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Taxonomic and functional variation of carabid beetles (Coleoptera: Carabidae) diversity in pioneer black pine and secondary broad-leaved Karst forests

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ABSTRACT

Carabid beetles are widely used as bioindicators because they respond rapidly to changes in near-ground microclimate, litter and understory structure, and habitat continuity. In the Classical Karst of the North Adriatic region, forest management is shaped by two concurrent trajectories: the aging of *Pinus nigra* stands established during late 19th-century afforestation and the recovery of secondary thermophilous broad-leaved forests. Pine plantations, although now old and prone to biotic and abiotic disturbances, have played an important role in shaping present forest ecosystems, and their future is currently debated. To evaluate the effectiveness of pioneer pine plantations in reconstructing forest conditions, we assessed differences in carabid species composition and functional structure between the two forest types using long-term pitfall-trap data collected across multiple sites and years. We quantified taxonomic diversity through richness-based comparisons, rarefaction and additive partitioning, and examined compositional turnover using β-diversity contribution metrics and ordination with permutation-based testing. Functional structure was evaluated using distance-based functional diversity indices, functional rarefaction based on expected Rao's Q and decomposition of functional α-β-γ components, and a ternary framework separating dominance, functional diversity and redundancy. Finally, we used indicator-oriented analyses (species-level and trait-informed) to identify taxa associated with each forest type. Overall, broad-leaved and pine stands showed limited divergence in mean richness and in conventional functional indices, whereas clearer differences emerged in turnover, site uniqueness and diagnostic species subsets. Functional rarefaction indicated that expected functional diversity may differ even when aggregate indices appear similar. Overall, results support the contribution of black pine stands to the maintenance of forest ground-dwelling biodiversity and functional structure in karst forests and suggest that conversion strategies should prioritise continuity of microhabitat conditions and microclimatic buffering rather than assuming that replacement by broad-leaved stands will automatically increase biodiversity.

1. Introduction

Carabid beetles (Coleoptera: Carabidae) are diverse and abundant, have relatively well known ecologies and systematics, and are easily collectable using pitfall traps. They are sensitive to environmental factors and respond rapidly to habitat changes (Amori et al., 2021; Osawa et al., 2005; Shibuya et al., 2008), making them particularly suitable for detecting stand-level changes in forest structure, microclimate, and resource availability that follow both natural succession and management interventions. A substantial fraction of ground-dwelling forest-associated taxa is characterized by limited dispersal and strong habitat specialization; this is often (though not exclusively) linked to wing

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reduction or wing polymorphism, which increases their sensitivity to habitat alteration and fragmentation (Duchesne et al., 1999; Niemelä, 1997; Yu et al., 2008, 2006). Thus, they are used as bioindicators in investigations into the biodiversity in forests managed in different ways in Europe (Finch, 2005; Humphrey et al., 1999; Karen et al., 2008; Koivula, 2002; Lange et al., 2014; Lövei et al., 2006; Magura, 2002; Magura et al., 2001; Negro et al., 2014), Africa (Rainio and Niemelä, 2006), Central and North America (Klimaszewski et al., 2005; Ulyshen et al., 2006) and Japan (Fujita et al., 2008; Kaizuka et al., 2020). Many studies on carabid assemblages in forests have covered various topics, such as age of forests and effect of replanting after logging and deforestation (Rogerson et al., 2025; Skłodowski, 2021; Wu et al., 2020), effects of fragmentation on assemblages (Fujita et al., 2008; Marrec et al., 2021), effect of edges between forest and clear-cut grassland (Heliölä et al., 2001; Magura and Lövei, 2024), impacts of invasive alien species in forested habitats (Kotze et al., 2011; Uboni et al., 2019) and comparison of conifer and broad-leaved forests (Fuller et al., 2008; Kriegel et al., 2021; Wehnert et al., 2021). The differences between carabid assemblages in various landscapes are also studied in ecotones between natural forests and mature pine plantations (Yu et al., 2010), urban landscapes (da Silva et al., 2008; Zara et al., 2021) and farmland (Purtauf et al., 2005).

From a management perspective, comparisons between coniferous and broad-leaved stands are especially relevant because tree species identity and canopy architecture jointly control key drivers of carabid assemblages, such as litter quality and depth, soil moisture, thermal buffering, understory development, and the spatial continuity of suitable microhabitats (Kriegel et al., 2021). In European forest landscapes, planted conifer forests and mixed stands can therefore host assemblages that differ markedly from those of native broad-leaved forests, but the direction and magnitude of change depend on stand age, structural heterogeneity, and the broader landscape context (including proximity to source populations) (Kriegel et al., 2021). This point is not trivial in conservation terms: planted stands may function either as biodiversity-poor "filters" dominated by generalists, or as habitat surrogates that maintain subsets of forest fauna under certain conditions, and these alternatives imply very different outcomes when plantations are converted or removed. Carabids, already widely used as indicators of sustainable forest management, are an appropriate model group for evaluating such trade-offs because they integrate microhabitat conditions and landscape constraints, and they often respond rapidly to changes in forest structure (Grodsky et al., 2019). Moreover, they are extremely sensitive to soil properties and microclimate and respond also to fine-tuned changes in vegetation composition (Thiele, 1973).

The North Adriatic Karst offers a particularly instructive context in which to address these issues, because its current forest mosaic is tightly linked to historical land use, afforestation, and ongoing management debates (Pafumi et al., 2023; Poldini, 1989; Uboni et al., 2019). Large areas of *Pinus nigra* forests in the Karst region were established through afforestation starting in the mid–late 19th century as a restoration response to severe land degradation, and many of these pine stands are now aging and increasingly prone to disturbances, pests, and drought stress, which motivates active discussion about conversion to broad-leaved forests and/or restoration of open habitats where appropriate (Candel-Pérez et al., 2022; Diaci et al., 2019; Trotta et al., 2024). At the same time, broad-leaved forests (notably thermophilous oak-dominated communities) are recovering in many sectors as a consequence of land-use abandonment and successional dynamics, yet their future trajectories will be strongly conditioned by climatic warming and the increasing frequency and intensity of drought and heat events (Čarni et al., 2021; Sutanto et al., 2025). In this setting, decisions on pine stand maintenance, gradual conversion, thinning, gap creation, or removal are not merely silvicultural choices: they are expected to reshape forest microclimates and habitat continuity, with potential consequences for both taxonomic and functional dimensions of biodiversity (Santi et al., 2024).

Research on the impacts of environmental change on carabid diversity has traditionally adopted a taxonomic approach by focusing on the composition and diversity of particular groups of species in a community. However, taxonomic turnover alone may be difficult to interpret mechanistically, because different species can perform similar ecological roles and respond similarly to the same environmental filters. For this reason, functional-trait approaches have become increasingly used to complement taxonomic analyses by explicitly considering the morphological, anatomical, biochemical, physiological, or phenological traits that influence a species' ability to acquire resources, disperse, reproduce, and persist in the environment (Kleyer et al., 2012; Violle et al., 2007). Functional-trait analysis offers several advantages over taxonomic composition analysis for both conceptual and management purposes (Kleyer et al., 2012; McGill et al., 2006; Pavanetto et al., 2025): it facilitates an understanding of the mechanisms that underlie both community responses to environmental change and ecosystem functioning. In particular, trait-based approaches allow one to distinguish between compositional turnover that is largely "taxonomic" (species replacement with limited consequences for functional strategies) and turnover that entails substantive shifts in resource use, dispersal potential, phenology, or trophic roles (Pavanetto et al., 2025).

In this study, we aimed to assess patterns of carabid beetle species composition and associated functional diversity in North Adriatic Karst forest types with the purpose to evaluate the contribution of pine afforestation in the restoration of a karstic forest ecosystem. Specifically, we aimed to: (1) assess differences in patterns of species richness (α diversity) and composition (β diversity) in deciduous and coniferous forests; (2) determine the functional variation of these assemblages in these forest types; and (3) compare taxonomic and functional diversities to understand the main responses of carabids to different forest types. By embedding these comparisons in a landscape where pine plantations are historically contingent and currently debated, while broad-leaved stands are expanding but simultaneously facing climate-driven constraints, the study also provides an empirical basis to anticipate biodiversity consequences of alternative management trajectories (retention vs. conversion vs. removal) in the Karst forest mosaic. This information will contribute to clarify whether carabid assemblages signal potential gains or losses in functional strategies under ongoing forest transitions, and how these signals may interact with the increasing relevance of climatic stress in sub-Mediterranean forests.

