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Higher levels of protection do not consistently improve habitat quality: Insights from Mediterranean and Alpine shrublands

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ABSTRACT

Protected areas are recognized as a crucial tool to mitigate ongoing trends of biodiversity loss. The effect of different levels of protection and their subsequent conservation efficiency remains, however, largely unexplored. To fill this gap, we present here an integrated approach that combines taxonomic analysis based on typical species to evaluate habitat quality and functional analysis based on plant traits to define habitat structure and functions. We focused on shrubland habitats across levels of protection in two different biogeographical areas. We found that habitat quality does not change linearly with levels of protection. Furthermore, the increase in habitat quality is characterized by a homogenization of habitat structure and functions, mostly driven by an increase in typical species. Our study suggests the level of protection afforded by protected areas is not necessarily indicative of their quality. A combined taxonomic and functional approach in protected areas can offer a thorough appraisal of habitat quality.

1. Introduction

Biodiversity is continuously declining because of land-use intensification and land-use change at the global, regional and local scales (Ceballos et al., 2015; Díaz et al., 2019). Conservation measures have been widely adopted to safeguard natural and semi-natural ecosystems and to reduce biodiversity loss (Maxwell et al., 2020). Governments, policymakers and researchers recognized that protected areas (PAs) are fundamental tools for biodiversity conservation (Barnes et al., 2016; Adams et al., 2019). Europe hosts one of the world's largest networks of PAs called Natura 2000 (European Commission, 2016), to support biodiversity conservation and favour restoration of habitats with high conservation values (Kati et al., 2015; Ricci et al., 2023). Natura 2000 stems from the Birds directive and the Habitats directive. A specific goal stated by the latter is the achievement and the preservation over time of a "favorable conservation status" of habitats, which implies the long-term maintenance of their specific structure and functions (European Commission, 1992). Accordingly, Natura 2000 network constraints and limits human activities across its entire area. Despite this, active management is not centralized at the European level but mostly relies on the local administration.

Assessing habitat conservation status involves a holistic approach based on four criteria: i) area, ii) range, iii) structures and functions, and iv) future prospects and trends. Among these, evaluating habitat structures and functions is pivotal and relies on habitat-specific characteristics that indicate the quality of ecosystems (Tsiripidis et al., 2018). Traditionally, such evaluations have been conducted considering habitat-specific species (hereafter "typical species"; Biondi et al., 2009; Bonari et al., 2021a; Jung et al., 2021; Dalle Fratte and Cerabolini, 2023). These species are specialist species strictly linked to the specific environmental conditions of a given habitat and are highly sensitive to variations in disturbance regimes (Evans and Arvela, 2011; Wohlgemuth et al., 2022). A deviation from optimal disturbance conditions for a given habitat might produce a decrease in typical species coupled with

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an increase in ruderal or highly competitive species ("land-use-moderated conservation effectiveness hypothesis"; Kleijn et al., 2011). For example, semi-natural grasslands strictly depend on specific anthropogenic disturbances. Abandonment or intensification of anthropogenic disturbances can trigger processes of forest recolonization or ruderalization, respectively (Giarrizzo et al., 2017). Although the number of typical species represents good qualitative information on habitat quality (Sperandii et al., 2020), it cannot be translated into quantitative consideration about "functions and structures" that habitats provide (e.g., Del Vecchio et al., 2015; Napoleone et al., 2021).

In this context, the use of plant functional traits (for definition, see Violle et al., 2007) might increase the efficiency of conservation status assessment. Plant traits not only describe how the environmental conditions (e.g., disturbance) influence community composition ("response traits", Lavorel and Garnier, 2002; Götzenberger et al., 2012; Bricca et al., 2023a, 2023b) but also how community composition affects the habitats structures and functions ("effect traits"; Lavorel and Garnier, 2002; Violle et al., 2007; Grigulis et al., 2013; Hanisch et al., 2020). Among a large number of traits (Perez-Harguindeguy et al., 2016), plant growth height (H) and leaf dry matter content (LDMC) are key components of "plant size spectrum" and "leaf economic spectrum" (Wright et al., 2004; Díaz et al., 2016; Bruelheide et al., 2018). Plant size spectrum depicts a gradient of short-tall plant communities while the leaf economic spectrum aligns plant communities along a gradient of acquisitive-conservative resource exploitation which reflects fast-slow relative growing rates. Most importantly, H and LDMC values can be in turn connected to ecosystem processes. For example, taller and more conservative species indicate overall higher carbon sequestration (de Bello et al., 2010; Conti and Díaz, 2013; Grigulis et al., 2013). Moreover, these traits respond to variations in disturbance regimes and can therefore be used as complementary information to typical species variation. Disturbance regimes can be partitioned into two main dimensions: severity and frequency. These two dimensions can influence plant traits differently at species level (Herben et al., 2018). However, studies at community level are mostly lacking, relying mainly on the effect of the last disturbance event (Backhaus et al., 2021 and references therein). Despite the widespread use of plant traits in ecological studies (Funk et al., 2017; Chelli et al., 2019), the translation of trait information into conservation practice remains surprisingly rare in conservation biology (but see Napoleone et al., 2021). Nonetheless, including traits in conservation status assessments might expand our understanding of conservation effects, leading to more informed decisions (Cadotte et al., 2011; Cadotte and Tucker, 2018; Gallagher et al., 2021; Mendes et al., 2023). Integrating current taxonomic indicators of habitat quality, such as typical species richness, with functional indicators of habitat structure and functions, such as plant traits, could provide a holistic approach to the conservation status assessment that is also more in line with the goal of Natura 2000 network (Del Vecchio et al., 2015).

