNIS
European Nature Information System
HCR
Heterogeneity–Constrained Random resampling
MA
Marine habitats (EUNIS Level 1)
N
Coastal habitats (EUNIS Level 1)
P
Inland waters (EUNIS Level 1)
Q
Wetlands (EUNIS Level 1)
R
Grasslands and lands dominated by forbs, mosses or lichens (EUNIS Level 1)
S
Heathlands, scrub and tundra (EUNIS Level 1)

T
Forests and other wooded land (EUNIS Level 1)
U
Inland habitats with no or little soil and mostly with sparse vegetation (EUNIS Level 1)
V
Vegetated man–made habitats (EUNIS Level 1)
WEPs
Wild edible plants

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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Author Contribution

Conceptualization RG, CM; Data curation EG, VH, CG, ASG, RG, CM; Formal analysis CM, EG, RG; Funding acquisition RG, CM, BP; Investigation RG, CM, EG, MB, AG, GG, VI, ALR, SP, RV; Methodology CM, RG, EG, ASG; Project administration RG, CM, BP; Resources RG, CM, GB, AG, RL, BP; Supervision RG, CM, BP; Writing – original draft RG, EG; Writing – review & editing CM, GB, AG, GG, ASG, RL, SP.

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Not applicable.

Data Availability

The plots used in the dataset are available upon request in an internal repository in the European Vegetation Archive (EVA). The name of the internal repository is “35-2016-05-02”

References

1. Agrillo E, Alessi N, Massimi M, Spada F, De Sanctis M, Francesconi F, Cambria VE, Attorre F (2017) Nationwide Vegetation Plot Database – Sapienza University of Rome: state of the art, basic figures and future perspectives. Phytocoenologia 47:221–229. 10.1127/phyto/2017/0139
2. Arts GH, Watson M, Solheim AL, Schaminée JHJ, Evans D, Lund MP, Tryfon E (2022) Revision of the EUNIS inland surface water habitat group: finalisation of level 3 and outlook to level 4. ETC/BD Technical Paper 2/2022. European Topic Centre on Biological Diversity
3. Bacchetta L, Visioli F, Cappelli G, Caruso E, Martin G, Nemeth E et al (2016) A manifesto for the valorization of wild edible plants. J Ethnopharmacol 191:180–187. 10.1016/j.jep.2016.05.061
4. Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19:134–143
5. Blasi C, Capotorti G, Copiz R, Guida D, Mollo B, Smiraglia D, Zavattero L (2014) Classification and mapping of the ecoregions of Italy. Plant Biosyst 148:1255–1345
6. Blondel J, Aronson J, Bodiou JY, Boeuf G (2010) The Mediterranean region: biological diversity in space and time, 2nd edn. Oxford University Press, Oxford
7. Buhk C, Alt M, Steinbauer MJ, Beierkuhnlein C, Warren SD, Jentsch A (2017) Homogenizing and diversifying effects of intensive agricultural land-use on plant species beta diversity in Central Europe – a call to adapt our conservation measures. Sci Total Environ 576:225–233
8. Chytrý M, Hennekens SM, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F et al (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Appl Veg Sci 19:173–180. 10.1111/avsc.12191
9. Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS et al (2020) EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. Appl Veg Sci 23:648–675. 10.1111/avsc.12519
10. Chytrý M, Řezníčková M, Novotný P, Holubová D, Preislerová Z, Attorre F et al (2024) FloraVeg.EU – an online database of European vegetation, habitats and flora. Appl Veg Sci 27:e12798. 10.1111/avsc.12798
11. Couplan F (2009) Le régal végétal: plantes sauvages comestibles, vol 1. Éditions Ellebore, Paris
12. de Cortes Sánchez-Mata M, Tardío J (eds) (2016) Mediterranean wild edible plants: ethnobotany and food composition tables. Springer, New York
13. Dengler J, Jansen F, Glöckler F, Peet RK, De Cáceres M, Chytrý M et al (2011) The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. J Veg Sci 22:582–597.