2. Materials and methods

2.1. Study area

The study was carried out in the Italian sector of the Classical Karst, in north-eastern Italy (provinces of Trieste and Gorizia), a limestone plateau spanning from sea level up to ca. 600 m a.s.l. and characterized by strong environmental heterogeneity over short distances. This portion of the Karst is embedded in the wider transboundary karst system between Italy and Slovenia above the Gulf of Trieste and includes a fine-grained mosaic of natural and semi-natural habitats, where forests, grasslands, and shrublands form a highly interdigitated landscape. In the same region, several areas fall within the Natura 2000 network, including the Special Area of Conservation "Carso Triestino e Goriziano" (IT3340006) and the Special Protection Area "Aree carsiche della Venezia Giulia" (IT3341002) (Fig. 1), underscoring both the conservation relevance of the system and the practical need to understand biodiversity responses to management and ongoing environmental change (Pafumi et al., 2023). From a biogeographic and climatic standpoint, the Classical Karst represents a transitional zone between Mediterranean and continental influences (often referred to as sub-Mediterranean), producing pronounced gradients in moisture availability and thermal regime across topographic positions and exposures. For the Italian Karst sector, mean annual temperature has been reported around 12.5 °C, with average annual precipitation near 1200 mm, although local

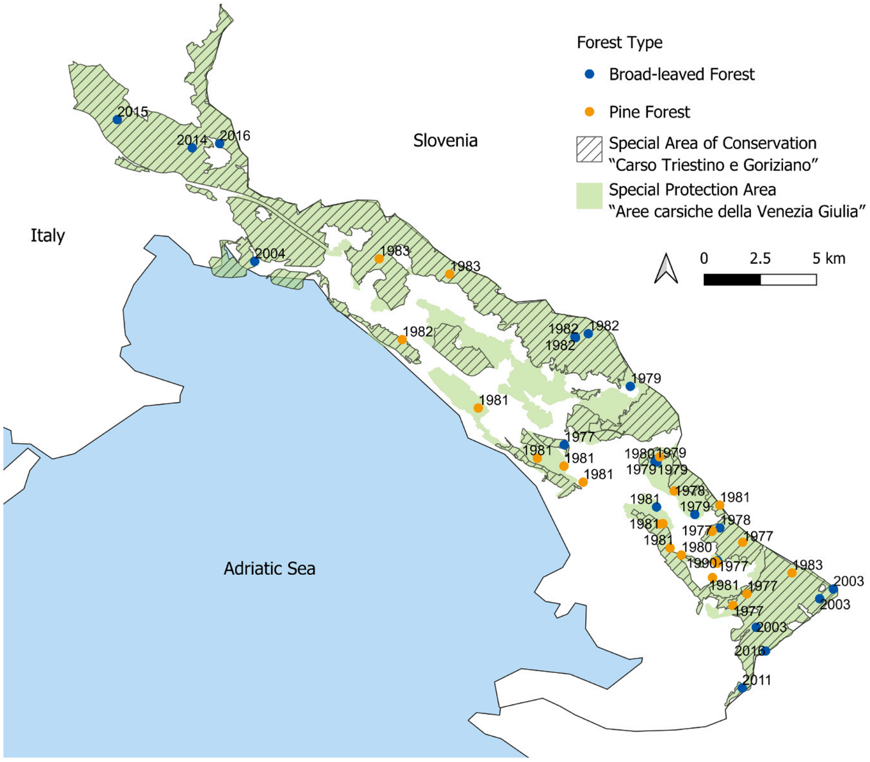

Fig. 1. Location of sampling sites in the Karst area of north-eastern Italy (Friuli Venezia Giulia region). Points indicate carabid beetle sampling plots, classified by forest type (blue = broad-leaved forest; orange = pine forest). Numbers next to points denote the year of sampling. The hatched polygon represents the Special Area of Conservation (SAC) "Carso Triestino e Goriziano", and the light-green polygon the Special Protection Area (SPA) "Aree carsiche della Venezia Giulia".

variability is substantial and tightly coupled with elevation and aspect. Geologically, the plateau is dominated by karstified Mesozoic limestones and typical shallow, well-drained soils; in the broader Kras/Karst area immediately adjacent to the Italian sector, rendzinas and cambisols are commonly reported as prevailing soil groups, consistent with the hydrologically "leaky" nature of karst terrains and the strong coupling between substrate, water balance, and vegetation structure (Pafumi et al., 2023; Uboni et al., 2019; Zara et al., 2021). The vegetation matrix is dominated by three major physiognomic components that are particularly relevant for ground-dwelling arthropods: (i) semi-natural dry grasslands, (ii) thermophilous broad-leaved woodlands (notably downy oak, *Quercus pubescens*, often with hop hornbeam *Ostrya carpinifolia* and flowering ash *Fraxinus ornus* in the regional context), and (iii) Austrian black pine (*Pinus nigra* subsp. *nigra*) plantations (Poldini, 2009, 1989). Karst grasslands are among the most species-rich herbaceous habitats in the region and are historically linked to long-term grazing and traditional land use. However, these grasslands are currently undergoing widespread shrub encroachment and woodland expansion following land-use abandonment. In parallel, secondary broad-leaved woodland has expanded and now represents a major land-cover component across many parts of the Karst landscape, reflecting successional trajectories that remain spatially heterogeneous (Pafumi et al., 2023). Black pine is not native to the Karst but it naturally occurs in the nearby mountain regions of Italy, Slovenia and Austria, as a pioneer, stress-tolerant species on poor, shallow rocky calcareous soils: *Pinus nigra* stands introduced through afforestation programs starting in the mid-19th century, initially aimed at stabilizing severely degraded landscapes and restoring tree cover. These plantations are typically structurally simpler and floristically less diverse than native broad-leaved forest types, and in several areas *Pinus nigra* has also expanded beyond planted cores through spontaneous spread (Trotta et al., 2024). Silvicultural debates triggered by plantation aging, changing disturbance regimes, and regeneration dynamics motivate alternative strategies ranging from maintenance with thinning to gradual conversion towards mixed or broad-leaved stands via gap-based approaches and assisted regeneration. In the nearby Slovenian Karst, for example, gradual conversion of *P. nigra* plantations through intermediate canopy gaps has been explicitly framed as a silvicultural pathway to achieve more stable future stands under sub-Mediterranean constraints, highlighting the broader relevance of plantation-to-broad-leaved transitions for this biogeographic context (Diaci et al., 2019).

2.2. *Carabids survey and measured functional traits*

The analyses are based on a set of independent forest stands treated as "sites" for statistical purposes. Overall, the dataset includes 46 sites, split evenly between pine forests (n = 23) and broad-leaved forests (n = 23). Sampling data were collected in different periods, pine sites are represented in surveys spanning 1977–1990, while broad-leaved sites span 1977–2016 (Fig. 1). Because the dataset integrates surveys conducted across multiple years and decades, the study design should be interpreted as a multi-temporal compilation of comparable site-level assemblage samples within the same region and forest macro-types, rather than as a single synchronized sampling campaign.

Carabid beetles were sampled using pitfall trapping, following the standard approach widely adopted in regional carabid monitoring and forest ecology studies (see for instance Brandmayr et al., 2005; Uboni et al., 2019). Each pitfall trap (plastic cups approximately 9 cm in diameter and ~11 cm deep) was randomly placed within forest patches (coniferous or broad-leaved) and partially filled with a preservative plus attractant solution based on wine vinegar saturated with sodium chloride. Trap contents were collected every three weeks, usually for an entire season (March-November), and specimens preserved in ethanol for identification. In the present dataset, the number of traps deployed per site ranged from 2 to 6 (typically 3), reflecting differences among survey years and/or site-specific logistical constraints; only two single sites were exceptions, with 1 and 8 traps, respectively. The abundance was standardised using an "activity density" metric, i.e., captures expressed as individuals per trap referred to a standardised trapping period, usually corresponding to the entire activity season of the beetles (March-November), expressed as individuals·trap^{-1} ·10 days^{-1} . The annual activity density (year sample) standardisation is necessary in historical and multi-source datasets to ensure that differences in trap number and exposure time do not propagate as artefacts in comparisons among sites and is used at international level (Kotze et al., 2011). All captured individuals were identified to species level using standard taxonomic keys and specialist expertise consistent with the regional Carabidae tradition (Kotze et al., 2011), and species nomenclature was harmonised across survey years to produce a single, internally consistent community matrix. The resulting assemblage dataset is structured as site-by-species activity-density (hereafter standardised abundance) values, and each site is attributed to one of the two forest macro-types (pine vs broad-leaved) used in the comparative analyses.

