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RESEARCH ARTICLE

Below-ground traits, rare species and environmental stress regulate the biodiversity–ecosystem function relationship

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Abstract

1. Understanding the relationship between biodiversity and ecosystem functioning (BEF) is crucial to predicting the consequences of ongoing global biodiversity loss. However, what drives BEF relationships in natural ecosystems under globally changing conditions remains poorly understood.
2. To address this knowledge gap, we applied a trait-based approach to data from coastal dune plant communities distributed along a natural environmental stress gradient. Specifically, we compared the relative importance of below-ground and above-ground traits in predicting productivity, decomposition, water regulation, carbon stock and nutrient pools, and tested how these BEF relationships were modulated by environmental stress and the presence of rare species that are typically excluded from experimental systems.
3. Below-ground traits were just as important as above-ground traits in driving ecosystem functioning. Moreover, despite having low abundances, rare species positively influenced ecosystem multifunctionality (EMF). However, most biodiversity effects became weaker as environmental stress increased.
4. Our study shows that to understand variation in ecosystem functioning we must consider below-ground traits as much as above-ground ones. Moreover, it highlights the importance of conserving rare species for maintaining EMF. However, our findings also suggest that rapid global change could dampen the positive effects of diversity on ecosystem functioning.

KEYWORDS
BEF relationships, below-ground traits, biodiversity, coastal dunes, ecosystem functioning, environmental stress gradient, multifunctionality, rare species

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1 | INTRODUCTION

Despite considerable evidence that species-rich communities support a greater range of ecosystem functions (i.e. ecosystem multifunctionality [EMF], Allan et al., 2015; Gross et al., 2017; Le Bagousse-Pinguet et al., 2021; Maestre et al., 2012), our current understanding of biodiversity–ecosystem functioning (BEF) relationships remains limited (Laliberté, 2017; Freschet, Roumet, et al., 2021; van der Plas et al., 2020). In particular, while the effects of some biodiversity attributes (e.g. species richness [SR] and above-ground traits) have been extensively studied in plant communities, the role of below-ground traits is largely unexplored, despite their potentially important contribution to soil functionality as well as nutrients and water uptake (de Bello et al., 2010; Freschet, Roumet, et al., 2021). Moreover, while a growing number of studies suggest that environmental conditions can alter BEF relationships, research has predominantly focused on a few ecosystem types, mainly grasslands, forests and on experimental setups subject to weak or no environmental pressures (Garland et al., 2021; van der Plas, 2019). As a result, how strongly the environmental context influences ecosystem functioning and how ongoing global environmental changes will impact BEF relationships remains unclear. Nevertheless, identifying which community traits contribute most to specific ecosystem functions, and how this varies depending on the environmental conditions, is critical to accurately predict how changes in species composition will impact ecosystems.

Plant functional traits can explain the effect of SR on ecosystem functioning (Cernansky, 2017; Eisenhauer et al., 2018; Garnier et al., 2015). As the number of species increases in a community, so does the probability of including (1) functionally distinct species specialised on different resources and potentially influencing different ecosystem processes (i.e. niche complementarity hypothesis; Petchey & Gaston, 2006; Tilman, 1997) and (2) some dominant species with a combination of traits strongly influencing ecosystem functioning (Grime, 1998; Smith & Knapp, 2003). These two mechanisms, that is the biodiversity effects driven by, respectively, trait complementarity and dominance (Cadotte, 2017; Loreau & Hector, 2001), can be related to two components of community functional structure, specifically the variability and the mean in species functional traits within the community (Cadotte, 2017; Loreau & Hector, 2001) that can be quantified through the indices of functional diversity (FD) and the traits' community-weighted mean (CWM) (Cadotte, 2017; Ricotta & Moretti, 2011). Functional complementarity and dominant species' traits can simultaneously influence ecosystem functioning (Le Bagousse-Pinguet et al., 2019), but their relative importance remains a subject of debate (Diaz et al., 2007; Garnier et al., 2015). Recent studies suggested that the balance between these two effects depends on the environmental context (Hodapp et al., 2016; Ratcliffe et al., 2017) as well as on the ecosystem functions and species traits analysed (de Bello et al., 2010; Hanisch et al., 2020; Lavorel & Garnier, 2002).