The "Kunming-Montreal Global Biodiversity Framework" developed by the Convention on Biological Diversity proposes to ensure the effective protection of at least 30 % of the land, inland waters, coastal and marine areas by 2030 (Joly, 2022). Accordingly, the EU Biodiversity Strategy for 2030 is planning to expand the Natura 2000 network to cover at least 30 % of the EU's terrestrial and marine territory (European Commission, 2021). This enlargement is expected to foster the current globally widespread phenomenon of overlapping PAs with different designation types (Wu et al., 2020). Although all PAs have been created for nature conservation purposes, they legally respond to different designation types. For example, besides the European Natura 2000 network, National Parks are different nationally designated PAs. Nonetheless, European directives are more binding than national legislation. Thus, it is expected that the management of National Parks aligns with the objectives declared by Natura 2000 for enhancing the quality of habitats, especially in cases where Natura 2000 network sites are established within their boundaries. However, to our knowledge, no studies have addressed the effect of different levels of protection (i.e., Natura 2000 and National Parks), leaving conservation implications unexplored. The underlying idea is therefore that an area protected by both designations should host higher habitat quality associated with a particular habitat structure and functions and a given disturbance regime. By combining the protection actions of Natura 2000 and National Parks, a wider range of typical species should, theoretically, be better conserved, since these areas receive double levels of protection.

Accordingly, this study aims to investigate the efficiency of different levels of protection on two distinct shrubland habitats occurring in two Italian biogeographical contrasting regions, which are a Mediterranean and an Alpine region. As such, we adopted an integrated approach based on taxonomic aspects (typical species) to evaluate the quality of the habitats and functional aspects (plant traits) to assess the habitat's structure and functions across levels of protection. Specifically, we asked:

i) Does the relative contribution of typical species richness increase alongside the levels of protection?
ii) Does functional diversity change across levels of protection, and, if yes, how?
iii) What is the relationship among different disturbance conditions, typical species, and functional diversity?

2. Methods

2.1. Study area

We focus on two Italian biogeographically different study areas (NW Sardinia and SE Alps) with similar characteristics in terms of levels of protection, namely which have one and two levels of protection each (Fig. 1). For each habitat type, we considered three different sites subjected to different designation types. Specifically, sites without any legal protection outside PAs (PL0); sites within the Natura 2000 network (PL1); sites with two levels of protection where the Natura 2000 network overlaps with a National Park (PL2). We adopted this approach because the comparison of protected and non-protected areas is a common practice for the evaluation of the efficiency of conservation measures (Deák et al., 2020; Ricci et al., 2023). The first study area was located in the Mediterranean biogeographic region and includes the National Park of the Island of Asinara (41°3′14″N 8°16′45″E; IUCN category II; Dudley and Stolton, 2008; ProtectedPlanet, 2023) and the Stintino peninsula in the northwestern part of Sardinia (Italy). On the whole Island of Asinara, Natura 2000 network overlaps with the National Park, while Stintino peninsula includes a sector in the Natura 2000 network and a sector outside. The second area is located in the Alpine biogeographic region (southeastern Alps, Italy) and includes Stelvio National Park (46°24′15″N 10°41′19″E; IUCN category II; Dudley and Stolton, 2008; ProtectedPlanet, 2023) and nearby zones. In the Stelvio National Park, there are areas belonging to the Natura 2000 network (Fig. 1). Detailed descriptions of the National Parks and Natura 2000 PAs are given by Pisanu et al. (2014) and Orlandi et al. (2016). For further information, see Appendices A and B.

2.2. Sampling design and data collection

As recommended for the robustness of ecological studies, we developed an ad hoc sampling design to collect data properly so that data can be used to test our hypotheses (Popovic et al., 2024). We retrieved available Natura 2000 habitat maps from park administrations and identified one Natura 2000 target habitat for each study area according to the following criteria: i) sharing physiognomically similar vegetation structure for the sake of the comparison, and ii) presence of the habitat within all three levels of protection (Fig. 1). To do this, we overlapped maps of Natura 2000 habitats and PAs (i.e., Special Areas of Conservation and National Parks) in a GIS environment (QGIS, 2023). A preliminary inspection outside the PAs was carried out to verify the