Functional trait information was compiled for all recorded species from literature (Brandmayr et al., 2005; Brandmayr and Colombetta, 2025) to allow functional diversity analyses in parallel with taxonomic analyses. Trait selection was constrained to a small set of ecologically interpretable traits that capture key axes of carabid responses to forest structure and microhabitat conditions, and that are commonly used in functional ecology applications of ground beetles (Brandmayr and Colombetta, 2025; Gobbi et al., 2022; Kotze et al., 2011). Specifically, we used four traits: (1) wing morphology (as a measure of dispersal power), (2) adult diet (trophic strategy), (3) larval development/phenology (reproduction rhythm), and (4) mean body length (proxy for body size and microhabitat use). This trait set is consistent with recent functional trait applications in ground beetle ecology and available in a recent database on ground beetles of the Triestine Karst (Brandmayr and Colombetta, 2025; Gobbi et al., 2022). In addition to these four traits, we assigned each species to a chorological category (hereafter ‘chorology’) as a biogeographic/ecological descriptor of species distribution. Chorology was used exclusively for descriptive purposes (i.e., to summarise the biogeographic structure of the assemblages and to support the trait-composition figure) and was not included in any functional distance matrix or in the computation of functional diversity indices.

Wing morphology was classified into discrete categories reflecting hind-wing development, following standard definitions: brachypterous (reduced wings; functionally flightless), macropterous (fully winged; potentially volant), and dimorphic (polymorphic wing development within species). These categories correspond to the dispersal axis and were treated as nominal trait levels (Gobbi et al., 2022). Adult diet was encoded using the trophic categories reported in the trait matrix and subsequently interpretable within the broader functional distinction between predatory (zoophagous/polyphagous predators) and non-strictly predatory strategies (e.g., omnivory and granivory), which is the operational framing commonly used in trait-based analyses of carabids (Brandmayr et al., 2005; Brandmayr and Colombetta, 2025; Gobbi et al., 2022). Subcategories of predation (e.g., specialist predation) and mixed strategies were also identified, and the information was used as the basis for any necessary aggregation steps in functional distance calculations. Larval development (phenology/reproductive rhythm) was also encoded categorically. In line with recent trait-based work, this trait captures whether larval development occurs predominantly in particular seasons (e.g., spring, summer, autumn, winter) and whether the life cycle may extend over more than one year (biennial cycles), reflecting differences in sensitivity to seasonal microclimatic buffering and resource availability. Mean body length (in mm) was treated as a quantitative trait; values were taken from the compiled trait table and represent species-level averages used consistently across sites. Species traits are updated based on Brandmayr et al. (2005) and Brandmayr and Colombetta (2025).

All trait data (nominal and quantitative), with the exclusion of chorology, were assembled into a single species-by-trait matrix (Supplementary Materials, Table S1), which also reports abbreviations and forest-type occurrences used for data management.

2.3. *Statistical analysis*

To address our research questions, we applied a multi-metric framework integrating taxonomic and functional approaches. Because different metrics capture complementary facets of community structure, analyses were organised by ecological dimension (taxonomic vs. functional) and by the level at which diversity is expressed (within-site vs. among-site variation). In this study, α diversity refers to within-site diversity (e.g. species richness or functional diversity), whereas β diversity refers to variation in species or trait composition among sites.

2.3.1. *Patterns of α and β taxonomic diversity*

To characterise taxonomic diversity patterns, we analysed α diversity (within-site richness) and β diversity (variation of species composition among sites) using complementary metrics that capture both average diversity and compositional turnover. Differences in carabid species richness between broad-leaved and pine forests were evaluated using a non-parametric Wilcoxon test (Mann–Whitney U), treating sites as independent sampling units. Species richness represents a basic measure of α diversity, describing the average number of species per site without accounting for differences in sampling effort or spatial structure. Species accumulation curves (SACs; Ugland et al., 2003) were computed to describe richness accrual through the temporal sequence of sampling and to provide an overview of completeness and turnover over the sampling period. Sample-based rarefaction curves (RCs) and spatially explicit rarefaction curves (SERs; Bacaro et al., 2016, 2012; Chiarucci et al., 2009) were calculated separately for each forest type using the “vegan” (Oksanen et al., 2013) and “Rarefy” (Thouverai et al., 2025) R packages, respectively. Rarefaction approaches complement raw richness estimates by accounting for sampling effort and spatial configuration, allowing more robust comparison between forest types.

The contributions of α and β taxonomic diversity to overall (γ) diversity were assessed for each forest type using additive diversity partitioning (Crist et al., 2003; Lande, 1996) implemented in the “vegan” package (Oksanen et al., 2013). This approach explicitly separates α and β components of diversity, allowing us to quantify the relative importance of within-site diversity versus compositional turnover at different spatial levels. Specifically, γ diversity was decomposed into α diversity and two hierarchical β components: β among sites within forest type, and β between forest types. Statistical significance of observed partitions was assessed using a null model with 999 permutations, comparing observed α and β components to their expected values under randomised assemblage structure.

To further characterise β diversity, we estimated the total variance of the community matrix (Bdtotal) and its two complementary attributes: local contributions to β diversity (LCBD) and species contributions to β diversity (SCBD) (Heino and Grönroos, 2017; Legendre and De Cáceres, 2013). LCBD quantifies the uniqueness of each site in terms of species composition (i.e., how much each site contributes to the overall β diversity), whereas SCBD quantifies the contribution of each species to the overall compositional variation across the study area. In addition to analyses on the full dataset, Bdtotal, LCBD and SCBD were also computed separately within each forest type to describe within-habitat compositional variation, ignoring the sampling year as a grouping factor for these within-type summaries. Analyses were performed on Hellinger-transformed abundance data using the “beta.div” function in the “adespatial” package (Dray et al., 2025). Statistical significance of LCBD values was assessed by permutation (999 permutations). Differences in carabid species composition between broad-leaved and pine forests were visualised using non-metric multidimensional scaling (NMDS). Ordination was based on plot-to-plot Bray-Curtis dissimilarities computed on abundance data. Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001), using 9999 permutations and the same distance matrix, was then used to test for differences in community composition between forest types. NMDS provides a visual summary of β-diversity structure, while PERMANOVA tests whether compositional centroids differ between forest types under the chosen dissimilarity metric.

2.3.2. *Functional traits and pattern of functional diversity*

Functional diversity indices were calculated separately for each forest type using the "FD" package (Laliberté et al., 2014) via the 'dbFD' function. Differences in functional diversity between broad-leaved and pine forests were evaluated using non-parametric Wilcoxon tests applied to distance-based functional diversity indices. We computed functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al., 2008), functional dispersion (FDis) (Laliberté and Legendre, 2010), and Rao's quadratic entropy (Rao's Q) (Botta-Dukát, 2005). These indices capture complementary aspects of functional structure: FRic describes the extent of trait space occupied by the assemblage, i.e. the range of ecological strategies present. FEve quantifies how regularly species abundance are distributed within the trait space. FDiv indicates whether dominant species are located at the extremes of trait space. FDis measures the average distance of species from the community centroid, proving an abundance-weighted estimate of trait dispersion. Finally, Rao's Q integrates both pairwise functional dissimilarities and species abundance into a single measure of overall functional diversity. Subsequently, to complement plot-level functional indices, we compared functional diversity between broad-leaved and pine forests using functional rarefaction curves. Sample-based functional rarefaction curves (FRCs) and spatially explicit functional rarefaction curves (SEFRs), derived from the expected value of Rao's Q (Ricotta et al., 2012), were calculated separately for each forest type using "Rarefy" (Thouverai et al., 2025). Functional rarefaction describes how expected functional diversity accumulates with sampling effort and spatial extent, allowing comparisons that are less sensitive to differences in sample size.