10.1111/j.1654-1103.2011.01265.x

14. Di Marzio P, Di Iorio A, Giancola C, Paura B (2025) AlimurgITA: a database of the Italian alimurgic flora. Data 10:209. 10.3390/data10120209
15. Duchesne LC, Wetzel S (2002) Managing timber and non-timber forest product resources in Canada's forests: needs for integration and research. Chron 78:837–842
16. Falla NM, Ravetto Enri S, Nota G, Lonati M, Scariot V (2025) Wild edible plants oxymoron: higher abundance in lower wilderness. CABI Agric Biosci 6:0087. 10.1079/ab.2025.0087
17. Fischer HS (2015) On the combination of species cover values from different vegetation layers. Appl Veg Sci 18:169–170. 10.1111/avsc.12130
18. Gori B, Cossu T, El Zein H, Liu U, Ulian T, Bacchetta G (2026) A comprehensive checklist of Mediterranean wild edible plants: diversity, traditional uses, and knowledge gaps. Plants People Planet 8:1616–1633. 10.1002/ppp3.70137
19. Granath G, Strengbom J (2017) Nitrogen fertilization reduces wild berry production in boreal forests. Ecol Manage 390:119–126
20. Guadilla-Sáez S, Pardo-de-Santayana M, Reyes-García V (2019) The role of traditional management practices in shaping a diverse habitat mosaic in a mountain region of Northern Spain. Land Use Policy 89:104235
21. Knollová I, Chytrý M, Tichý L, Hájek O (2005) Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. J Veg Sci 16:479–486
22. Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. Glob Ecol Biogeogr 23:1324–1334
23. Lengyel A, Chytrý M, Tichý L (2011) Heterogeneity-constrained random resampling of phytosociological databases. J Veg Sci 22:175–183
24. Mori AS, Isbell F, Seidl R (2018) β-diversity, community assembly, and ecosystem functioning. Trends Ecol Evol 33:549–564
25. Moss D (2008) EUNIS habitat classification—a guide for users. European Environment Agency, Copenhagen
26. Nowak-Olejnik A, Mocior E (2022) Provisioning ecosystem services of wild plants collected from seminatural habitats: a basis for sustainable livelihood and multifunctional landscape conservation. Mt Res Dev 42:R11–R19
27. Oksanen J, Kindt R, O'Hara B (2005) Community ecology package (vegan). R package. https://cran.r-project.org/package=vegan. Accessed 15 Jan 2026
28. Pasta S, La Rosa A, Garfì G, Marcenò C, Gristina AS, Carimi F, Guarino R (2020) An updated checklist of the Sicilian native edible plants: preserving the traditional ecological knowledge of century-old agro-pastoral landscapes. Front Plant Sci 11:388. 10.3389/fpls.2020.00388

29. Paura B, Di Marzio P, Salerno G, Brugiapaglia E, Bufano A (2021) Design a database of Italian vascular alimurgic flora (AlimurgITA): preliminary results. Plants 10:743
30. Pohjanmies T, Jašková A, Hotanen JP, Manninen O, Salemaa M, Tolvanen A, Merilä P (2021) Abundance and diversity of edible wild plants in managed boreal forests. Ecol Manage 491:119151
31. Raab-Straube E (2006) Euro + Med PlantBase—the information resource for Euro-Mediterranean plant diversity. https://europlusmed.org. Accessed 15 Jan 2026
32. Schaminée JHJ, Hennekens SM, Ozinga WA (2007) Use of the ecological information system SynBioSys for the analysis of large datasets. J Veg Sci 18:463–470
33. Shirsat R, Koche D (2024) Wild edible plants (WEPs): a review on their importance, possible threats, and conservation. In: Son L (ed) Contemporary research and perspectives in biological science, vol 2. BP International, Hong Kong, pp 97–115. doi:10.9734/bpi/crpbs/v2/1897
34. Stinca A, Musarella CM, Rosati L, Laface VLA, Licht W, Fanfarillo E et al (2021) Italian vascular flora: new findings, updates and exploration of floristic similarities between regions. Diversity 13:600. 10.3390/d13110600
35. Zerbe S (2022) Restoration of multifunctional cultural landscapes: merging tradition and innovation for a sustainable future. Landscape series, vol 30. Springer, Cham. 10.1007/978-3-030-95572-4