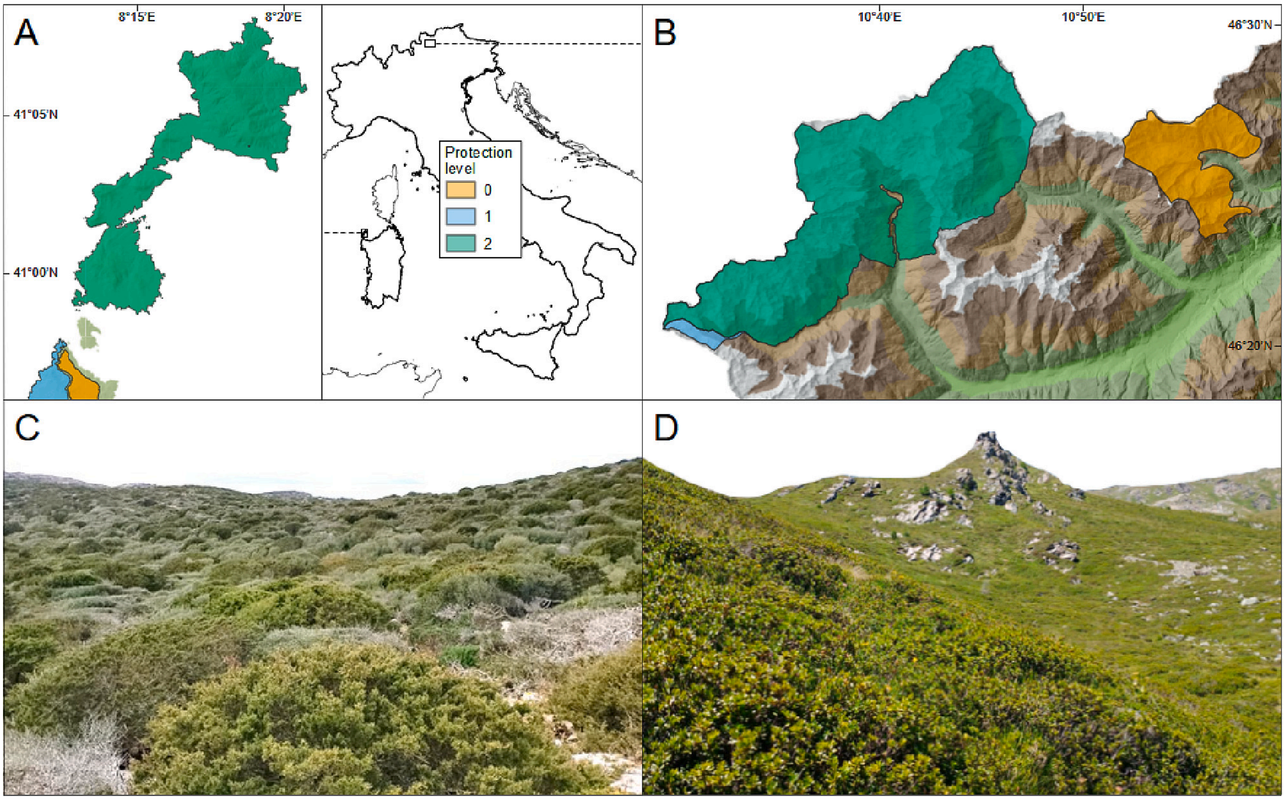

Fig. 1. Protection levels in **(A)** the Mediterranean study area (Italy - NW Sardinia) and in **(B)** the Alpine study area (Italy - SE Alps) with **(C)** the target habitat "Arborescent matorral of *Juniperus* spp." (code 5210 Natura 2000) and **(D)** the target habitat "Alpine and boreal heaths" (code 4060 Natura 2000). Photographs were taken in 2022. Levels of protection are expressed as: 0, absence of any legal protection of PAs; 1, one level of legal protection exerted by Natura 2000 network; 2, two levels of legal protection exerted by the combined presence of Natura 2000 network and National Park.

suitability of the potential habitat within the PAs. Two habitats met the criteria: "Arborescent matorral of *Juniperus* spp. (habitat code 5210 according to Natura 2000) for the Mediterranean region, and "Alpine and boreal heaths" (habitat code 4060 according to Natura 2000) for the Alpine region.

To sample vegetation plots, we used a random stratified sampling design according to the following criteria: i) at least 50 m between plots to avoid spatial autocorrelation; ii) at least 50 m between plots and boundaries of level of protection as well as roads and paths to avoid edge effect; iii) numerically similar south-exposed vs. north-exposed plots (7 vs 8) for each level of protection in each study area. Then, for each level of protection and biogeographical area, we generated in the GIS environment 15 random points (for a total of 90 plots). This environmental stratification allowed us to reduce the influence of environmental factors as much as possible (Vaughan and Ormerod, 2003; Ricci et al., 2023).

Field survey activity was performed during the respective growing season which was in April 2022 in the Mediterranean region and in July 2022 in the Alpine region. The size of the plots was 7 × 7 m in both habitats, in line with the Manual for the Monitoring of Habitats of Community Interest (Allegrezza et al., 2016; Spampinato et al., 2016). The advantage of using the same plot size for different habitats is that biodiversity patterns can be compared. We recorded vegetation data for each plot estimating species cover projection of vascular plants on the ground as percentage values.