To mirror the taxonomic additive partitioning, we performed a functional decomposition of α and β components following De Bello et al. (2010), using the 'Rao' function and Gower distances to estimate functional diversity. In this framework, functional α diversity represents within-community functional diversity (interpretable as the effective number of functionally distinct species, with a minimum value of 1), functional β diversity represents the additional functional diversity gained when pooling communities, and functional γ diversity represents total functional diversity across all sampled sites. A hierarchical null-model test was performed using the 'hiersimu' function in "vegan", using the same spatial levels as the 'adipart' procedure (plots; forest types) and 999 permutations, to test whether observed α, β and γ components differed from expectations under random assembly.

To describe the variation and complementarity of traits across communities, we computed plot-level functional uniqueness (U), defined as the functional contribution of individual species to the overall functional diversity of a community (Ricotta et al., 2016). U ranges from 0 (minimum uniqueness) to 1 (maximum uniqueness) and was calculated separately for broad-leaved and pine forest assemblages using the "adiv" package (Pavoine, 2020) and Gower distances. This metric complements community-level indices by describing how functional dissimilarity is distributed among species within each assemblage.

Finally, to represent how functional diversity and redundancy relate to species dominance, we adopted the approach proposed by Ricotta et al. (2023), which decomposes community structure into three complementary fractions: functional diversity (Rao's Q), species dominance (Simpson dominance, D) and functional redundancy (i.e. the amount of species diversity not expressed by functional diversity, R). These components sum to one and can therefore be represented in a ternary diagram. In this representation, the contrast between each vertex and the opposite edge summarises three alternative structural conditions: (i) D versus Simpson diversity (R + Q), with D = 1 indicating a single-species assemblage; (ii) Q versus functional homogeneity (D + R), with Q approaching 1 indicating high species diversity with maximal functional dissimilarity; and (iii) R versus functional uniqueness (D + Q), with R approaching 1 indicating high species diversity but functional equivalence among species (Ricotta et al., 2023).

The three components were computed for broad-leaved and pine forest sites based on four functional traits (wing morphology, adult diet, larval development category, and mean body length). Trait data were classified as nominal (wing morphology, adult diet, larval category) and quantitative (body length). Quantitative traits were linearly scaled to the range [0, 1]. Pairwise species distances were computed using the appropriate mixed-trait distance (Modified Gower Distance; Pavoine et al., 2009), then scaled by their maximum value to obtain a [0,1] distance matrix. Using relative species abundances per plot and the scaled distance matrix, we computed Rao's quadratic diversity (Q), functional redundancy (R), and the Simpson dominance component (D) for each plot using "adiv" (Pavoine, 2020). The ternary diagram was generated using "ggtern" (Hamilton and Ferry, 2018).

To test for differences in the multivariate structure of ternary components between broad-leaved and pine forest sites, we performed a distance-based MANOVA (db-MANOVA) using the "PERMANOVA" package (Vicente-Gonzalez and Vicente-Villardon, 2021), with Bray-Curtis dissimilarities computed among plots based on their (Q, R, D) values and 9999 permutations.

2.3.3. *Species and functional trait indicator analyses*

To assess whether particular carabid species were significantly more abundant in broad-leaved or pine forests, or in a particular year, we performed an indicator species analysis (ISA) (Dufrêne and Legendre, 1997) using the "multipatt" function available in the "indicspecies" R package (De Cáceres et al., 2010). Because sampling year varies among sites and is not fully balanced between forest types, we conducted the ISA primarily by forest type. To account for multiple comparisons across species, p-values from ISA were adjusted using the Holm procedure. In addition, using the framework proposed by Ricotta et al. (2015), we identified potential diagnostic species for both broad-leaved and pine forests, taking into account the functional traits of species as well as their occurrence and abundance. Specifically, the species that best characterise each group of sites were identified using species abundance data, and the functional association between the abundance-based indicator species and each group of forest type (broad-leaved or pine forests) was tested by calculating the functional distance between the indicator species and the functional centroids of all plots in each forest type. P-values of positive functional association (ϕ) between a given species (j) and each forest type (k) were calculated as the proportion of permutation-derived values of ϕjk equal to or greater than the actual value (999 permutations, two-tailed test). Because these tests are repeated across species, p-values were also Holm-adjusted.

All the statistical analyses were run under the R statistical environment v. 4.4 (R, 2025).

3. Results

3.1. *Taxonomic diversity*

A total of 103,113 individuals belonging to 57 species were recorded across the study area (Supplementary Materials, Table S1). Species richness at the forest-type scale was higher in broad-leaved forests (47 species) than in pine forests (41 species). Seventeen species occurred exclusively in broad-leaved forests and ten species exclusively in pine forests (Supplementary Materials, Table S1), implying a shared pool of 30 species across the two forest types.

Mean plot-level species richness (α diversity) did not differ significantly between forest types across the whole sampling period (broad-leaved forests: 15.65 ± 3.63 species; pine forests: 14.35 ± 3.67 species; Wilcoxon test $p = 0.15$). Species accumulation curves (SACs) calculated over years indicated that the SACs for the overall dataset and for broad-leaved forests reached an asymptote, whereas the pine-forest SAC did not fully saturate, although it showed a clear tendency towards flattening (Fig. 2a). Sample-based rarefaction and spatially explicit rarefaction patterns were consistent with a larger expected species pool in broad-leaved forests than in pine forests for comparable sampling effort (Fig. 2). In the spatially explicit comparison, the SER for pine forests increased less steeply than the corresponding classical rarefaction curve, yielding lower richness estimates for a given spatial extent (Fig. 2b).

Additive diversity partitioning showed that the β component among plots within forest types contributed more to γ diversity than the β component between forest types (Fig. 3), indicating that compositional turnover among plots was more pronounced than differentiation between broad-leaved and pine forests. Specifically, γ diversity was dominated by within-site (α) richness (81.4%), while turnover among plots within forest types (β) accounted for 14.4% and turnover between forest types (β) for 4.2% (Fig. 3).

The NMDS ordination (non-metric fit: $R^2 = 0.99$; stress = 0.09) did not show a statistically significant separation of assemblages between forest types (PERMANOVA: F = 1.82, p = 0.10; Fig. 4), consistent with relatively weak β diversity between forest types compared with the overall among-site variation.

Total β diversity for the whole dataset was Bdtotal = 0.330, and LCBD values ranged from 0.006 to 0.070, with five sampling sites showing significant LCBD values (Fig. 5). All significant LCBD sites were located in broad-leaved forests, occurred in five different years, and were positioned in peripheral sectors of the study area (four sites in the north-western sector and one in the south-eastern sector; Fig. 5). When calculated separately by forest type (ignoring year), total β diversity was 0.369 in broad-leaved forests and 0.276 in pine forests. Within each forest type, only one LCBD value was significant: LCBD = 0.124 in broad-leaved forest (2015) and LCBD = 0.108 in pine forest (1982).

Across the entire dataset, SCBD ranged from < 0.001–0.362; within broad-leaved forests it ranged from < 0.001–0.402, and within pine forests from < 0.001–0.346. The species contributing most to overall β diversity (highest SCBD) was *Aptinus bombarda* in both forest types (Supplementary Materials, Figure S1).

3.2. Functional diversity

Across the two forest types, carabid assemblages encompassed a wide range of dispersal and trophic strategies as reflected by the four functional traits considered (wing morphology, adult diet, larval ecology, and body length; Supplementary Materials, Table S1). Most species were brachypterous or macropterous, and trophic categories ranged from strict zoophagy to omnivory and granivory. Broad-leaved sites hosted a higher number of omnivorous species, whereas pine forests included a relatively higher number of collembolan-hunting taxa. Reproduction season categories likewise ranged from more generalist strategies to specialised ones, whereas body size varied from small-sized taxa (e.g., *Tachyta nana*) to large-bodied species within Carabini (e.g., *Carabus coriaceus*). In parallel, the species pool included multiple chorological categories (Fig. 6), indicating that the assemblages combine taxa with different biogeographic affinities.

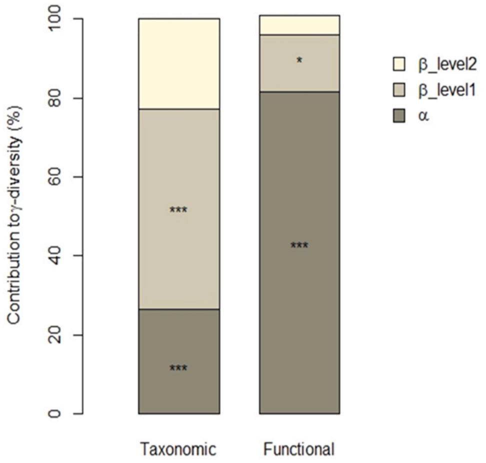

Fig. 3. The contribution of α, β_level1 and β_level2 to taxonomic and functional diversity. α is the average diversity, β_level1 is the among-sites diversity and β_level2 is the between-forest types (broad-leaved and pine forests) diversity. *** the expected diversity values are highly statistically different from the observed at $p < 0.001$, * the expected diversity values are statistically different from the observed at $p < 0.05$.