Figures

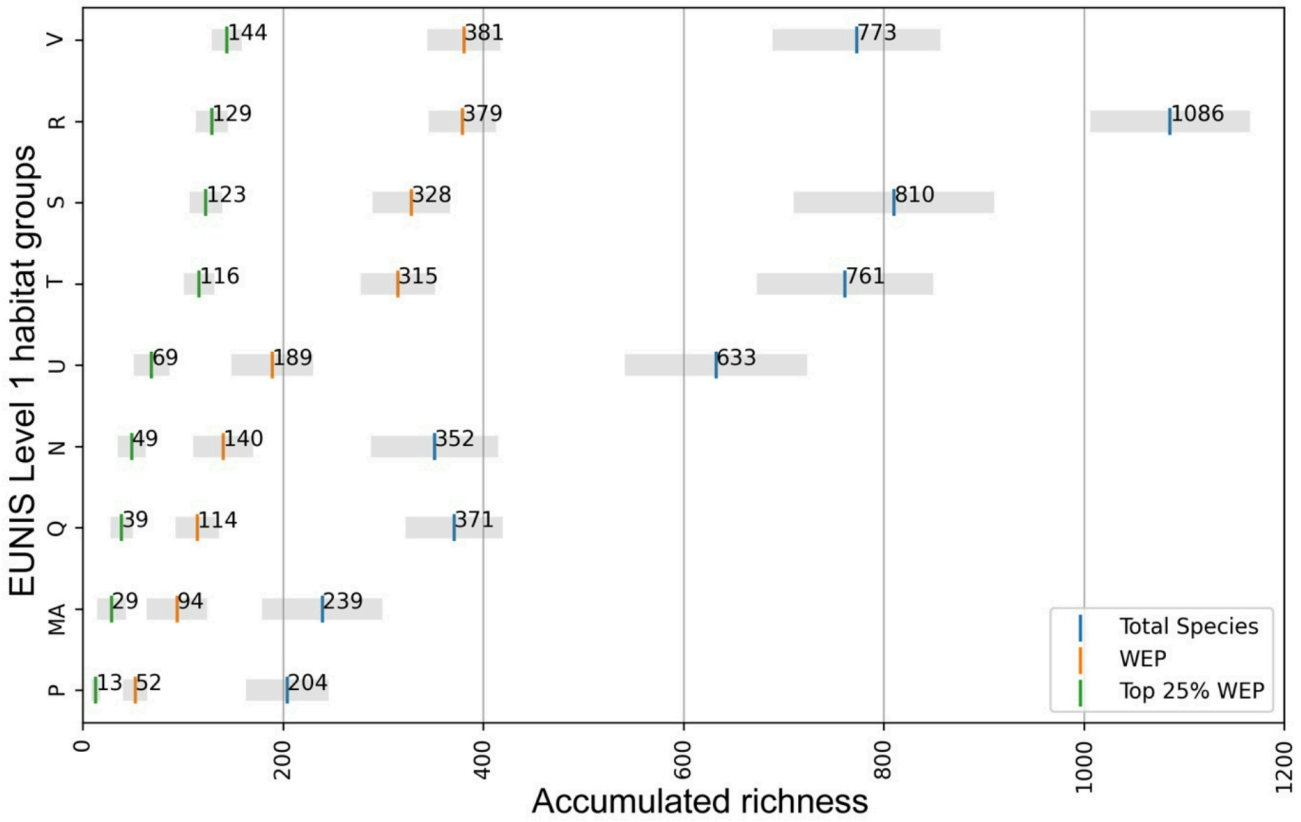

Figure 1

Species accumulation values (at *n = 100* plots) for total species richness, total WEPs richness, and the top 25% most frequent WEPs across habitat groups. Grey bars represent 95% confidence intervals. While WEPs richness generally increases with total species richness, vegetated man-made habitats (Group V) accumulate a higher number of WEPs at lower levels of total richness compared to the other groups. **Abbreviations**: MA = Marine habitats; N = Coastal habitats; P = Inland waters; Q = Wetlands; R = Grasslands and lands dominated by forbs, mosses or lichens; S = Heathlands, scrub and tundra; T = Forests and other wooded land; U = Inland habitats with no or little soil and mostly with sparse vegetation; V = Vegetated man-made habitats.