We selected plant growth height (H) and leaf dry matter content (LDMC) as plant traits. Considering that traits of more abundant species exert a key effect on ecosystem functioning ("biomass-ratio hypothesis"; Grime, 1998) and that measuring plant traits for all species in all plots is time-demanding (Lepš et al., 2011), we measured plant traits for those species whose aggregated relative cover reached at least 80 % of the total cover in each plot (Pakeman and Quested, 2007). We measured H and LDMC for ten individuals of each selected species according to a standardized protocol (Perez-Harguindeguy et al., 2016). We adopted this approach separately for each level of protection and biogeographical area. For instance, we collected three mean H and LDMC values for *Cistus monspeliensis* L., since this species was abundant in at least one plot in all three levels of protection in the Mediterranean area. Overall, we sampled a total of 1090 individuals. More information on species sampled is reported in Appendices C and D.

2.3. Calculation of taxonomic, functional and disturbance indices

Firstly, we calculated species richness for both habitats. Then, we identified the typical species (Appendix E) using the Italian Interpretation of the Manual of the 92/43/EEC Habitats Directive (Biondi et al., 2009), while the other were defined as "non-typical species". We then quantified the typical species richness for each plot as an indicator of habitat quality (Sperandii et al., 2020; Bonari et al., 2021b). Both indices were calculated with *specnumber* function in the vegan package (Oksanen et al., 2022). Then, we calculated the ratio between typical species richness and species richness (hereafter "typical ratio index"; Dalle Fratte and Cerabolini, 2023). This index represents a standardized measure across habitats ranging from 1 if the plot is constituted exclusively by typical species and 0 if no typical species are present.

To quantify the disturbance regime in each plot, we calculated the community unweighted mean (CM) of disturbance severity and disturbance frequency (Midolo et al., 2023) as the average disturbance indicator values of the species present in each plot. To calculate the CM, we used the *cwm* function in the weimea package (Zelený, 2020) and the function *decostand* in the vegan package to standardize species cover in 0/1 (absence/presence) (Oksanen et al., 2022). When species are used to depict ecological gradients, presence/absence species data provides more robust estimates being less affected by Type II Error rate (Tölgyesi et al., 2014).

As an indicator of habitat structure and functions, we selected two complementary functional metrics which are functional diversity (FD) and community weighted mean (CWM) (Ricotta and Moretti, 2011). FD has been widely used in the evaluation of ecosystem functionality, with higher values related to higher multifunctionality (Cadotte et al., 2011). As a measure of FD, we selected Rao's Quadratic Entropy which quantifies the expected dissimilarity between species within the plot (Ricotta and Moretti, 2011). To calculate FD, we considered Gower distance which standardized the functional distance between each pair of species (i.e., $d_{ij} = 0$ when two species assume the same trait values and $d_{ij} = 1$ when two species have opposite trait values) (Pavoine et al., 2009). Instead, CWM is widely used to quantify shifts in dominant functional strategies due to environmental selection and is calculated as the sum of the product between the trait values of a given species with its relative cover. By describing the dominant strategies, the CWM variation is indicative of the ecosystem processes rate. For example, higher/lower CWM of LDMC reflects lower/higher litter decomposition rates (Grigulis et al., 2013). We calculated CWM for single traits with the function *cwm* in the weimea package, while we calculated the FD using both traits together with the function *RaoRel* in the cati package (Taudiere and Violle, 2016). Before calculating FD and CWM we log10-transformed trait values of H and LDMC to have a normal distribution (Schleuter et al., 2010).

Lastly, we calculated species functional redundancy (FR), i.e., how much each species is functionally similar to other species of the same plant community. Functional redundancy quantifies the effect that species loss has on ecosystem functions (Mouillot et al., 2014; Ricotta et al., 2016). Functional redundancy for each species was calculated with Gower distance, considering both plant traits (H and LDMC) and species cover. Then, we calculated the average values of functional redundancy for typical and non-typical species at the plot level. Species functional redundancy was calculated with the function *uniqueness* provided by Ricotta et al. (2016).

2.4. Statistical analyses

We analyzed the variation of species richness, typical species richness, typical ratio index, FD and CWM by running separate analyses of variance (ANOVAs). We considered level of protection (categorical variables with three levels) as a predictor. Also, we included the habitat type (categorical variable with two levels) to account for the effect of different study areas. We considered the interaction between levels of protection and habitat types to test whether the effect of levels of protection was consistent across habitats. To run ANOVA, we used *aov* function in the stat package (R Core Team, 2022).