Functional diversity indices computed for each plot (FRic, FEve, FDiv, FDis and Rao's Q) did not differ significantly between broad-leaved and pine forests (all tests $p > 0.05$; Supplementary Materials, Tables S2 and S3).

Functional rarefaction curves indicated that the sampling effort was sufficient to capture the functional diversity of the assemblages, as

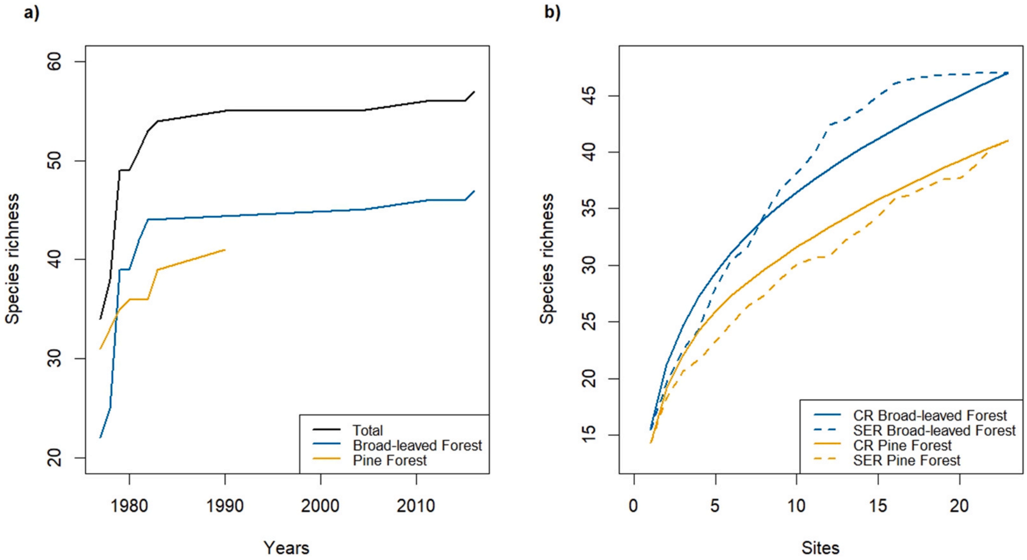

Fig. 2. a) Species accumulation curves (SACs) over years calculated from the whole dataset (black), broad-leaved forest (blue) and pine forest (orange). b) Spatially explicit rarefaction curves (SER, dashed line) and classical rarefaction curves (CR, solid line) of the two forest types.

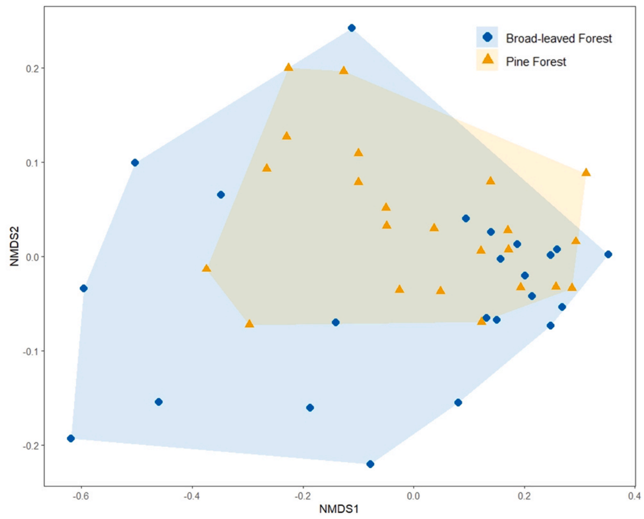

Fig. 4. Non-metric multidimensional scaling (NMDS) on the plot-to-plot Bray–Curtis dissimilarity matrix for community of carabids in broad-leaved and pine forests.

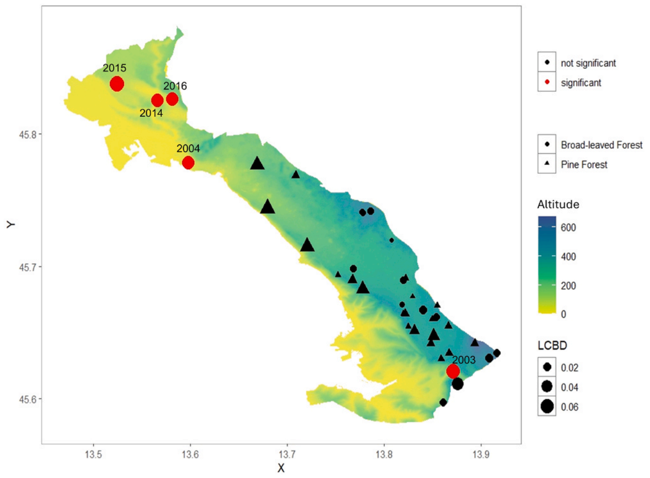

Fig. 5. Local contribution to β diversity (LCBD) values of sampling sites in the study area calculated from the whole dataset. Larger circles indicate higher values; symbols indicate forest type and red colour p-value < 0.05.

sample-based functional rarefaction curves reached an asymptote both for the overall dataset and within each forest type (Fig. 7). Both sample-based and spatially explicit functional rarefaction curves based on expected Rao's Q suggested higher Rao's Q values in pine forests than in broad-leaved forests for comparable sampling effort/extent (Fig. 7).

Functional uniqueness values (U) spanned a limited range in both forest types (Table 1). In broad-leaved forests, U ranged from 0.52 to 0.68 (mean 0.60; $\Delta U = 0.16$), while in pine forests U ranged from 0.54 to 0.68 (mean 0.61; $\Delta U = 0.14$). This narrow range indicates limited variation in the distribution of trait dissimilarity across plots within each forest type (Table 1).

The ternary decomposition of community structure into functional diversity (Q), redundancy (R) and dominance (D) did not differ significantly between broad-leaved and pine forest sites ($p = 0.30$; Fig. 8). In both forest types, the distribution of points in the ternary diagrams was shifted towards the D vertex, indicating assemblage structure characterised by relatively high dominance (Fig. 8). The pattern appeared more sharply concentrated in broad-leaved forests in the current figure rendering (Fig. 8), although the overall multivariate comparison of ternary composition did not detect a significant forest-type effect ($p = 0.30$).

3.3. Indicator analysis

Abundance-based indicator species analysis (ISA) and the trait-informed diagnostic framework suggested weak, exploratory signals of species-forest type association (Supplementary Materials, Tables S4-S6). Using unadjusted p-values, ISA highlighted a small set of taxa with the highest IndVal scores in broad-leaved forests (e.g., *Molops striolatus*, *Anchomenus dorsalis*, *Licinus hoffmanseggii*) and in pine forests (e.g., *Carabus caelatus schreiberi*, *Tachyta nana*, *Abax parallelepipedus* subsp. *subpunctatus*, *Abax carinatus* subsp. *sulcatus*, *Molops ovipennis*) (Table S4). However, after Holm correction for multiple comparisons across species, no taxa remained statistically significant in the abundance-based ISA (Table S4). We therefore treat these outputs as candidate diagnostic taxa rather than as statistically supported indicators, and we report both raw and Holm-adjusted p-values in the Supplementary Materials for transparency (Tables S4-S6).

The trait-informed diagnostic framework produced qualitatively congruent patterns, highlighting partially overlapping candidate taxa across forest types (Tables S5-S6). As for ISA, Holm correction removed formal significance across species-level tests, and results are therefore presented as exploratory evidence based on the magnitude of association and consistency with other community-level patterns (turnover and site uniqueness) rather than as definitive indicator sets. Some additional taxa of conservation interest were recorded sporadically and are best interpreted as qualitative signals of local environmental conditions rather than as statistically supported indicators. *Carabus hortensis*, recorded mainly in cooler broad-leaved sites close to the Slovenian boundary, may reflect locally buffered microclimates and associated substrate–vegetation conditions in that sector of the study area. Rare taxa with a Dinaric biogeographic affinity, such as *Leistus magnicollis* and *L. parvicollis*, were detected only in the south-eastern corner of the Triestine Karst, in two pine stands, highlighting the potential role of geographically peripheral sites as refugial localities for regionally uncommon species.

