Biodiversity and Conservation (2026) 35:216
https://doi.org/10.1007/s10531-026-03425-6

ORIGINAL RESEARCH

Contrasting effects of protected areas on understory plant diversity in broadleaved deciduous forests

Lorenzo Ricci[1,2] · Jonas Geldmann[3] · Nicola Alessi[4] · Anna Rita Frattaroli[1] · Jacob Heilmann-Clausen[3] · Francesco Maria Sabatini[2] · Alessandro Chiarucci[2] · Fabio Attorre[5] · Gianmaria Bonari[6,7] · Michele Di Musciano[1,2]

Received: 16 June 2025 / Revised: 1 June 2026 / Accepted: 11 July 2026

Abstract
Protected areas are essential for preserving forest ecosystems and maintaining their ecological integrity. Nonetheless, their role in conserving understory plant species in Italy remains understudied. We analysed 5,423 vegetation plots sampled in Italian broadleaved deciduous forests between 1980 and 2020. Using propensity score matching, we controlled for potential confounding factors such as elevation, climate, proximity to roads, and plot size, enabling an unbiased assessment of the effect of protection status on understory plant diversity. We compared alpha and gamma diversity between protected and unprotected areas, considering both the total number of species and separately for understory plant species associated with forest- or open-habitats. Differences in alpha diversity were assessed using generalized linear models, while gamma diversity was evaluated by quantifying the number of species exclusive to protected areas, exclusive to unprotected areas, and shared between the two. Protected areas generally tended to support higher levels of both alpha and gamma diversity, although patterns varied among habitat types. Alpha diversity was generally higher within protected areas, with statistically significant differences observed only in some habitats. Similarly, forest-associated species showed higher gamma diversity within protected areas than outside across all habitat types, whereas patterns for open-habitat species were more variable and did not consistently differ between protected and unprotected areas. Overall, our results suggest that Italian protected areas represent an important portion of understory plant diversity, particularly for forest-associated species. However, the presence of habitat-specific assemblages suggests that additional conservation efforts may still be needed beyond protected areas boundaries.

Keywords Forest biodiversity · Protected areas · Propensity score matching · Understory vegetation

Communicated by Daniel Sanchez Mata.

Extended author information available on the last page of the article

Introduction

Protected areas have been established worldwide as a key conservation tool aimed at preserving biodiversity and ecosystem functions (Bruner et al. 2001; Chape et al. 2005; Yang et al. 2019) and are today one of the main instruments implemented to halt biodiversity loss (Watson et al. 2014). Acknowledging that the current protected area system has proven insufficient to halt biodiversity loss on a continental scale (Hermoso et al. 2022), the Convention on Biological Diversity's Kunming-Montreal Global Biodiversity Framework, the United Nations Sustainable Goals, and the European Union's commitments mandate an expansion of protected areas globally (European Commission 2020; UNEP-WCMC and IUCN 2023).

Given the resources and commitment required to ensure effective protection (Geldmann et al. 2018; Coad et al. 2019; Rodrigues and Cazalis 2020; Geldmann 2023), it is crucial that new sites are selected efficiently and improve the representation of the regional diversity of species and habitats within the protected area system (Butchart et al. 2012, 2015; Delso et al. 2021). This expansion must overcome some of the limitations of the current protected area system, where protected area allocation is not always based on ecological criteria but is rather commonly biased toward less accessible or unproductive areas (Joppa and Pfaff 2009; Elbakidze et al. 2013; Velazco et al. 2019). In response to these challenges, systematic conservation planning has shifted toward scientifically grounded approaches, emphasizing ecological representativeness in protected area design (McIntosh et al. 2017; Jantke et al. 2019; Hoffmann 2022). A reliable assessment of the effect of protected areas in representing biodiversity requires a meaningful comparison of the species diversity inside and outside protected areas to identify potential gaps in biodiversity protection. Such a comparison requires good quality biodiversity data, which, ideally, should be collected over large geographic areas (country to regional) according to a probabilistic sampling design that controls for the main environmental factors affecting biodiversity distribution, such as elevation, climate, and disturbances (Chen et al. 2023). Unfortunately, data collected using such an approach is rarely available, particularly for direct measures of biodiversity, like changes in abundance and distribution of species (Cazalis et al. 2020). Most large-scale biodiversity datasets are haphazard assemblages of observations originally collected with different purposes, often without a proper sampling design (Chiarucci et al. 2011; Chytrý et al. 2016; Alessi et al. 2023), and this hinders our ability to robustly assess biodiversity contained in protected versus unprotected areas.

While primarily used to evaluate conservation outcomes, counterfactual analysis and matching techniques offer a novel tool when assessing the effect of protected areas in representing biodiversity. The main advantage is that these techniques can account for the non-random location of protected areas (Schleicher et al. 2020). This allows for not only assessing patterns of biodiversity inside protected areas, but also for understanding if and how these patterns differ from areas with similar characteristics, but which are not protected. Thus, our integration of matching provides a more robust assessment of the state of biodiversity compared to an appropriate counterfactual. Yet, this does not come without challenges, including the choice of an appropriate set of environmental factors to consider to account for the full complexity of biodiversity patterns (Rodrigues and Cazalis 2020), and the fact that the amount of data needed for such a comparison to be robust is substantial (Rodrigues and Cazalis 2020).

Forest ecosystems have experienced substantial biodiversity decline over the last centuries due to significant human-driven forest loss and degradation (Márialigeti et al. 2016; Douda et al. 2017). The overall decline in forest cover has been reversed in most of Europe during the second half of the last century leading to net afforestation at national and regional scales (Cervera et al. 2019; Bricca et al. 2025), also leading to local recovery of forest-associated species (see e.g. Lelli et al. 2021). Yet, this expansion in forest cover may not necessarily confer benefits to biodiversity conservation, as many newly-established forests lack a suite of structural features and specialized biodiversity which are commonly associated with primary and old-growth forests (Burrascano et al. 2013; Gloor et al. 2024), besides being typically homogeneous and managed for commercial exploitation (Angelstam et al. 2020, 2021; Gauthier et al. 2023).

Within forest ecosystems, trees dominate the living biomass, yet understory plants, mainly restricted to the ground layer, are an important part of the biodiversity and play a critical role by providing essential habitat and forage for many animals and fungi. In temperate forests, understory plants typically represent over 80% of vascular plant species diversity (Gilliam 2007; Spicer et al. 2022). These species respond fast to both natural and anthropogenic disturbances. They also play a crucial role in stabilizing soil and creating suitable microenvironments that support the development of other species (Simonson et al. 2014; Atrena et al. 2024). Thus, understory species constitute a fundamental component of forest biodiversity and serve as a reliable indicator for monitoring changes in forest conditions (Landuyt et al. 2019; Oettel and Lapin 2021; Chelli et al. 2024).

In addition to typical forest understory species, the occurrence of species commonly associated with open-habitats within forest stands provides important ecological information. These species may reflect disturbance regimes, canopy openness, edge effects, or historical land-use legacies, and are therefore informative of habitat conditions and ecosystem dynamics (Landuyt et al. 2019; Oettel and Lapin 2021). In managed or fragmented landscapes, such species may persist within forest stands due to ongoing disturbance or past land use, whereas their occurrence in protected areas may be linked to natural disturbance processes or transitional successional dynamics (Lelli et al. 2021). Considering the co-occurrence of species with different ecological affinities thus allows for a more comprehensive assessment of biodiversity patterns and the processes shaping them across protection regimes (Brockerhoff et al. 2017; Landuyt et al. 2019).