Similarly, we tested the effect of levels of protection, habitat type and their interaction on the CM of disturbance indicators (severity and frequency) using ANOVA. However, to remove the influence of species composition from disturbance indicator values which can produce confounded results, we compared the observed R^2 value of ANOVA model with a distribution of 999 expected R^2 values of ANOVA model (Zelený and Schaffers, 2012; Zelený, 2018). If the observed R^2 value is significantly higher than 999 expected R^2 values, the results of ANOVA model can be considered reliable and not false positives (Zelený, 2018). To calculate expected R^2 values, disturbance indicator values were shuffled 999 times across species before calculating the CM index ("column-based permutation test"; Zelený, 2018). This approach was not adopted for analysis of CWM for two reasons: i) plant traits are not derived by species composition matrix; and ii) using permutation models to explore the link between plant traits to ecosystem processes increases the Type II Error rate (Lepš and de Bello, 2023). Additionally, we used structural equation models (SEMs; Grace, 2006) to quantify the presumed causal relationships between CM of disturbance indicators, typical ratio index and functional diversity for each biogeographical region. Specifically, each structural equation model has been built with two separate regression models, one testing the effect of the CM of disturbance indicator values for severity and frequency on the typical ratio index and another testing the effect of all these three parameters on the functional diversity. In contrast to the Mediterranean region where disturbance severity and frequency were weakly correlated according to Pearson correlation (coefficient = 0.41), in the Alpine region these disturbance regimes were highly correlated (coefficient = −0.98). Therefore, we included in SEMs only the disturbance frequency for the Alpine region (Evans, 1996). Nonetheless, we checked the presence of multicollinearity between predictors for each regression model using variation inflation factor (VIF). We discarded disturbance frequency from the regression model with three predictors (disturbance severity and frequency, and typical species ratio) for the Mediterranean region since it showed higher multicollinearity values (VIF > 3; Zuur et al., 2010). We compared the R^2 values of the observed model with a distribution of 999 expected R^2 values by shuffling disturbance indicator values across species 999 times (Zelený, 2018).

We ran SEMs with the *psem* function in the piecewiseSEM package (Lefcheck, 2016) and variation inflation factors with the *vif* function in the car package (Fox and Weisberg, 2019).

Lastly, we tested if the amount of functional redundancy significantly differed between typical species and non-typical species for each habitat using two-paired *t*-test with *t.test* function in the stat package.

We used diagnostic plots to check ANOVA and SEMs assumptions (i.e., normal distribution of residuals, equal variance in the residuals and lack of autocorrelation in the residuals; Zuur et al., 2010).

All the computations were performed with R 4.1.3 software (R Core Team, 2022).

3. Results

3.1. Taxonomic, functional and disturbance variation along levels of protection

Levels of protection affected all taxonomic metrics (species richness, typical species richness and typical ratio index) and their interaction with habitat types, while the effect of the habitat type was mostly neglected (Fig. 2). However, while species richness and typical species richness were independent according to Pearson correlation test (coefficient = −0.1; $p > 0.05$), typical ratio index results significantly correlated with a negative trend to species richness (coefficient = −0.7; $p < 0.05$) and with a positive trend to typical species richness (coefficient = 0.7; $p < 0.05$). The ANOVA model for species richness (Fig. 2a) showed 25 % of explained variation (R^2; $p < 0.05$). When we partitioned the total explained variation into the relative contribution of each predictor, we found that level of protection explained 46 % ($p < 0.05$), interaction term 53 % ($p < 0.05$), and the effect of habitat type 1 % ($p > 0.05$). The ANOVA model for typical species (Fig. 2b) explained 47 % of the variation (R^2; $p < 0.05$) with a higher contribution of the level of protection 49 % ($p < 0.05$), slightly higher than the interaction term with 48 % ($p < 0.05$), followed by habitat type with 3 % ($p > 0.05$). The ANOVA model for the typical ratio index (Fig. 2c) explained a total of 43 % (R^2; $p < 0.05$) partitioned into 64 % ($p < 0.05$) due to interaction term, 35 % ($p < 0.05$) level of protection, and only 1 % due to the habitat type ($p > 0.05$).

The ANOVA model for functional diversity (Fig. 2d) explained 26 % of the variation (R^2; $p < 0.05$). However, contrary to taxonomic metrics, for functional diversity we found a higher contribution of habitat type with 48 % ($p < 0.05$), followed by very similar values of interaction terms of 45 % ($p < 0.05$) and by level of protection with 7 % ($p > 0.05$). For details see Appendix F.

Regarding the analysis of CWM, we found the ANOVA model for plant growth height explained 91 % of the variance (R^2; $p < 0.05$) with a significant effect of habitat type (98 % of relative contribution; $p < 0.05$)

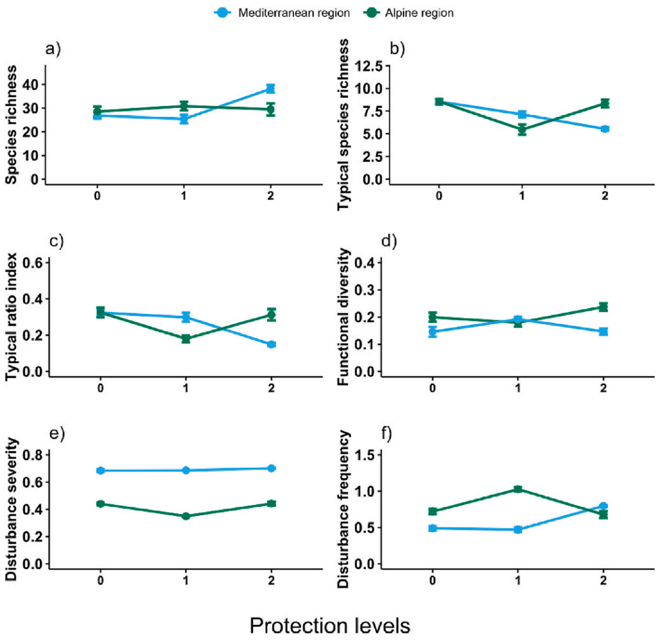

Fig. 2. Trends (mean ± s.e.) per shrubland habitat of **a)** species richness, **b)** typical species richness, **c)** typical ratio index, **d)** functional diversity, **e)** disturbance severity and **f)** disturbance frequency across protection levels with 0 = absence of protection; 1 = one level of protection (Natura 2000); and 2 = two levels of protection (Natura 2000 + National Park). Blue lines represent trends for the Mediterranean area, green lines represent the trends for the Alpine area.