4. Discussion

This study combined long-term, multi-site pitfall-trap data with trait-based metrics to evaluate how carabid assemblages respond to two widespread forest types in the North Adriatic Karst: secondary broad-leaved stands and historically established *Pinus nigra* forests. Overall, differences between forest types were subtle when viewed through coarse community-level summaries, yet they became clearer when the analysis focused on turnover, site uniqueness and diagnostic taxa. In parallel, functional metrics suggested broad similarity in trait space between forest types, while differences in functional structure were largely driven by dominance patterns and the way rare or specialised species contribute to expected functional diversity under effort-explicit comparisons.

A key outcome is that broad-leaved and pine stands did not diverge strongly in simple richness-based summaries, suggesting that overstory identity alone is not a sufficient predictor of carabid diversity in this system. This is consistent with a growing body of forest biodiversity research showing that many ground-dwelling arthropods respond at least as much to near-ground conditions (litter amount and quality, moisture, temperature buffering, understory structure, deadwood and microhabitat continuity) as to canopy composition per se, and that the "tree-species signal" is often mediated by stand structure and microclimate rather than being purely taxonomic (Kriegel et al., 2021; Thiele, 1973; Uhl et al., 2025; Zara et al., 2021). In other words, broad-leaved versus conifer stands can host similar overall richness while still differing in which species dominate, which species are locally unique, and how assemblages vary across space.

The more informative patterns emerged from β-diversity components

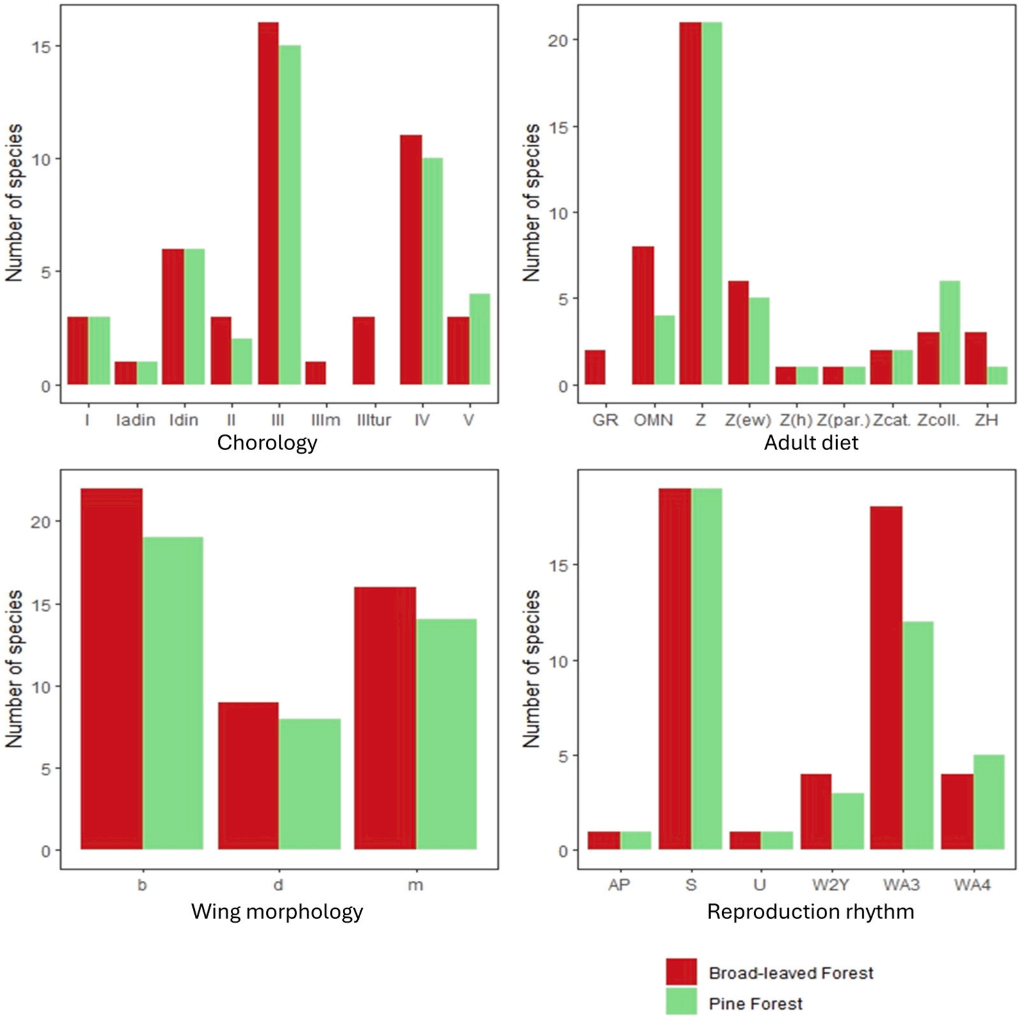

Fig. 6. Species number of carabids recorded during the surveys categorized by their ecological and biogeographical traits: chorology (I: endemic of South-Eastern Europe; Iadin: endemic of Alps and Dinaric mountains; Idin: endemic of Dinaric mountains; II: central European; III: European; IIIm: Euro-Mediterranean; IIItur: turanic-European; IV: Euro-Siberian, west-palearctic; V: palearctic, Holarctic), diet of the adults (GR: granivorous; OMN: omnivorous; Z(ew): adult generalist larva earthworm predator; Z(h): adult generalist; larva snail predator; Z(par.): larva parasitoid; Zcat.: caterpillar predator; Zcoll.: springtail predator; ZH: imago and larvae snail or mollusc predators), wing morphology (b: brachypterous; d: dimorphic; m: macropterous) and reproduction rhythm (AP: aperiodic; S: spring breeder (summer larvae); U: unstable reproductive season; W2Y: biennial cycle; WA3: autumn breeder, winter larvae; WA4: late autumn breeder, winter larvae and aestivation of adults).

and from the identification of sites with distinctive compositions. In our dataset, turnover within forest types contributed substantially to overall diversity, and a subset of plots, particularly in broad-leaved stands, appeared to contribute disproportionately to compositional uniqueness. Ecologically, this pattern is consistent with fine-grained habitat heterogeneity within the broad-leaved forest mosaic, which is typical of the karst landscape, thus showing diverse topography, soil features, exposure and successional stage over short distances. Such heterogeneity can promote high among-site compositional variation even when average α-diversity is comparable across forest types. From a monitoring perspective, this implies that preserving a diversity of stand structures and microhabitat conditions within each forest type may be at least as important as favouring a single "target" overstory, a conclusion that aligns with recent synthesis work emphasising structural heterogeneity as a key lever for multi-taxon biodiversity in managed forests (Uhl et al., 2025). A second, management-relevant implication concerns detectability: weak separation in ordination space does not necessarily mean ecological equivalence (Anderson and Walsh, 2013): when broad patterns overlap, diagnostic and contribution-based approaches (species-level diagnostics, site uniqueness and contribution metrics) can capture differences that community-level ordination summarises only partially (Legendre and De Cáceres, 2013). This is particularly relevant in karst forests where dispersal limitation and microrefugia, such as dolines, can generate patchy distributions, and where functionally similar forest conditions may be produced by different canopy types under comparable structural settings (Bátori et al., 2023, 2021; Frei et al., 2023).