Protected areas may prevent forest loss by prohibiting, or limiting, logging and other threats and disturbances such as agriculture, mining, and road construction activities that often accelerate biodiversity loss (Kleinschroth and Healey 2017). Nevertheless, in Italy and many European countries, logging and other land-use activities are not entirely excluded from protected areas but instead vary according to protection level and specific conservation strategies (Agnoletti et al. 2022; Cazzolla Gatti et al. 2023). In some cases, selective logging can create canopy gaps, enhance habitat heterogeneity, and promote the regeneration of open-habitat vegetation, potentially increasing species diversity (Götmark 2013; Schall et al. 2018). Consequently, biodiversity patterns may partly reflect differences in forest management regimes rather than solely the effects of protection status (Powlen et al. 2021; Agnoletti et al. 2022). In addition, plant diversity of forest ecosystems at local scale is also affected by landscape processes and land use diversity at a large spatial extent around the focal area (Amici et al. 2015). However, while protected areas can be effective in conserving forest species, overall species richness often declines after protection is established, mainly

due to the loss of open-habitat species that thrive in managed landscapes (Petermann and Buzhdygan 2021). On the flip side, protection leads to an increase in specialized late-successional forest species, promoting the development of old-growth features, such as deadwood accumulation and the creation of tree-related microhabitats (Amici et al. 2013; Lelli et al. 2021). Nonetheless, the overall impact of protection on plant biodiversity remains complex, highlighting the need for further understanding of how protected areas can effectively represent biodiversity throughout the forest succession (Heywood 2019; Corlett 2020). A major challenge is to understand the role of protected areas in representing and conserving understory plant diversity within forests (Lindenmayer and Franklin 2013; Viña and Liu 2017), based on solid data permitting counterfactual analyses (Ribas et al. 2021).

In this study, we leveraged a newly aggregated and extensive dataset of vegetation plots (Alessi et al. 2023), enabling a detailed assessment of the effect of Italian protected areas in representing forest understory plant diversity. Italian forests are highly diversified because of the existence of major natural gradients in biogeographical regionalization (Chiarucci et al. 2019), a high rate of plant endemism (Orsenigo et al. 2021) combined with the long-term interactions with humans which led to a transition from natural to human-dominated landscapes (Marignani et al. 2017).

Given the different dominant disturbance regimes (natural versus anthropogenic) occurring in protected and unprotected areas, we hypothesized that: (i) At local scale, forests in protected areas contain a higher number of forest-associated species compared to forests located outside protected areas. (ii) At the landscape scale, the pool of species associated with open-habitats is only marginally shared between protected and unprotected areas, with most open-habitat species being either exclusively found inside or outside protected areas.

Materials and methods

Data collection

We obtained data on understory plant species co-occurrences within Italian broadleaved deciduous forest ecosystems from a countrywide vegetation-plot dataset (Alessi et al. 2023). This comprehensive dataset includes 16,259 preferential forest vegetation plots and contains information on 2,948 vascular plant species. Taxonomy was standardized according to *Flora d'Italia* (Pignatti et al., 2017–2019), and species names were harmonized accordingly across the dataset.

The dataset contains data on vegetation plots, from 1 m^2 to 2000 m^2 in size, collected between 1935 and 2020. For the purpose of this study, the dataset was refined by filtering plots based on different specific criteria. We only retained plots between 100 m^2 and 400 m^2 in size, reflecting the plot sizes traditionally used by European vegetation scientists to sample forest habitats (Chytrý and Otýpková 2003). Additionally, we only retained plots sampled between 1980–2020, a temporal range chosen to align with the establishment of most protected areas in Italy.

Vegetation plots were assigned to EUNIS habitat types using an expert system (Version v2021-06-01- https://doi.org/10.5281/zenodo.4812736) based on species composition (Chytrý et al. 2020). The 4,192 unassigned plots were chord-transformed and assigned to an EUNIS habitat type using the hard noise clustering model (De Cáceres et al. ytr2010).

Based on the EUNIS classification, we retained only plots classified as "broadleaved deciduous forests". We further excluded habitat types that were not classified at Level 3 by the expert system and those represented by fewer than 100 vegetation plots. The final number of vegetation plots was 5,423, distributed across eight Level 3 EUNIS habitats (hereafter habitat types): acidophilous *Quercus* forests, *Quercus* mesic deciduous forests, *Fagus* forests on acid soils, *Fagus* forests on non-acid soils, riparian forests, ravine forests, thermophilus deciduous forests, and temperate hardwood riparian forests (Fig. 1). The geographical boundaries of protected areas were acquired from the World Database on Protected Areas (WDPA) (UNEP-WCMC and IUCN 2023) and then clipped to the geographical area of Italy. The WDPA contains 3,948 protected areas for Italy, encompassing national