and its interaction with level of protection (1.7 % of relative contribution; $p < 0.05$). Lastly, for CWM of LDMC, the ANOVA model explained 78 % of the variation (R^2; $p < 0.05$) with a significant effect for each of the three predictors. Specifically, the interaction term had higher explanatory power (77 % of relative contributions; $p < 0.05$), followed by habitat type (16 %; $p < 0.05$) and level of protection (6 %; $p < 0.05$). For model results see Appendices G and H. Patterns in variation of typical species richness and CWM for H and LDMC between levels of protection and habitat types were confirmed when species were split into woody and herbaceous species (for details see Appendix I).

The model results emerging from the analysis of disturbance regime across levels of protection, habitat type and their interactions showed significant variation. Regarding CM of disturbance severity (Fig. 2e), the model showed significant results with 97 % of the total explained variation (R^2; $p < 0.05$), partitioned into 95 % due to the habitat type ($p < 0.05$), 3 % for level of protection ($p < 0.05$) and 2 % for their interaction ($p < 0.05$). Similarly, for CM of disturbance frequency (Fig. 2f), the ANOVA model results were significant with 70 % of the total explained variation (R^2; $p < 0.05$). However, in this case, variations across levels of protection were more marked compared to disturbance severity (Fig. 2f). This emerges also from the partitioning of total explained variation that revealed different contributions with 54 % of the total explained variation due to interaction term ($p < 0.05$), 34 % due to habitat type ($p < 0.05$) and 12 % due to level of protection ($p < 0.05$). Detailed information on model performance and its comparison against expected models is reported in Appendix J.

3.2. Relationship among disturbance, typical species and functional diversity

Our SEMs highlighted multiple causal relationships between disturbance indicators, typical species and functional diversity for each habitat type (Fig. 3a, c). For the Mediterranean region, we found only direct (and negative) effects of disturbance indicator values of frequency on the typical ratio index ($R^2 = 75$ %), and direct (and negative) effects of the typical ratio index on functional diversity ($R^2 = 24$ %). For the Alpine region, disturbance indicator values of frequency directly affected both the typical ratio index (negatively) ($R^2 = 61$ %) and functional diversity (positively) ($R^2 = 46$ %), whereas the negative relationship between typical species ratio and functional diversity was not significant. Overall, the SEMs pointed out that increased disturbance frequency directly and indirectly influences different biodiversity facets.

Additionally, the increase of typical species in the plant community tended to decrease overall functional diversity. This negative effect of typical species on functional diversity was also confirmed by the comparison of the functional redundancy between typical species and non-typical species. *t*-test showed significant differences in the redundancy values between the two groups, with typical species having a higher degree of functional redundancy compared with non-typical species both in the Mediterranean ($t = 4.3$; $p < 0.05$) and Alpine region ($t = 2.9$; $p < 0.05$) (Table 1; Fig. 3b, d).

4. Discussion

This study is one of the first that combined empirically into a unique framework the taxonomic and functional facets of biodiversity in defining habitat conservation status on different levels of protection. Our results suggest habitat quality quantified by means of typical species richness does not increase consistently with levels of protection. Against our expectations, European Natura 2000 sites do not host habitats with the highest quality when they fall within the two Italian National Parks considered in our study. This suggests that variation in disturbance regimes represents a key factor in shaping habitat quality more than levels of legal conservations. Additionally, plant traits represent a valid tool to describe habitat structure and functions, a complementary information fundamental for conservation assessment. Overall, we found that the habitats having better quality are characterized by a functional homogenization towards specific strategies expressed by typical species. We suggest a combination of a taxonomic approach based on typical species and a functional approach based on plant traits can offer a good assessment of habitats' structure and functions, which can help in prioritizing conservation actions in PAs.