Trait-based metrics indicated broadly similar functional diversity across forest types, which suggests functional convergence between assemblages in pine and broad-leaved stands. Functional convergence is plausible here because both forest types share a set of near-ground environmental filters typical of karst systems (shallow soils, high spatial variability in moisture, and strong seasonal thermal contrasts), which can constrain the viable trait combinations for ground beetles (Thiele, 1973). Recent studies have highlighted that functional diversity may remain relatively stable across habitat categories if different species "replace" one another without expanding the occupied functional space (i.e., taxonomic change with limited functional change), particularly when the trait set primarily captures dispersal, feeding and size-related ecological strategies (Kriegel et al., 2021; Ricotta et al., 2023). At the same time, rarefaction-based functional comparisons suggested that expected functional diversity can differ between forest types even when

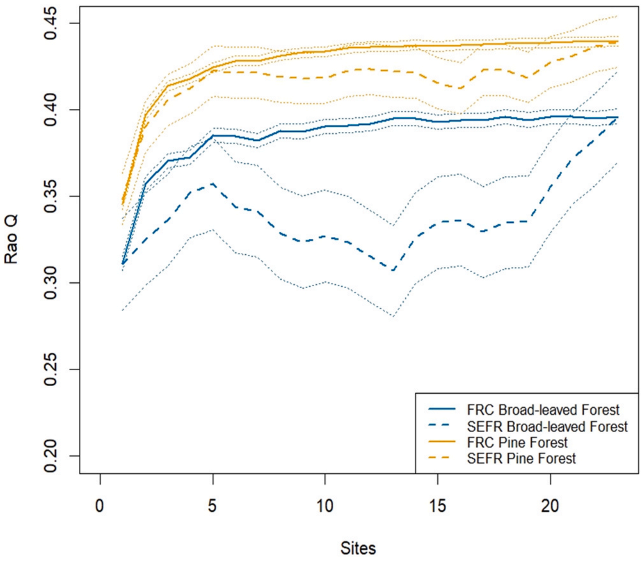

Fig. 7. Functional rarefaction curves (FRC, solid line) and spatially explicit functional rarefaction curves (SEFR, dashed line) derived from the computation of Rao's Q index for the carabids community in the broad-leaved forest (blue) and in the pine forest (orange).

Table 1
Summary statistics (minimum, maximum, mean and range) of functional uniqueness values U within the two forest types, the broad-leaved and pine forests.

	Broad-leaved forest	Pine forest
Min	0.52	0.54
Mean	0.60	0.61
Max	0.68	0.68
ΔU (Max - Min)	0.16	0.14

conventional functional indices do not (Ricotta et al., 2012). This is an important nuance: functional diversity is sensitive not only to which trait values are present, but also to how abundances are distributed across species and how quickly rare trait combinations accumulate with sampling effort (Pavoine, 2020; Ricotta et al., 2012). In practice, pine stands may contribute disproportionately to expected functional diversity if they harbour a subset of taxa with trait combinations that are uncommon in broad-leaved stands or if they support a more even representation of certain ecological strategies at comparable sampling effort (Jung et al., 2020). Conversely, broad-leaved stands can show high taxonomic turnover without a commensurate increase in trait space if turnover mostly involves species that are functionally similar (functional redundancy), a pattern that would be consistent with dominance-driven assemblages (Ricotta et al., 2023, 2015).

The ternary decomposition framework is useful to interpret these patterns mechanistically because it explicitly separates the role of dominance (D), functional diversity (Q) and redundancy (R) (Ricotta et al., 2023). The tendency of plots to align toward dominance-dominated configurations indicates that a limited set of taxa accounts for a substantial fraction of individuals, which is common in carabid datasets and can also emerge clearly in forest contexts where catches are strongly uneven (Mei et al., 2023; Skłodowski, 2023). The relative abundance structures of the karst forests are dominated by *Aptinus bombarda*, a carabid which lives as parasitoid in the larval phase and whose adults crowd in the pit falls because of an intraspecific aggregation process. In such cases, management actions that modify near-ground conditions via canopy structure and associated litter/understory development are expected to shift community structure primarily by changing dominance and relative abundances rather than by adding entirely new trait combinations, because carabid activity-density and richness respond measurably to stand structure, canopy cover/maturity, and disturbance legacies that buffer microhabitats (Konrad et al., 2024; Pereira et al., 2024; Skłodowski, 2023).

Even when overall richness and broad functional indices show limited differences between forest types, species-level screening can still suggest candidate diagnostic taxa. This is precisely the context in which carabids function well as bioindicators: they can provide diagnostic signals of microhabitat continuity, disturbance intensity, and near-ground climatic conditions, often responding rapidly to structural changes that are not immediately reflected in canopy-based classifications (Ludwiczak et al., 2020; Pereira et al., 2024; Skłodowski, 2023, 2021). Importantly, the trait-informed diagnostic approach further refines this by identifying not only which species are associated with each forest type, but also whether those species are functionally close to the centroid conditions of the plots they characterise (Pereira et al., 2024). However, after Holm correction for multiple comparisons, none of the species-level tests remained statistically significant (Tables S4-S6). We therefore interpret the indicator outputs as exploratory evidence, and focus on the taxa with the highest association statistics as candidate diagnostic species to be interpreted in conjunction with turnover and site-uniqueness patterns. Under this conservative framing, the broad-leaved stands were characterized by a diagnostic subset including *Molops striolatus*, *Anchomenus dorsalis*, and *Licinus hoffmanseggii*. These three species are characteristic of well-developed, deep soils found in dolines or in cooler forest stands. *M. striolatus* also shows a limited

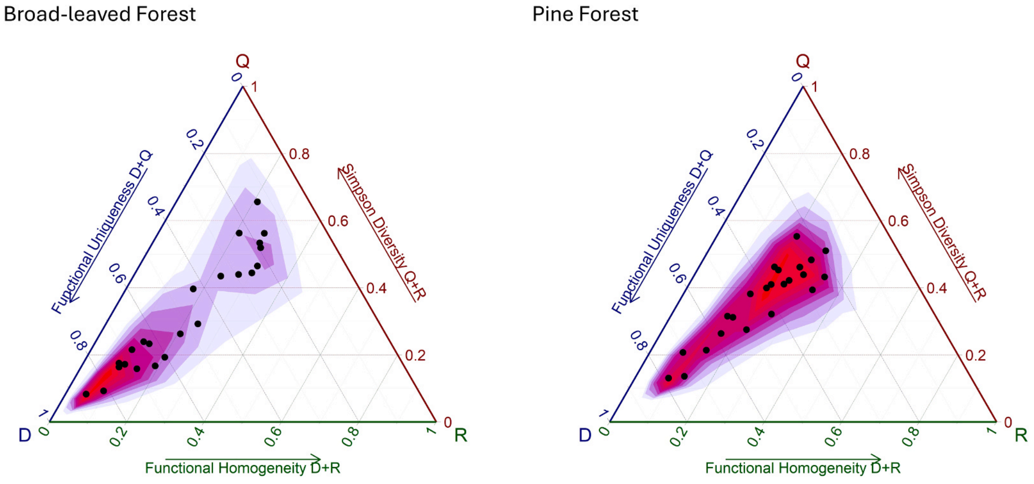

Fig. 8. Ternary diagrams for the broad-leaved and pine forests. Q: Rao's Q, D: Simpson's dominance and R: redundancy - (D+Q).

distribution in northeastern Italy and is of conservation concern (Brandmayr and Colombetta, 2025). Pine stands were characterised by *Carabus caelatus* ssp. *schreiberi*, *Tachyta nana*, *Abax parallelepipedus* ssp. *subpunctatus*, *Carabus germarii* ssp. *germarii*, *Abax carinatus* ssp. *sulcatus* and *Molops ovipennis*. Ecologically, this partition is coherent with the expectation that forest-floor assemblages often segregate along near-ground microclimatic buffering, litter/soil moisture regimes, and disturbance histories, with large predatory and low-dispersal taxa being particularly sensitive to abrupt canopy opening and to drought-driven stress (Růžičková et al., 2025; Weiss et al., 2024a). In more detail, the broad-leaved diagnostic group reflects cool moist forests of higher elevations or dolines with deeper soils (*Fagetalia*), whereas the pine indicator species characterize lower altitudes or less developed soils, *Tachyta nana* in particular is a small under-bark predator strictly bound to dead or perishing conifers. In parallel, the appearance of more mobile taxa among diagnostic sets is consistent with evidence that certain carabids (including *Anchomenus dorsalis*) peak in structurally open or edge-like situations and can exploit habitat interfaces, which are common in karst woodland mosaics where small-scale heterogeneity is pervasive (Bennewicz and Barczak, 2020). Finally, the fact that some diagnostic taxa belong to lineages with strong regional structuring in the North Adriatic–Dinaric sector (e.g., *Carabus caelatus* within the Dinaric system) is consistent with the broader view of this biogeographic region as a hotspot. In this predominantly karstic area, topographic complexity and historical contingencies contribute to fine-grained species turnover and patchiness, reinforcing the value of species-level diagnostics for bioindication in karst forests (Kuralt et al., 2022; Vladić et al., 2019). *Carabus caelatus*, in particular, with its snail-catching larvae, shows a marked preference for the shallower rendzina soils of pine plantations, which readily grow even on the deeply karstified outcropping rocks of the area, where these molluscs are abundant.