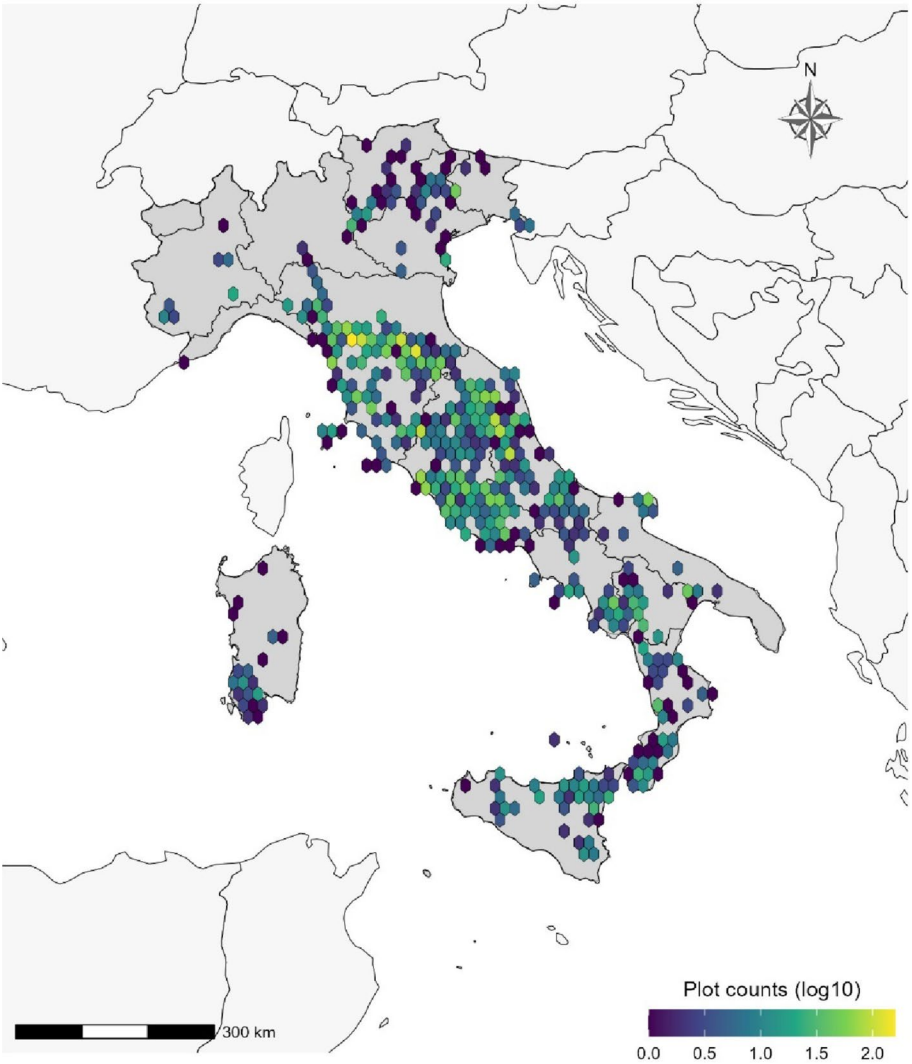

Fig. 1 Geographical distribution of vegetation plots across Italy after filtering, with plot counts presented on a $\log_{10}$ scale

and regional parks, nature reserves, biotopes, natural monuments, and Natura 2000 sites. Subsequently, vegetation plots were classified as "protected" (3,638 plots) if they intersected with protected area polygons, or "unprotected" otherwise (1,785 plots).

Candidate covariates

We used the geographical coordinates to retrieve, for each selected vegetation plot, the elevation (European Union 2021), as well as the annual mean precipitation and temperature, which were extracted from the CHELSA dataset at 1 ArcSec resolution (~1000 m at the equator; Karger et al. 2017). To account for the human disturbance of forest habitat, we used Open Street Map to calculate the minimum distance of each plot from the nearest forestry roads, as this distance affects not only the probability of silvicultural activities, but also the presence of species typical of disturbed habitats, such as ruderal and alien species (Kleinschroth and Healey 2017). Data preparation, as well as all statistical analysis, were conducted with the software R 4.2.3 (R Core Team 2023) using the packages *terra* (Hijmans et al. 2022), *rgdal*, *sf* (Pebesma 2018), and *tidyverse* (Wickham et al. 2019).

Data analyses

Species categorization

To better interpret diversity patterns in relation to disturbance regimes and habitat conditions, we categorized understory plant species into two groups: forest and open-habitat associated species (see Appendix 1), following a previous study on forest dynamics in complex Mediterranean ecosystems (Amici et al. 2013). Appendix 1 contains the complete lists of forest- and open-habitat associated species used for the classification, together with a separate sheet reporting the species retained for the analyses and their corresponding habitat association. The classification was conducted by assessing each species' fidelity to the forest vegetation relative to open-habitats, following the approach outlined by Chytrý et al. (2002). We used the phi coefficient of association as a measure of species fidelity, comparing species occurrences in the full dataset of 16,259 forest vegetation plots (Alessi et al. 2023) with 26,161 vegetation plots from open-habitats, obtained by aggregating plots excluded from the forest selection procedure described in Alessi et al. (2023). Both forest and open-habitat plots originated from the vegetation databases used in Alessi et al. (2023). A threshold of phi > 0.20 was used to identify species-habitat associations. The phi coefficient was corrected for unequal cluster size following Tichý and Chytrý (2006).

Propensity score matching

To account for confounding factors related to the non-random location of vegetation plots in the landscape within and outside protected areas, we used propensity score matching. Here protected plots function as the treatment. Based on previous studies (Joppa and Pfaff 2009; Arriagada et al. 2012; Geldmann et al. 2019), we identified as matching covariates: (1) size of the vegetation plots, (2) elevation, (3) annual mean temperature, (4) annual precipita-

tion, (5) minimum distance from forestry roads, and (6) habitat types. For each protected plot (treatment group), propensity score matching selects the most similar unprotected plot (control group). We used exact matching for the habitat type, i.e., we only compared protected and unprotected vegetation plots inside the same habitat. Propensity score matching was done using the *MatchIt* package (Ho et al. 2018). The 'nearest' method was chosen, the parameter 'ratio' was set to 1, and the caliper was set to 0.25 (Cuenca et al. 2016). To verify the validity of propensity score matching, we checked the balance between the treated sites and the control sites (Appendix 2) using the standardized mean difference tests from the *cobalt* package by Greifer and Greifer (2020).

Alpha and gamma diversity

We quantified alpha diversity in two ways: as the number of species occurring in a vegetation plot, as well as the average number of forest and open-habitat specialist species. Differences in alpha diversity between protected and unprotected areas across various habitat types were analysed using the Wilcoxon Rank Sum Test, without adjusting for potential confounding variables. Additionally, we fitted generalized linear models (GLMs) with a Poisson distribution (Quinn and Keough 2002) to further evaluate changes in alpha diversity of forest and open-habitat associated species in relation to the protection status and habitat types. In these models, alpha diversity of forest- and open-habitat species served as response variables. GLMs were built allowing for the interaction between protection status and habitat type, using as explanatory variables all those included in the propensity score matching, except for annual mean temperature. To avoid multicollinearity, we checked correlation among all pairs of explanatory variables using the Pearson correlation coefficient. We found a strong negative correlation between elevation and annual mean temperature (Pearson's correlation coefficient, r_p = -0.92), and only retained the former, as it offers more specific insights into the geographical setting (Graham 2003; Joly et al. 2012). Pairwise contrasts between protected and unprotected plots within each habitat type were estimated by the GLMs using estimated marginal means, as implemented in the *emmeans* package (Lenth et al. 2019). Gamma diversity was assessed by calculating the total number of species, as well as the number of forest- and open-habitat species, within each habitat type. All estimates were calculated separately for protected and unprotected plots. In addition, we identified the number of forest- and open-habitat associated species exclusive to protected areas, exclusive to unprotected areas, and shared between the two. We further assessed gamma diversity of species endemic to Italy using the national checklist of the Italian vascular flora (Bartolucci et al. 2018). Endemic species richness was subsequently summarized across habitat types and protection categories.

To evaluate sampling completeness and expected species richness, rarefaction curves were generated using the iNEXT package (Hsieh et al. 2016) on the matched dataset. We performed separate analyses for all species, as well as for forest- and open-habitat associated species, within both protected and unprotected areas. By examining how closely the rarefied accumulation curve approached its theoretical asymptote, which represents the overall expected species richness in each group, we were able to assess the completeness of species representation (Koellner et al. 2004; Chiarucci et al. 2008; Chao et al. 2014). This approach provides insights into the completeness of species representation and helps assess whether overall species richness, as well as the richness of forest- and open-habitat

associated species, is adequately captured in both protected and unprotected areas (Chao et al. 2014).

A summary of diversity patterns across habitat types and protection status is provided in Appendix 3.

Results

The final dataset included 5,423 vegetation plots and 1,028 plant species. Alpha diversity of understory plants was generally higher inside protected areas than in otherwise comparable outside areas (Fig. 2). When considering individual habitat types, alpha diversity was significantly different only for ravine forests, *Fagus* forests on non-acidic soils and Thermophilus deciduous forests (e.g. mean alpha = 20.82, 16.04 and 18.81 respectively; Fig. 2 and Appendix 3). All other habitats did not show statistically significant differences between protected and unprotected sites.