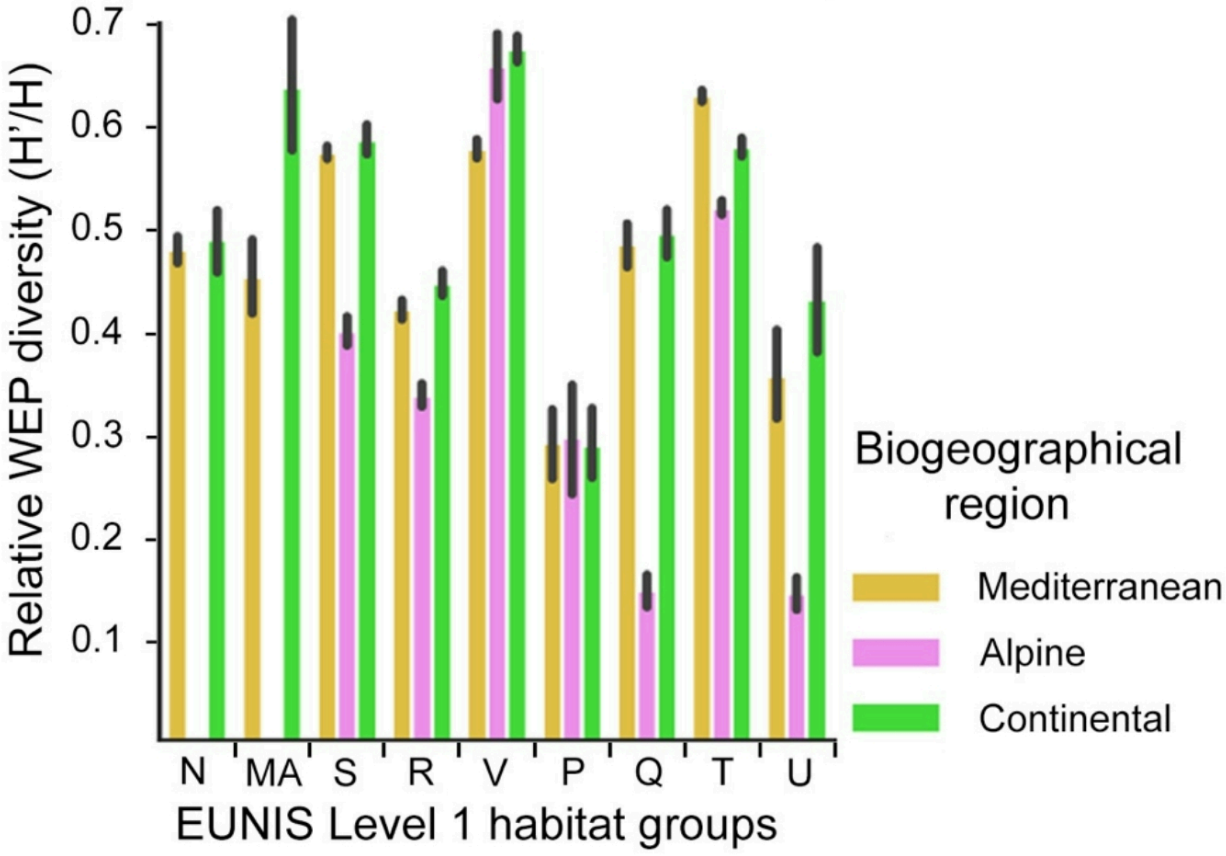

Figure 2

Mean WEPs contribution to alpha diversity by habitat group and biogeographical region (sensu Blasi et al., 2014). The Continental region shows the highest values, especially in groups V, MA, R, and U. Mediterranean forests (Group T) exhibit high values with low variance compared to counterparts in other regions. The Alpine region generally shows significantly lower WEPs contributions, with wetlands and sparsely vegetated habitats displaying the lowest values. **Abbreviations**: MA = Marine habitats; N = Coastal habitats; P = Inland waters; Q = Wetlands; R = Grasslands and lands dominated by forbs, mosses or lichens; S = Heathlands, scrub and tundra; T = Forests and other wooded land; U = Inland habitats with no or little soil and mostly with sparse vegetation; V = Vegetated man-made habitats.