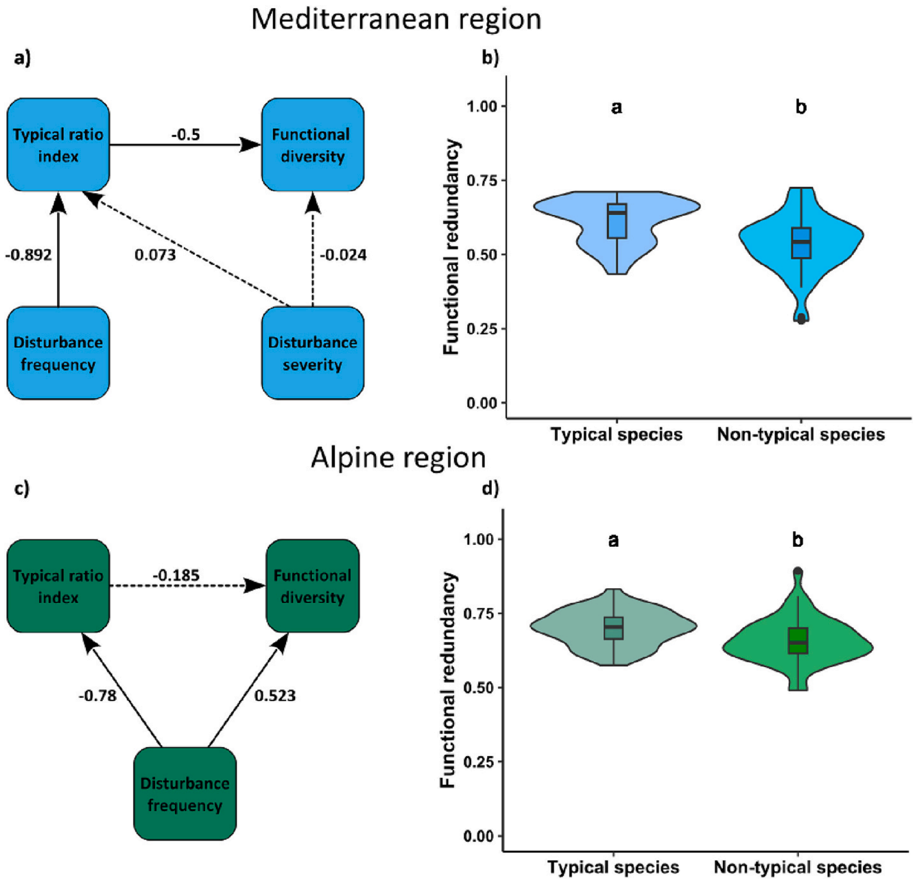

Fig. 3. Structural equation models (SEMs) explaining causal relationships among functional diversity, disturbance severity and frequency based on community mean of species disturbance indicator values and typical ratio index for the a) Mediterranean region and the c) Alpine region. Continuous lines and dotted lines represent significant ($p < 0.05$) and non-significant ($p > 0.05$) paths. Disturbance severity and frequency have been expressed as community unweighted mean of species disturbance indicators, typical ratio index as the number of typical species on the species richness and functional diversity with Rao's Quadratic Entropy considering plant growth height and leaf dry matter content. Standardized coefficients are also shown. Comparison of functional redundancy between typical species and non-typical species for the b) Mediterranean region and the d) Alpine region. Functional redundancy has been calculated with plant growth height (H) and leaf dry matter content (LDMC). Different letters mean significantly different ($p < 0.05$) according to *t*-test.

Table 1
Mean values of functional redundancy and mean values of measured plant traits (H, plant growth height; LDMC, leaf dry matter content) of typical ($N = 19$) and non-typical ($N = 40$) species for a habitat type.

	Habitat type	Functional redundancy	H (cm)	LDMC (mg/g)
Typical species	Arborescent matorral of *Juniperus* spp.	0.59	137.9	349.5
Non-typical species		0.53	35.8	190.00
Typical species	Alpine and boreal heaths	0.70	18.9	291.4
Non-typical species		0.65	14.7	253.9

4.1. Variation of habitat quality along levels of protection

In the Mediterranean study area, the lowest habitat quality (i.e., lowest typical species richness) was found at sites under two levels of protection. These sites hosted the highest species richness. Similarly, for the Alpine region, we found the lowest habitat quality (i.e., lowest typical species richness) associated with highest species richness but for sites under one level of protection. In both cases, these habitats were associated with highest disturbance frequency. Therefore, our results suggest that species richness might not be a reliable standalone indicator of habitat quality (Boch et al., 2013) as habitats with favorable conservation status can be species-poor (Hunter et al., 2021), and that designation of PAs alone does not ensure habitat preservation (Kindermann et al., 2024). The effect of disturbance regime variation in enhancing plant diversity is well-known in the literature. According to the intermediate disturbance hypothesis (Connell, 1978), further adopted in conservation science as the "land-use-moderated conservation effectiveness hypothesis" (Kleijn et al., 2011), variation of disturbance regime can be harmful to conservation efforts of a specific habitat (Xu et al., 2023). While the disturbance regimes present in the PL2 sites in the Mediterranean study area could be attributed to human-land use, like overgrazing by domestic species occurring with different frequencies (Appendix K; Drissen et al., 2022), sites experiencing one level of protection in the Alpine region were characterized by natural disturbance occurring with mostly similar frequencies (rock movements on screes; Appendix K). This suggests how, for the Alpine region, the PL1 sites hosted a habitat representing more a natural deviation from a reference condition, rather than a degraded human-induced form. These considerations hold even when we consider a direct connection between the effect of disturbance regimes (frequency) variation in decreasing typical species richness. Overall, our results highlight a context-dependent relationship between anthropogenic and natural disturbances and shrubland habitat quality in PAs.