The GLMs showed that for forest-associated species, alpha diversity was generally higher within protected areas than in unprotected areas, except for the acidophilous *Quercus* forests (Fig. 3 and Appendix 4–5). A broadly similar pattern was observed for open-habitat species, where alpha diversity tended to be higher in protected areas, except for the riparian forests, temperate hardwood riparian forests, and *Quercus* mesic deciduous forests (Fig. 3 and Appendix 6–7).

Patterns in gamma diversity largely mirrored those observed for alpha diversity, with higher values within rather than outside protected areas for most, but not all, habitat types

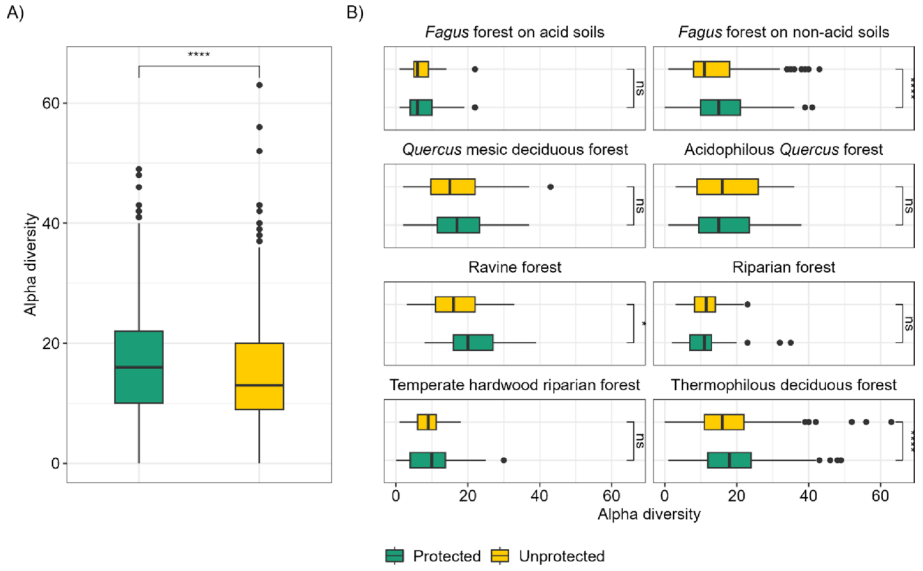

Fig. 2 Boxplots of post-matching overall alpha diversity (A) comparing protected and unprotected areas, and (B) divided by different habitat types within these areas. Asterisks indicate significant differences in the pairwise comparison (Wilcoxon Rank Sum test) between protected and unprotected areas. (*ns* not significant; * P value < 0.05; ** P value < 0.01; *** P value < 0.001; **** P value < 0.0001)

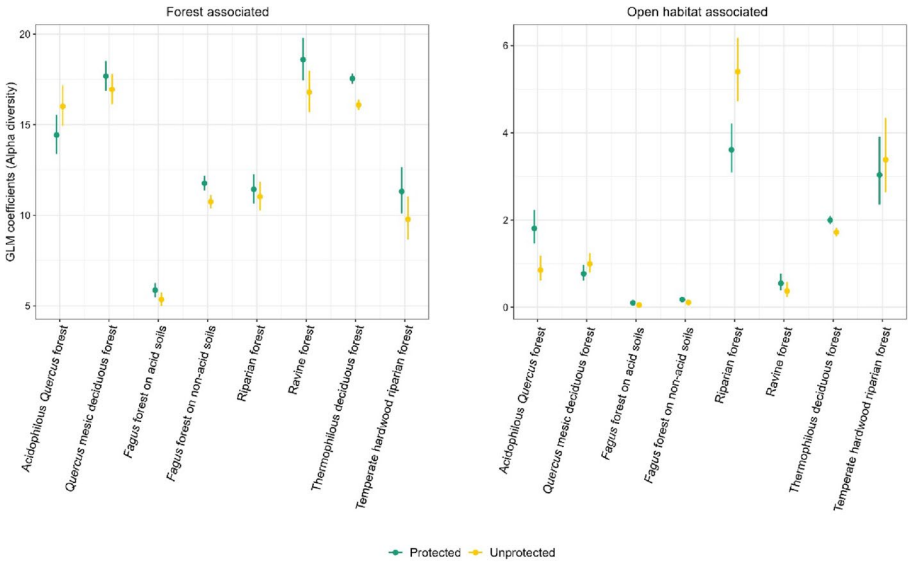

Fig. 3 GLM coefficients of post-matching alpha diversity across habitat types for forest- and open-habitat associated species within protected areas (yellow) and outside (green) (lines, standard error; dots, estimated regression coefficients as obtained by GLMs for the different groups).

(Fig. 4, Appendix 8). For example, *Fagus* forests on non-acid soils showed higher gamma diversity within protected areas (315 species) than outside (277 species; Appendix 3). Exceptions were limited to riparian forests and *Quercus* mesic deciduous forests, where gamma diversity was higher outside protected areas.

Overall, 21% of the species were found exclusively within protected areas, 16% exclusively outside, and 63% were shared between both. Across habitat types, species exclusive to protected areas generally outnumbered those exclusive to unprotected areas, although most species remained shared between the two (Figs. 4 and 5; Appendix 3). For instance, in Thermophilus deciduous forest, shared species (481) greatly exceeded the number of exclusive species (209 inside vs. 133 outside protected areas; Appendix 3).

When examining gamma diversity for forest- and open-habitat species separately, we found that protected areas exhibited higher gamma diversity for forest-associated species across all habitat types (Fig. 5, Appendix 3). The magnitude of these differences varied, however, with *Fagus* forests on non-acid soils and *Quercus* mesic deciduous forests showing only minor differences between protected and unprotected areas. For open-habitat species, gamma diversity generally showed a tendency towards higher values in protected areas, although the pattern was less consistent among habitats than for forest-associated species. While protected areas contained more unique open-habitat species in most forest types, *Fagus* forests on non-acid soils and *Quercus* mesic deciduous forests showed the opposite pattern, with a greater number of unique species occurring in unprotected sites (Fig. 5). A total of 32 endemic species were recorded, with their distribution across habitat types and protection categories broadly reflecting the patterns observed for overall gamma diversity (Appendix 3).