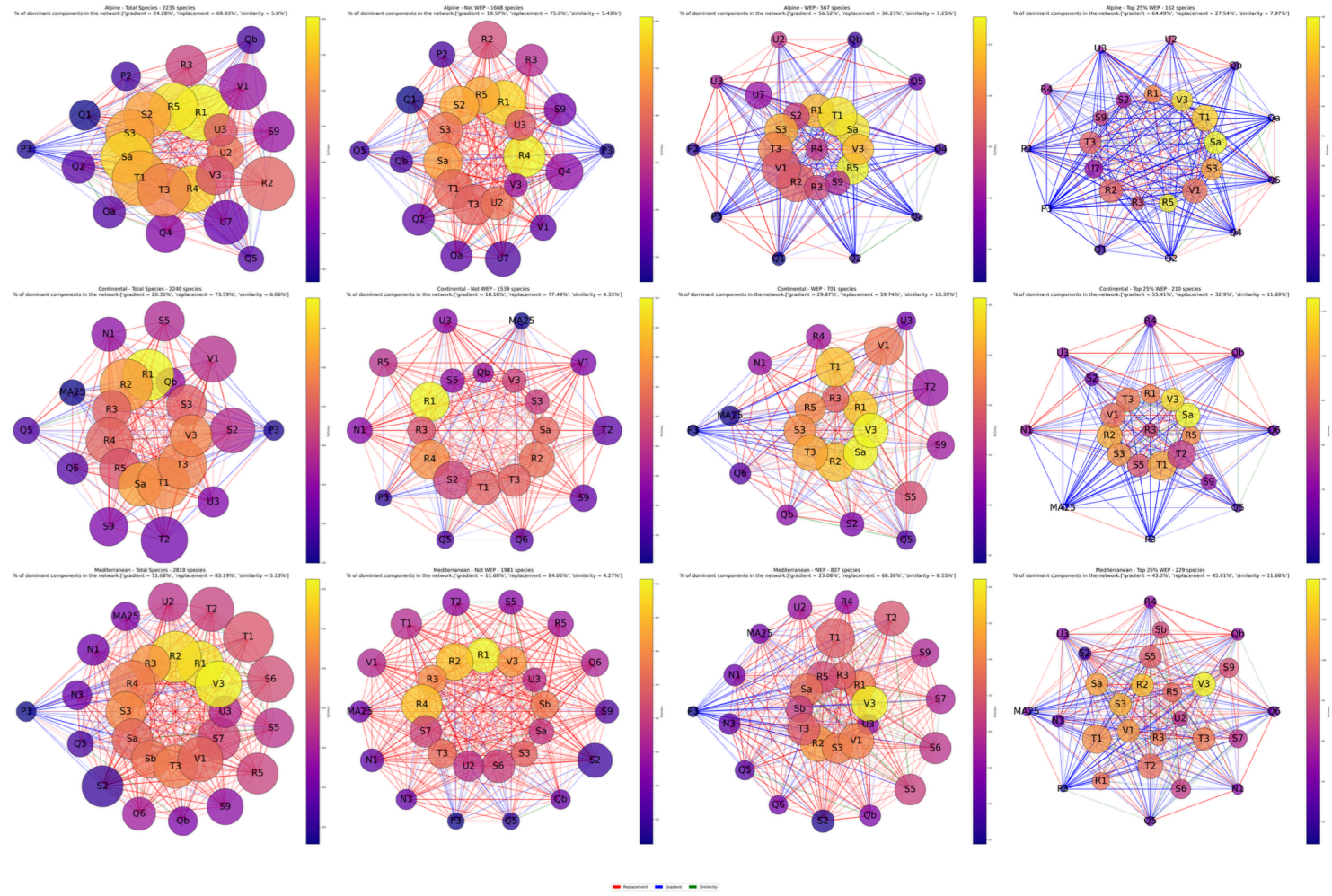

Figure 3

Network analysis of beta-diversity drivers across habitats in the three biogeographic regions. Beta-diversity was calculated using Bray-Curtis dissimilarity on mean species frequencies and decomposed following the decomposition method for abundance data (Podani & Shmera, 2011). **Columns**: The panels show four species subsets: (a) Total species, (b) Non-WEPs, (c) All WEPs, and (d) Top 25% WEPs. **Nodes**: Node size represents the cumulative frequency of the species subset within the habitat; node color indicates species richness. **Edges**: Edges represent the additive beta-diversity components (summing to 1): Similarity (green), Abundance difference (blue), and Replacement (red). For clarity, only the dominant component is displayed. Arrows originate from the habitat with higher species richness, and stroke width reflects the component's magnitude. **Layout**: Nodes are arranged in concentric shells based on their dominant role: inner shells contain nodes dominated by outgoing replacement (1st) or abundance difference (2nd), while outer shells contain nodes dominated by incoming replacement (3rd) or abundance difference (4th). **Abbreviations**: MA25 = saltmarshes, N1 = sandy coasts, N3 = rocky coasts, P2 = running water, P3 = aquatic communities, Q1 = raised bogs, Q2 = poor fens, Q4 = rich fens, Q5 = helophyte beds, Q6 = periodically exposed shores, Qa = unclassified mires, Qb = unclassified helophyte vegetation, R1– dry grasslands, R2 = mesic grasslands, R3 = moist grasslands, R4 = alpine grasslands, R5 = forest fringes, Sa = unclassified shrub dominated by tall shrubs, Sb = unclassified shrub dominated by dwarf shrubs, S2 = alpine shrub, S3 = temperate and mediterranean-mountain shrub, S4 =

temperate heatlands, S5 = maquis and arborescent matorral, S6 = garrigue, S7 = spiny Mediterranean heats, S9 = riverine shrub, T1 = deciduous forest, T2 = evergreen forest, T3 coniferous forest, U2 = inland cliffs, U3 = screes, U7 = gravel bars, V1 = arable crops, V3 = anthropogenic grasslands.

Supplementary Files

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- Appendix1AdditionalTables.docx
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