Conversely, sites with the highest habitat quality (i.e., highest typical species richness) were PL0 and PL1 in the Mediterranean region, and PL0 and PL2 in the Alpine region, also characterized by lowest disturbance frequencies. We can assume that they are representative of less deviated conditions from their reference habitat state, which could result from the abandonment of traditional silvo-agro-pastoral activities (Zerbe, 2022). The rural exodus started after World War II and persisted over time across all of Europe (MacDonald et al., 2000; Ricotta et al., 2012), is triggering processes of natural vegetation re-growth. The abandonment of grazing, timber use, and other agricultural activities, followed by the onset of natural succession processes, is promoting shrub and forest encroachment. While in the initial phase, shrubland habitats should benefit from this trend, if abandonment of land use persists longer, there is a chance they will be replaced by forest ones (Ferrara et al., 2021). This calls for further studies to identify the optimal disturbance condition these habitats benefit from to avoid their transformation towards grasslands or forests.

4.2. *Habitat structure and functions associated with habitat quality*

Variations of functional diversity across levels of protection can be associated with changes in disturbance regimes. As such, in the lowest habitat quality of both biogeographical regions (PL2 Mediterranean region and PL1 Alpine region), a peculiar disturbance regime was mirrored by greater functional diversity. This supports the concept that more disturbed communities are characterized by functionally distinct species (Grime, 2006). In these habitats, we found the dominance of shorter species (mean values: 49.5–11.8 cm) displaying more acquisitive (i.e., faster relative growing rates) strategy, functional adaptations favored by disturbance conditions (Backhaus et al., 2021 and reference within). This functional portfolio suggests for both habitats lower stability (defined as higher resistance to environmental changes; Majeková et al., 2014) and that eventually the loss of species will be coupled with the loss of functions uniquely associated with the given species (Díaz and Cabido, 2001; Majeková et al., 2014). Scaling up from the community to ecosystem level, these functional plant communities suggest a higher diversity of habitat structure and functions (FD) but lower carbon sequestration (shorter species) with higher litter decomposition rates (acquisitive strategies) (Conti and Díaz, 2013; Grigulis et al., 2013). Overall, this relationship between disturbance and functional diversity holds if we consider the relationship between disturbance frequency and functional diversity even with slight differences. For example, in the Mediterranean region we found disturbance frequency altered the functional diversity, while for the Alpine region, we found both direct and indirect effects. This consideration strengthened the concept that drivers can influence the component of plant diversity differently (Cadotte and Tucker, 2018; Napoleone et al., 2021).

Conversely, sites with the highest habitat quality (i.e., highest typical species richness; PL0 and PL1 for the Mediterranean region and PL0 and PL2 for the Alpine region) were characterized by lower functional diversity, with a dominance of taller species (97.1 and 94.9 cm for PL0 and PL1 in Mediterranean region - 18.3 and 18.5 for PL0 and PL2 for the Alpine region) with more conservative (i.e., slower relative growing rates) strategies. This functional portfolio reflects that of a less disturbed plant community (Backhaus et al., 2021). Here, the loss of species slightly affected variation in structure and functions of habitats thanks to the presence of other functionally similar species (higher stability; Díaz and Cabido, 2001; Majeková et al., 2014). In terms of ecosystem processes, these functional plant communities suggest a lower diversity of habitat structure and functions (FD) but higher carbon sequestration (taller species) and lower decomposition rates (conservative strategies) (Conti and Díaz, 2013; Grigulis et al., 2013). Our results confirm maintenance of habitat structure and functions in shrublands is driven by typical species and provide empirical evidence on the relation between typical species and structure and functions of habitats.

Lack of management actions in National Parks hosting Natura 2000 habitats showed a mismatch with the main aim of Natura 2000 network of improving habitat quality. Given the large extension of Natura 2000 sites within National Parks in the European territory and our limited possibility of assessing this scenario in two study areas, we call for further studies. Traditionally, conservation assessments have focused solely on qualitative information about habitat-specialist species, considering them as keystone species in habitat structure and functions. Our study provides evidence of how typical species quantitatively define habitat structure and functions. In light of the strict relationship between disturbance regimes and typical species of a given habitat, a comprehensive outlook should encourage an integrated use of disturbance conditions (e.g., species disturbance indicator values) within the purview of habitat quality assessment. From a conservation planning point of view, conserving typical species will enhance the stability of ecosystem processes provided by the habitat and will produce functional homogenization. Nonetheless, the level of protection afforded by protected areas is not necessarily indicative of their quality. Conservation planning should thus prioritize facets that hold major ecological significance, recognizing its context-specific nature. A combined taxonomic and functional approach in PAs can hence offer a thorough understanding of habitat quality enabling more informed decision-making.

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Author statement

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Alessandro Bricca: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas Deola:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Stefan Zerbe:** Writing – review & editing. **Simonetta Bagella:** Writing – review & editing, Validation, Methodology. **Giovanni Rivieccio:** Writing – review & editing, Investigation. **Camilla Wellstein:** Writing – review & editing. **Gianmaria Bonari:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data used in the analysis are available in the Appendix L.

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Supplementary data

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