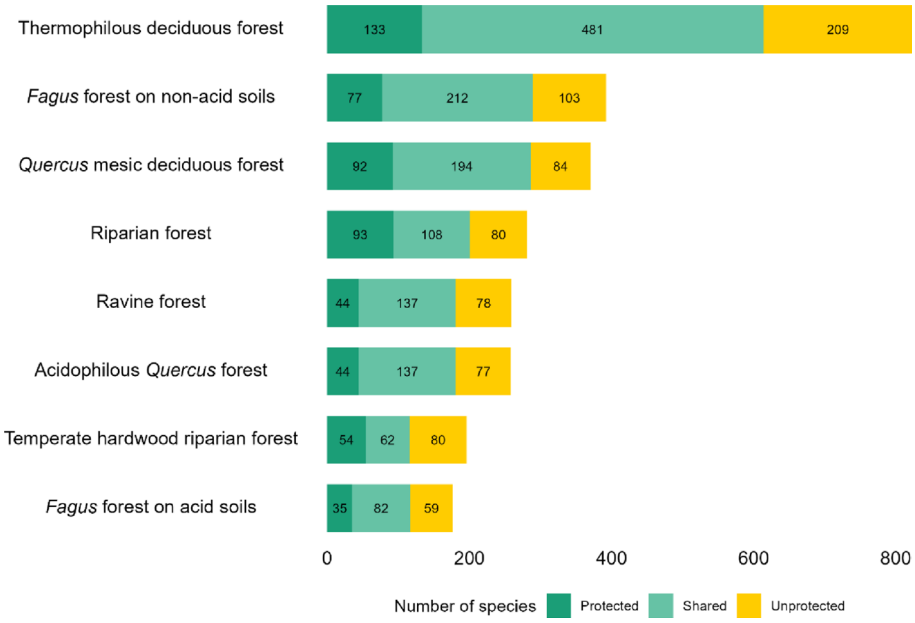

Fig. 4 Gamma diversity of understory plant species across the different habitat types, expressed as the absolute number of species. Bars are partitioned into species occurring exclusively inside protected areas (dark green), exclusively outside protected areas (yellow), and species shared between protected and unprotected areas (light green). The sum of exclusive and shared components represents the total gamma diversity within and outside protected areas, respectively. Numbers within bars indicate the observed number of species in each category

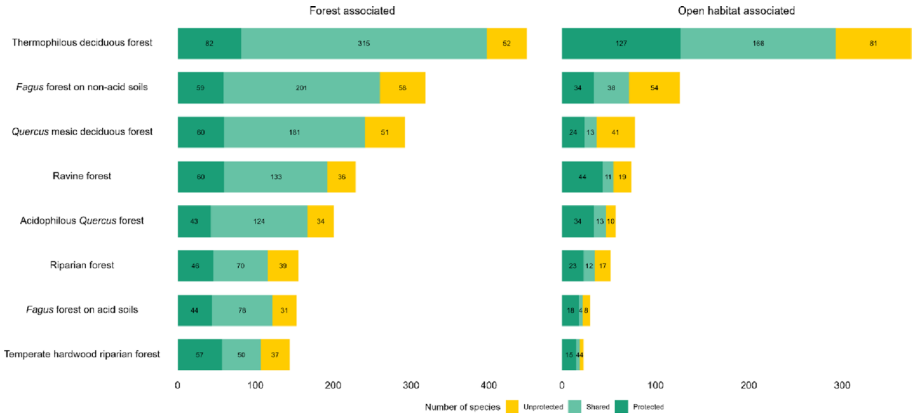

Fig. 5 Gamma diversity of understory plant species across the different habitat types, expressed as the absolute number of species and shown separately for forest- associated and open-habitat associated species. Bars are partitioned into species occurring exclusively inside protected areas (dark green), exclusively outside protected areas (yellow), and species shared between protected and unprotected areas (light green). The sum of exclusive and shared components represents total gamma diversity within and outside protected areas, respectively. Numbers within bars indicate the observed number of species in each category

Discussion

In contrast to many studies that have reported low alpha diversity (plot-level) of understory plant species in protected or otherwise unmanaged forests (Halpern and Spies 1995; Scheller and Mladenoff 2002; Boch et al. 2013; Kaufmann et al. 2017), or in forests that underwent natural successional dynamics (see e.g. Amici et al. 2013; Lelli et al. 2021), our results showed generally higher alpha diversity within protected areas, primarily driven by a greater abundance of forest-associated species. One possible explanation is the strategic selection of high-value sites for protection, combined with conservation measures within protected areas that promote the development and maintenance of intact, older and more natural forests (Hayes and Ostrom 2005; Koch 2005; Zannini et al. 2022). By reducing logging activities and human disturbance, protected areas can better preserve the complex structural and functional integrity of forests (Duguid and Ashton 2013; Anderson and Mammides 2020), which supports greater diversity of forest-associated plant species.

However, higher local species richness does not imply higher conservation value. Recent studies have reported limited or no significant difference in understory plant richness between strictly protected and managed forests in Europe (Leidinger et al. 2020; Elleason et al. 2021; Zhu et al. 2025), suggesting that the protection regime alone may not be the primary driver of local diversity patterns. Differences in historical land use, forest management practices or site selection process are also likely to have contributed to the observed patterns (Agnoletti et al. 2022). Therefore, our results should be interpreted as reflecting differences in species richness rather than broader biodiversity outcomes.

Our results further indicate that protected areas do not represent understory plant species diversity equally across habitat types. In fact, in acidophilous *Quercus* forests and riparian forests, alpha diversity was lower within protected areas than outside. Although the mechanisms underlying this pattern remain uncertain, it may reflect the cessation of traditional pastoral activities following rural depopulation, alongside long-term changes in forest management that may favour the expansion of open-habitat species (Malandra et al. 2019; Jiménez-Olivencia et al. 2021; Pallotta et al. 2022). In riparian forests, the linear structure of vegetation along watercourses likely promotes the persistence of open-habitats and disturbance-adapted species outside protected areas, as these regions are frequently shaped by periodic flooding and historical land-use practices (Broadmeadow and Nisbet 2004; Welsh et al. 2005; de Simone et al. 2025).

At the regional scale, gamma diversity, representing the overall number of understory plant species, was also generally higher within protected areas. These results may be linked to the type of forest management practices occurring outside protected areas, which could negatively affect plant gamma diversity (Kaufmann et al. 2017; Atrena et al. 2024). For example, Halpern and Spies (1995) observed higher plant species richness in old-growth forests compared to managed forests in North America. Similarly, other studies comparing managed and unmanaged forests have reported greater gamma diversity in unmanaged forests than in managed ones (Boch et al. 2013; Kaufmann et al. 2017).

In addition to overall species richness, we also considered endemic species, which represent a key component of biodiversity due to their restricted geographic distribution and higher conservation relevance (Orsenigo et al. 2021). Although the number of endemic species recorded was relatively low, their presence within protected areas supports the role of these areas in contributing to the conservation of species of higher conservation concern

(e.g., *Helleborus bocconei* or *Anemone apennina*). Thus, protected areas may also play a role in safeguarding geographically restricted components of the flora (de Lima et al. 2020).

When examining open-habitat and forest species separately, we found a higher number of exclusive species in the former group within than outside protected areas. The abundance of exclusive open-habitat species within protected areas may be driven by natural disturbances, such as treefall gaps in interaction with grazing, which likely contribute to higher diversity of open-habitat species by creating favourable microhabitats (van der Meer and Bongers 2001; Thom and Seidl 2016). These natural processes increase light availability, making suitable conditions for native grassland species to establish and thrive even in landscapes that are predominantly forested (Naaf and Wulf 2007; Kuuluvainen et al. 2021). Herbivore pressure may further contribute to these patterns. Changes in grazing regimes, including the decline of traditional livestock use and shifts toward wildlife-dominated browsing, are known to affect understory composition and the persistence of light-demanding species in European forests (Fløjgaard et al. 2018; Pringle et al. 2023). However, the presence of these species should be interpreted with caution. In forest ecosystems, open-habitat species may reflect a variety of ecological conditions and processes, including natural disturbance dynamics, edge effects, past and ongoing management activities, or variation in canopy structure and landscape context (Naaf and Wulf 2007; Bricca et al. 2023). Because we did not explicitly assess forest structure, disturbance regime, or canopy openness, the mechanisms underlying the occurrence of open-habitat species in protected areas remain uncertain. Therefore, while our results suggest that protected areas can host a broader spectrum of habitat-associated species, they should not be interpreted as evidence that the occurrence of open-habitat species necessarily reflects higher ecological integrity.