From a conservation and management standpoint, these diagnostic subsets matter because the Classical Karst is currently shaped by two concurrent, and partially competing, trajectories. First, *Pinus nigra* stands in the Classical Karst are largely the outcome of historical afforestation initiated in the second half of the nineteenth century; a substantial fraction of these stands is now ageing and, in several areas, increasingly exposed to drought stress and disturbance dynamics that can accelerate decline and motivate active discussion about conversion pathways and the role of natural regeneration (Diaci et al., 2019; González de Andrés and Camarero, 2020). Second, broad-leaved forests, often thermophilous oak-dominated communities, are recovering in various sectors due to land-use abandonment and successional dynamics, yet their future trajectories will be strongly conditioned by climatic warming and by increases in the frequency and intensity of drought and heat events (Mantero et al., 2020). In this setting, decisions about pine retention, gradual conversion, thinning/gap creation, or removal are not merely silvicultural: they reshape forest microclimates and the continuity of suitable ground-layer conditions, with direct consequences for forest-floor biodiversity (Skłodowski, 2023, 2021). Our results imply that pine stands should not be treated a priori as biodiversity-poor "non-habitats". Rather, they appear capable of supporting carabid assemblages with broadly comparable functional structure, while contributing to landscape-level heterogeneity through candidate diagnostic taxa and dominance–redundancy patterns. This resonates with recent evidence from temperate European forests showing that plantations and mixed stands can sustain diverse ground-beetle assemblages when structural conditions and landscape context are favourable, while still differing in composition from native broad-leaved forests (Kriegel et al., 2021; Pereira et al., 2024). The key message for the Karst debate is therefore conditional: removing or rapidly converting pine stands could lead to the loss of the diagnostic subset of species associated with those stands unless conversion pathways maintain microhabitat continuity (e.g., phased conversion, retention of shaded refugia, heterogeneous canopy openings, and avoidance of abrupt exposure of the forest floor), which is also consistent with evidence that structural legacies after disturbance can prolong the persistence of late-successional carabid assemblages (Skłodowski, 2023).

Climate change strengthens the need for this conditional framing. Long-term studies in European temperate forests document that drought and heat extremes can alter both α and β diversity of ground beetles and can trigger pronounced declines, with disproportionate impacts on less mobile, forest-associated taxa (Weiss et al., 2024a, 2024b). This implies that management choices that exacerbate near-ground warming and desiccation, through abrupt canopy removal, excessive thinning, or homogenisation, may amplify climate-driven pressures, while approaches that preserve microclimatic buffering and heterogeneity may enhance resistance and recovery (Weiss et al., 2024b, 2024a). In practical terms, diagnostic carabids can be used as early-warning indicators of microclimatic deterioration and habitat discontinuity along forest conversion gradients, complementing vegetation-based indicators and remote-sensing assessments of habitat mosaics developed for the North Adriatic Karst context (Pafumi et al., 2023).

In our study, two limitations deserve explicit acknowledgement. First, the temporal span of sampling, together with the fact that trapping periods differ among forest types, introduces a potential confounding between habitat effects and year/season effects. This is not a minor issue for pitfall-trap datasets, because pitfall catches reflect *activity-density* (i.e., a joint outcome of abundance and movement/phenology) rather than true density, and activity-density is strongly modulated, within and among years, by near-ground temperature and moisture conditions (Fülöp et al., 2021; Gardarin and Valantin-Morison, 2021). Recent long-term evidence based on monthly resolved carabid monitoring further reinforces that both richness and abundance can show pronounced seasonal structure and interannual shifts, such that changes in trapping windows can translate into changes in apparent dominance patterns even when the underlying species pool is stable (Irmler, 2022; Skarbek et al., 2021). In forest systems specifically, climatic anomalies (e.g., drought/heat) can also affect activity, biomass, and trait composition, which increases the plausibility of a time-related confounding if temporal replication is not balanced across habitats (Weiss et al., 2024a, 2024b). In our case, this concern is partly mitigated because inference does not rest solely on year-by-year contrasts: we rely on sample-based and spatially explicit rarefaction frameworks and on habitat-level β-diversity descriptors that are not exclusively parameterised as temporal comparisons. Moreover, progressive broad-leaved encroachment into pine stands over recent decades suggests that some pine sites may have undergone compositional transitions during the overall sampling window, which further supports treating the dataset as a multi-temporal compilation rather than a synchronised design. Nonetheless, the temporal imbalance remains a constraint on strict causal attribution that should therefore be kept in mind, particularly when interpreting dominance-sensitive outputs (e.g., metrics that can be disproportionately influenced by short seasonal windows or by interannual weather anomalies). The recommendation for future work is to adopt a more synchronised temporal design across forest types (or explicitly model seasonality and weather covariates), so that habitat effects can be separated more cleanly from phenological dynamics.

Second, trait-based analyses are inherently shaped by the selected trait set and by the way trait information is translated into distances. The four traits used here capture widely relevant axes for carabids-dispersal potential (wing morphology), trophic strategy (adult diet), life cycles seasonality, and body size, yet they do not exhaust the dimensions that may be mechanistically decisive in karst forests under climate stress, such as moisture affinity, microhabitat specialisation, phenology, or thermal tolerance. This matters because functional conclusions can be sensitive to trait choice and to the number/type of traits included, potentially altering the apparent strength and even the direction of functional contrasts among habitats (Ohlert et al., 2022; Zhu et al., 2017). In temperate forests, drought-related signals in carabid communities have been shown to align particularly with mobility and size dimensions, and to interact with landscape context and microclimatic exposure (Weiss et al., 2024b), which suggests that augmenting the trait set with moisture/thermal preference information could strengthen inference in future karst-focused works. Where feasible, expanding the trait matrix (or integrating species-level ecological indicator values from vetted sources) would help disentangle whether observed functional-structure patterns primarily reflect genuine shifts in ecological strategies versus abundance re-weighting among functionally similar taxa.

Despite these constraints, the combined use of compositional, functional, and diagnostic/indicator-oriented analyses provides a robust and management-relevant basis for interpretation. For the Classical Karst, the most defensible conclusion is not that "broad-leaved is always better" or that "pine is always poor", but that conversion strategies should be evaluated and implemented as *microclimate- and continuity-sensitive trajectories*. This is particularly pertinent because *Pinus nigra* stands in the region have a well-documented historical legacy and are embedded in an active management debate about retention, conversion, and, in some contexts, restoration of more open habitat mosaics (Diaci et al., 2019). The evidence base from forest management studies on carabids supports the general principle that *how* canopy structure is altered often matters as much as *which* canopy type replaces it: small-gap or structurally diversified interventions can be compatible with maintaining ground-beetle ecological networks (Amori et al., 2021; Růžičková et al., 2025). Conversely, larger or abrupt canopy openings can impose stronger near-ground exposure and thereby amplify climatic stressors that are already known to impact forest carabids (Weiss et al., 2024b, 2024a). In operational terms, a phased, structurally heterogeneous conversion, retaining shaded refugia, promoting mixed or multi-layer structures where appropriate, and avoiding abrupt exposure of the forest floor, appears most consistent with conserving both taxonomic and functional dimensions of diversity while still allowing long-term development of climate-resilient broad-leaved stands.

CRediT authorship contribution statement

Giovanni Bacaro: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Miris Castello:** Writing – review & editing, Data curation. **Federica Fonda:** Writing – review & editing, Visualization, Formal analysis, Data curation, Conceptualization. **Emilia Pafumi:** Writing – review & editing, Data curation. **Pietro Brandmayr:** Writing – review & editing, Supervision, Investigation, Conceptualization, Methodology, Data curation. **Giorgio Colombetta:** Writing – review & editing, Investigation, Data curation, Methodology, Validation. **Valentina Olmo:** Writing – review & editing, Formal analysis, Data curation. **Fredrick Ojija:** Writing – review & editing, Data curation. **Simona Maccherini:** Writing – review & editing, Data curation. **Gaia Foltran:** Writing – review & editing, Data curation.

Declaration of Competing Interest

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

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This work is dedicated to the memory of Professor Livio Poldini, botanist who stimulated some of the authors to explore the pioneer value of pine plantations for the restoration of forest biodiversity of the Triestine Karst.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123835.

Data availability

Data will be made available on request.

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