Notwithstanding the large collection of biodiversity data we used, our study does not come without limitations. First, selecting appropriate diversity metrics for conservation science depends heavily on the set of species that are analysed (Whittaker et al. 2005). In this study, we assessed the role of protected areas in representing understory plant diversity using multiple conservation metrics, including alpha and gamma diversity, which provide a more nuanced understanding of conservation needs. In addition, our gamma-diversity analyses allowed us to identify species occurring exclusively within protected or unprotected areas, thereby providing information on patterns of species uniqueness. However, we did not explicitly assess other dimensions of conservation value, such as species rarity, threat status, or phylogenetic distinctiveness. Future studies integrating these aspects could provide a more comprehensive evaluation of the conservation importance of protected areas for understory plant diversity. Furthermore, variations in sampling intensity and potential gaps in the floristic data, might affect the reliability of our results (Spyreas and Matthews 2006; Hughes et al. 2021). These shortfalls occur due to the presence of biases in sampling, when certain geographical regions and environmental conditions are overrepresented due to higher collection frequencies (Spyreas and Matthews 2006; Isaac and Pocock 2015; Večeřa et al. 2019). Yet, the use of matching at least alleviates this issue, by accounting for this very bias in the selection of plots being compared. Besides, our analysis does not assess the long-term effectiveness of protected areas in achieving conservation goals. While we observed higher understory plant diversity within protected areas, our data do not allow us to ascertain whether protection is effectively maintaining species or supporting their persistence over time. Future research should therefore integrate spatial conservation prioritization approaches with temporal biodiversity data (Kukkala and Moilanen 2013; Geldmann

et al. 2025). This will help to better understand the underlying ecological and management factors driving patterns of biodiversity in protected areas and develop more effective conservation strategies for both forest and open-habitat species in protected and unprotected areas (Hermoso et al. 2022).

Conclusion

This study suggests that protected areas in Italy are a cornerstone for biodiversity conservation, particularly for forest understory plant species. Our findings reveal that protected areas generally support higher alpha and gamma diversity compared to unprotected areas. Additionally, forest-associated species exhibited higher diversity within protected areas across all habitat types, reinforcing the role of these areas in safeguarding forest biodiversity. However, our results also highlight important exceptions. The lower diversity of open-habitat associated species in some protected habitats suggests that land-use changes can negatively impact species that thrive in managed or semi-natural landscapes. Overall, our study emphasizes the vital role of protected areas in representing plant biodiversity while highlighting the need for more nuanced conservation approaches to ensure the protection of diverse plant communities across different habitat types.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-026-03425-6.

Author contributions L.R. and M.D.M. designed the study, conducted the investigation, and performed the formal analysis and data visualization. L.R., J.G., N.A., F.M.S., A.C., and M.D.M. contributed to the conceptualization and methodology. N.A. curated the data. L.R., J.G., N.A., F.M.S., A.C., G.B., and M.D.M. wrote the original draftAll authors contributed to the review and editing of the manuscript. M.D.M. and J.G. supervised the work. All authors reviewed and approved the final manuscript.

Funding Open access funding provided by Università degli Studi dell'Aquila within the CRUI-CARE Agreement.

Data availability The vegetation plot data used to derive forest- and open-habitat species associations originated from the same databases reported in Alessi et al. (2023): VPD-Sapienza University of Rome, AMS-VegBank, HabItAlp, and CircumMed Forest database. Access to the original datasets is subject to the policies of the respective databases.

Declarations

Competing interests The authors declare no competing interests.

References

Agnoletti M, Piras F, Venturi M, Santoro A (2022) Cultural values and forest dynamics: The Italian forests in the last 150 years. For Ecol Manag 503:119655

Alessi N, Bonari G, Zannini P et al (2023) Probabilistic and preferential sampling approaches offer integrated perspectives of Italian forest diversity. J Veg Sci 34:e13175

Amici V, Santi E, Filibeck G et al (2013) Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. J Biogeogr 40:2335–2347

Amici V, Rocchini D, Filibeck G et al (2015) Landscape structure effects on forest plant diversity at local scale: Exploring the role of spatial extent. Ecol Complex 21:44–52

Anderson E, Mammides C (2020) The role of protected areas in mitigating human impact in the world's last wilderness areas. Ambio 49:434–441

Angelstam P, Manton M, Green M et al (2020) Sweden does not meet agreed national and international forest biodiversity targets: A call for adaptive landscape planning. Landsc Urban Plann 202:103838

Angelstam P, Albulescu A-C, Andrianambinina ODF et al (2021) Frontiers of protected areas versus forest exploitation: Assessing habitat network functionality in 16 case study regions globally. Ambio 50:2286–2310

Arriagada RA, Ferraro PJ, Sills EO et al (2012) Do payments for environmental services affect forest cover? A farm-level evaluation from Costa Rica. Land Econ 88:382–399

Atrena A, Banelytė GG, Bruun HH et al (2024) Plant communities and their relations to habitat and microhabitat features along a management gradient in beech forests in Denmark. For Ecol Manag 569:122162

Bartolucci F, Peruzzi L, Galasso G et al (2018) An updated checklist of the vascular flora native to Italy. Plant Biosystems 152:179–303

Boch S, Prati D, Müller J et al (2013) High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic Appl Ecol 14:496–505

Bricca A, Bonari G, Padulles Cubino J, Cutini M (2023) Effect of forest structure and management on the functional diversity and composition of understorey plant communities. Appl Veg Sci 26:e12710

Bricca A, Zerbe S, Fellin H, Alessi N, Maccherini S, Bonari G (2025) Passive rewilding of old-established plantations into native forests. J Veg Sci 36:e70085

Broadmeadow S, Nisbet TR (2004) The effects of riparian forest management on the freshwater environment: a literature review of best management practice. Hydrol Earth Syst Sci 8:286–305

Brockerhoff EG, Barbaro L, Castagneyrol B et al (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers Conserv 26:3005–3035

Bruner AG, Gullison RE, Rice RE, Da Fonseca GA (2001) Effectiveness of parks in protecting tropical biodiversity. Science 291:125–128

Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. For Ecol Manag 291:458–479

Butchart SH, Scharlemann JP, Evans MI et al (2012) Protecting important sites for biodiversity contributes to meeting global conservation targets. PLoS ONE 7:e32529

Butchart SH, Clarke M, Smith RJ et al (2015) Shortfalls and solutions for meeting national and global conservation area targets. Conserv Lett 8:329–337

Cazalis V, Princé K, Mihoub J-B et al (2020) Effectiveness of protected areas in conserving tropical forest birds. Nat Commun 11:4461

Cazzolla Gatti R, Zannini P, Piovesan G et al (2023) Analysing the distribution of strictly protected areas toward the EU2030 target. Biodivers Conserv 32:3157–3174

Cervera T, Pino J, Marull J et al (2019) Understanding the long-term dynamics of forest transition: From deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). Land use policy 80:318–331

Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67

Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Trans Royal Soc B: Biol Sci 360:443–455

Chelli S, Bricca A, Tsakalos JL et al (2024) Multiple drivers of functional diversity in temperate forest understories: Climate, soil, and forest structure effects. Sci Total Environ 916:170258

Chen H, Zhang T, Costanza R, Kubiszewski I (2023) Review of the approaches for assessing protected areas' effectiveness. Environ Impact Assess Rev 98:106929

Chiarucci A, Bacaro G, Rocchini D, Fattorini L (2008) Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. Community Ecol 9:121–123

Chiarucci A, Bacaro G, Scheiner SM (2011) Old and new challenges in using species diversity for assessing biodiversity. Philosophical Trans Royal Soc B: Biol Sci 366:2426–2437
Chiarucci A, Nascimbene J, Campetella G et al (2019) Exploring patterns of beta-diversity to test the consistency of biogeographical boundaries: A case study across forest plant communities of Italy. Ecol Evol 9:11716–11723
Chytrý M, Otýpková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. J Veg Sci 14:563–570
Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. J Veg Sci 13:79–90
Chytrý M, Hennekens SM, Jiménez-Alfaro B et al (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Appl Veg Sci 19:173–180
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
Coad L, Watson JE, Geldmann J et al (2019) Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. Front Ecol Environ 17:259–264
R Core Team (2023) A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. R Foundation for Statistical Computing; 2023
Corlett RT (2020) Safeguarding our future by protecting biodiversity. Plant Divers 42:221–228
Cuenca P, Arriagada R, Echeverría C (2016) How much deforestation do protected areas avoid in tropical Andean landscapes? Environ Sci Policy 56:56–66
De Cáceres M, Font X, Oliva F (2010) The management of vegetation classifications with fuzzy clustering. J Veg Sci 21:1138–1151
de Lima RAF, Oliveira AA, Colletta GD et al (2020) Defining endemism levels for biodiversity conservation: tree species in the Atlantic Forest hotspot. Biol Conserv 252:108825
de Simone L, Fanfarillo E, Fiaschi T et al (2025) Riparian structural vegetation types exhibit differential responses to local community drivers. Hydrobiologia 852:2971–2991
Delso Á, Fajardo J, Muñoz J (2021) Protected area networks do not represent unseen biodiversity. Sci Rep 11:12275
Douda J, Boublík K, Doudová J, Kyncl M (2017) Traditional forest management practices stop forest succession and bring back rare plant species. J Appl Ecol 54:761–771
Duguid MC, Ashton MS (2013) A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. For Ecol Manag 303:81–90
Elbakidze M, Angelstam P, Sobolev N et al (2013) Protected area as an indicator of ecological sustainability? A century of development in Europe's boreal forest. Ambio 42:201–214
Elleason M, Guan Z, Deng Y et al (2021) Strictly protected areas are not necessarily more effective than areas in which multiple human uses are permitted. Ambio 50:1058–1073
European Commission (2020) EU Biodiversity Strategy for 2030
European Union (2021) Copernicus land monitoring service. European Environment Agency (EEA)
Fløjgaard C, Bruun HH, Hansen MD, Heilmann-Clausen J, Svenning JC, Ejrnæs R (2018) Are ungulates in forests concerns or key species for conservation and biodiversity? Reply to Boulanger. Glob Change Biol 24:869–871. https://doi.org/10.1111/gcb.13899
Gauthier S, Kuuluvainen T, Macdonald SE et al (2023) Ecosystem management of the boreal forest in the era of global change.In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (eds) Boreal forests in the face of climate change: Sustainable management. Springer, pp 3–49
Geldmann J (2023) Safeguarding biodiversity requires understanding how to manage protected areas cost effectively. One Earth 6:73–76
Geldmann J, Coad L, Barnes MD et al (2018) A global analysis of management capacity and ecological outcomes in terrestrial protected areas. Conserv Lett 11:e12434
Geldmann J, Manica A, Burgess ND et al (2019) A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. Proceedings of the National Academy of Sciences 116:23209–23215
Geldmann J, Jones JP, Wauchope H, Ferraro PJ (2025) Causal claims, causal assumptions and protected area impact. Nature 638:E40–E41
Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858
Gloor R, Svitok M, Mikoláš M et al (2024) Sustaining forest biodiversity: Exploring the effect of long-term natural disturbance dynamics on contemporary lichen communities in primary forest ecosystems. Forest Ecosystems 100214
Götmark F (2013) Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications. For Ecol Manag 306:292–307

Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815
Greifer N, Greifer MN (2020) Package 'cobalt.' R Package Version 4
Halpern CB, Spies TA (1995) Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol Appl 5:913–934
Hayes T, Ostrom E (2005) Conserving the world's forests: Are protected areas the only way. Ind L Rev 38:595
Hermoso V, Carvalho SB, Giakoumi S et al (2022) The EU Biodiversity Strategy for 2030: Opportunities and challenges on the path towards biodiversity recovery. Environ Sci Policy 127:263–271
Heywood VH (2019) Conserving plants within and beyond protected areas–still problematic and future uncertain. Plant Divers 41:36–49
Hijmans RJ, Bivand R, Forner K et al (2022) Package 'terra.' Maintainer. Vienna, Austria
Ho D, Imai K, King G et al (2018) Package 'MatchIt'. Version [Google Scholar] 427:428
Hoffmann S (2022) Challenges and opportunities of area-based conservation in reaching biodiversity and sustainability goals. Biodivers Conserv 31:325–352
Hsieh TC, Ma Kh, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods Ecol Evol 7:1451–1456
Hughes AC, Orr MC, Ma K et al (2021) Sampling biases shape our view of the natural world. Ecography 44:1259–1269
Isaac NJ, Pocock MJ (2015) Bias and information in biological records. Biol J Linn Soc 115:522–531
Jantke K, Kuempel CD, McGowan J et al (2019) Metrics for evaluating representation target achievement in protected area networks. Divers Distrib 25:170–175
Jiménez-Olivencia Y, Ibáñez-Jiménez Á, Porcel-Rodríguez L, Zimmerer K (2021) Land use change dynamics in Euro-mediterranean mountain regions: Driving forces and consequences for the landscape. Land Use Policy 109:105721
Joly D, Bois B, Zakšek K (2012) Rank-ordering of topographic variables correlated with temperature. Atmospheric Clim Sci 2:139–147
Joppa LN, Pfaff A (2009) High and far: biases in the location of protected areas. PLoS ONE 4:e8273
Karger DN, Conrad O, Böhner J et al (2017) Climatologies at high resolution for the earth's land surface areas. Sci data 4:1–20
Kaufmann S, Hauck M, Leuschner C (2017) Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. For Ecol Manag 400:58–67
Kleinschroth F, Healey JR (2017) Impacts of logging roads on tropical forests. Biotropica 49:620–635
Koch G (2005) Protected areas in Europe and their importance for conservation. In: Geburek T, Turok J (eds) Conservation and management of forest ge netic resources in Europe Eds. Arbora, Zvolen, pp 513–534
Koellner T, Hersperger AM, Wohlgemuth T (2004) Rarefaction method for assessing plant species diversity on a regional scale. Ecography 27:532–544
Kukkala AS, Moilanen A (2013) Core concepts of spatial prioritisation in systematic conservation planning. Biol Rev 88:443–464
Kuuluvainen T, Angelstam P, Frelich L et al (2021) Natural disturbance-based forest management: moving beyond retention and continuous-cover forestry. Front Forests Global Change 4:629020
Landuyt D, De Lombaerde E, Perring MP et al (2019) The functional role of temperate forest understorey vegetation in a changing world. Glob Change Biol 25:3625–3641
Leidinger J, Weisser WW, Kienlein S et al (2020) Formerly managed forest reserves complement integrative management for biodiversity conservation in temperate European forests. Biol Conserv 242:108437
Lelli C, Nascimbene J, Alberti D et al (2021) Long-term changes in Italian mountain forests detected by resurvey of historical vegetation data. J Veg Sci 32:e12939
Lenth R, Singmann H, Love J et al (2019) Package 'emmeans'. R package version 1.3.2
Lindenmayer DB, Franklin JF (2013) Conserving forest biodiversity: a comprehensive multiscaled approach. Island
Malandra F, Vitali A, Urbinati C et al (2019) Patterns and drivers of forest landscape change in the Apennines range, Italy. Reg Envriron Chang 19:1973–1985
Márialigeti S, Tinya F, Bidló A, Ódor P (2016) Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary. Plant Ecol 217:549–563
Marignani M, Chiarucci A, Sadori L, Mercuri AM (2017) Natural and human impact in Mediterranean landscapes: An intriguing puzzle or only a question of time? Plant Biosystems-An International Journal Dealing with all Aspects. Plant Biology 151:900–905
McIntosh EJ, Pressey RL, Lloyd S et al (2017) The impact of systematic conservation planning. Annu Rev Environ Resour 42:677–697
Naaf T, Wulf M (2007) Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. For Ecol Manag 244:141–149

Oettel J, Lapin K (2021) Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecol Ind 122:107275
Orsenigo S, Fenu G, Gargano D et al (2021) Red list of threatened vascular plants in Italy. Plant Biosystems-An Int J Dealing all Aspects Plant Biology 155:310–335
Pallotta E, Boccia L, Rossi CM, Ripa MN (2022) Forest dynamic in the Italian Apennines. Appl Sci 12:2474
Pebesma EJ (2018) Simple features for R: standardized support for spatial vector data. R J 10:439
Petermann JS, Buzhdygan OY (2021) Grassland biodiversity. Curr Biol 31:R1195–R1201
Pignatti S, Guarino R, La Rosa M (2017–2019) Flora d'Italia, Vol 1–4, 2nd edn. Edagricole–New Business Media, Milano
Powlen KA, Gavin MC, Jones KW (2021) Management effectiveness positively influences forest conservation outcomes in protected areas. Biol Conserv 260:109192
Pringle RM, Abraham JO, Anderson TM, Coverdale TC, Davies AB, Dutton CL et al (2023) Impacts of large herbivores on terrestrial ecosystems. Curr Biol 33:R584–R610
Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press
Ribas LG, Pressey RL, Bini LM (2021) Estimating counterfactuals for evaluation of ecological and conservation impact: an introduction to matching methods. Biol Rev 96:1186–1204
Rodrigues AS, Cazalis V (2020) The multifaceted challenge of evaluating protected area effectiveness. Nat Commun 11:5147
Schall P, Gossner MM, Heinrichs S et al (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. J Appl Ecol 55:267–278
Scheller RM, Mladenoff DJ (2002) Understory species patterns and diversity in old-growth and managed northern hardwood forests. Ecol Appl 12:1329–1343
Schleicher J, Eklund J, Barnes D M, et al (2020) Statistical matching for conservation science. Conserv Biol 34:538–549
Simonson WD, Allen HD, Coomes DA (2014) Overstorey and topographic effects on understories: Evidence for linkage from cork oak (Quercus suber) forests in southern Spain. For Ecol Manag 328:35–44
Spicer ME, Radhamoni HVN, Duguid MC et al (2022) Herbaceous plant diversity in forest ecosystems: patterns, mechanisms, and threats. Plant Ecol 223:117–129
Spyreas G, Matthews JW (2006) Floristic conservation value, nested understory floras, and the development of second-growth forest. Ecol Appl 16:1351–1366
Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol Rev 91:760–781
Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. J Veg Sci 17:809–818.
UNEP-WCMC and IUCN (2023) Protected planet: the world database on protected areas (WDPA). UNEP-WCMC and IUCN, Cambridge, UK
van der Meer PJ, Bongers F (2001) Tree-falls and canopy gaps: patterns of natural disturbance. Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest 243–250
Večeřa M, Divíšek J, Lenoir J et al (2019) Alpha diversity of vascular plants in European forests. J Biogeogr 46:1919–1935
Velazco SJE, Villalobos F, Galvão F, De Marco Junior P (2019) A dark scenario for Cerrado plant species: Effects of future climate, land use and protected areas ineffectiveness. Divers Distrib 25:660–673
Viña A, Liu J (2017) Hidden roles of protected areas in the conservation of biodiversity and ecosystem services. Ecosphere 8:e01864
Watson JE, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. Nature 515:67–73
Welsh J, Hodgson GR, Karraker NE (2005) Influences of the vegetation mosaic on riparian and stream environments in a mixed forest-grassland landscape in Mediterranean northwestern California. Ecography 28:537–551
Whittaker RJ, Araújo MB, Jepson P et al (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11:3–23
Wickham H, Averick M, Bryan J et al (2019) Welcome to the Tidyverse. J open source Softw 4:1686
Yang H, Viña A, Winkler JA et al (2019) Effectiveness of China's protected areas in reducing deforestation. Environ Sci Pollut Res 26:18651–18661
Zannini P, Frascaroli F, Nascimbene J et al (2022) Investigating sacred natural sites and protected areas for forest area changes in Italy. Conserv Sci Pract 4:e12695
Zhu Z, Chelli S, Tsakalos JL et al (2025) How effective are different protection strategies in promoting the plant diversity of temperate forests in national parks? For Ecol Manag 584:122602

Authors and Affiliations

Lorenzo Ricci[1,2] · Jonas Geldmann[3] · Nicola Alessi[4] · Anna Rita Frattaroli[1] · Jacob Heilmann-Clausen[3] · Francesco Maria Sabatini[2] · Alessandro Chiarucci[2] · Fabio Attorre[5] · Gianmaria Bonari[6,7] · Michele Di Musciano[1,2]

✉ Michele Di Musciano
michele.dimusciano@univaq.it

[1] Department of Life, Health & Environmental Science, University of L'Aquila, L'Aquila, Italy

[2] BIOME Lab, BiGeA Department, Alma Mater Studiorum - University of Bologna, Bologna, Italy

[3] Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark

[4] Italian Institute for Environmental Protection and Research, Rome, Italy

[5] Department of Environmental Biology, Sapienza University of Rome, Rome, Italy

[6] Department of Life Sciences, University of Siena, Siena, Italy

[7] NBFC, National Biodiversity Future Center, Palermo, Italy