In this regard, much effort has been made to demonstrate the role of above-ground functional traits in regulating various ecosystem processes and functions, for example litter quality and quantity, carbon uptake, emissions of volatile organic compounds or herbivory dynamics (de Bello et al., 2010; Funk et al., 2017; Gross et al., 2017; Lavorel & Garnier, 2002; Le Bagousse-Pinguet et al., 2019, 2021). In contrast, on the below-ground side, the relative contribution of root traits on several EFs and particularly on EMF remains largely unexplored (Freschet, Roumet, et al., 2021; Laliberté, 2017; van der Plas et al., 2020). Roots are important for absorbing, transforming and conserving key resources for plant growth and fitness, such as nutrients and water (Freschet et al., 2018). Moreover, roots make up the large part of biomass that is decomposed directly in the soil, thus directly influencing soil biogeochemical cycles (de Bello et al., 2010). Roots also influence biogeochemical cycles by releasing carbon-rich exudates that nourish soil microbial communities in the rhizosphere and by forming symbiotic relationships, such as mycorrhizal and nitrogen-fixing associations (Freschet, Roumet, et al., 2021). Finally, compared with above-ground plant tissues (e.g. leaves), roots generally have lower nutrient contents but higher concentrations of large carbon-based molecules, making roots less decomposable than leaves, often resulting in greater contributions to below-ground carbon storage (Clemmensen et al., 2013). Consequently, below-ground traits can potentially explain soil-related functions, for example nutrient cycling or soil carbon sequestration, better than above-ground traits (Bardgett et al., 2014; Laliberté, 2017). However, root functional traits are difficult to measure, and consequently, less data are available compared with above-ground traits, which has so far prevented a deeper comprehension of the root–ecosystem function relationship (Freschet, Pagès, et al., 2021; Laliberté, 2017; van der Plas et al., 2020). Moreover, it remains unclear whether below-ground traits mirror the effects of above-ground traits or rather independently contribute to ecosystem functioning. Even if some studies investigated the effect of some root traits on a single ecosystem process (for a review see Freschet, Roumet, et al., 2021), a more comprehensive understanding of how roots influence multiple EMF is still missing (but see Butterfield & Suding, 2013) and the relevance of below-ground traits compared with above-ground ones.

Lastly, to date the effects of biodiversity on ecosystem functioning have been extensively tested in manipulative experiments (Lefcheck et al., 2015; Weisser et al., 2017), but less in natural ecosystems (Duffy et al., 2017; van der Plas, 2019). Consequently, there is large uncertainty about whether the insight derived from experimental studies can be applied to real-world ecosystems (Lepš, 2004; van der Plas, 2019; Wardle, 2016). There are several reasons why BEF relationships might differ between natural ecosystems and experiments. First, one of the main limitations of experiments is that they randomly simulate changes in species diversity, by casually removing and adding species or functional types to create diversity gradients (Balvanera et al., 2006; Cardinale et al., 2006; Duffy, 2009; but see Bruelheide et al., 2014; Schläpfer et al., 2005; Zavaleta & Hulvey, 2004 for experiments that have tested the impacts of non-random species losses). However, in natural systems, community assembly is not exclusively random, but results from a combination of biotic interactions (e.g. competition and facilitation) and environmental filtering (Götzenberger et al., 2012). Second, the environmental context defining community assemblages can also influence the BEF relationship, which has been shown to vary according to local climatic conditions (Jucker et al., 2016; Ratcliffe et al., 2017; Spohn et al., 2023), management (Allan et al., 2015; Tamburini et al., 2022) and disturbance regime (Valencia et al., 2015). These findings raise the need to investigate whether in real-world ecosystems BEF relationships shift along environmental gradients (Baert et al., 2018; De Boeck et al., 2008; Steudel et al., 2012). Third, natural and experimental communities greatly differ in the presence of regionally rare species. Experimental communities are mostly composed of common, dominant species (Dee et al., 2023; Enquist et al., 2019), thus overlooking the role of rare species, which recent work suggests play a key role in shaping BEF relationships (Dee et al., 2019; Gross et al., 2017; Le Bagousse-Pinguet et al., 2021; Wright et al., 2017).

Here, we used the strong sea–inland gradient of stress characterising coastal dunes as a model system to jointly investigate the influence of above and below-ground community functional structure, environmental conditions and rare species on the functioning of natural ecosystems. Specifically, we asked: (1) How does community functional structure drive variation in ecosystem functioning across real-world gradients? (2) How important are below-ground traits for ecosystem functioning compared with above-ground ones? (3) How does environmental stress modify the BEF relationship? (4) Do rare species influence ecosystem functioning? We hypothesised that below-ground traits would be just as relevant as above-ground traits to explain ecosystem functioning. We also expect that in this extreme natural system, rare species would promote functioning while the severity of environmental conditions would negatively impact the ability of the community to perform multiple ecosystem functions.

2 | MATERIALS AND METHODS

2.1 | Study area, vegetation and sea–inland gradient

The study was carried out on Mediterranean coastal dune systems of the region Lazio located along the Tyrrhenian coast of Central Italy (centred on latitude 41°44′20″ N longitude 12°14′18″ E). This area belongs to the Mediterranean climatic region and is composed of Holocene sandy dunes with low elevation (<10 m) occupying a narrow strip along the seashore (Acosta et al., 2009). Although the coast of Lazio extends for 250 km, it largely encompasses urbanised littorals. Consequently, the sampling area was limited to the last remaining intact dune systems within the region, which are distributed across six study sites covering a 90 km stretch along the Lazio coast (Figure 1a). Here, plant species and ecosystem functioning data were collected in 109 random vegetation plots of 4 m^2 distributed at different distances to the seashore in order to cover the coastal dune

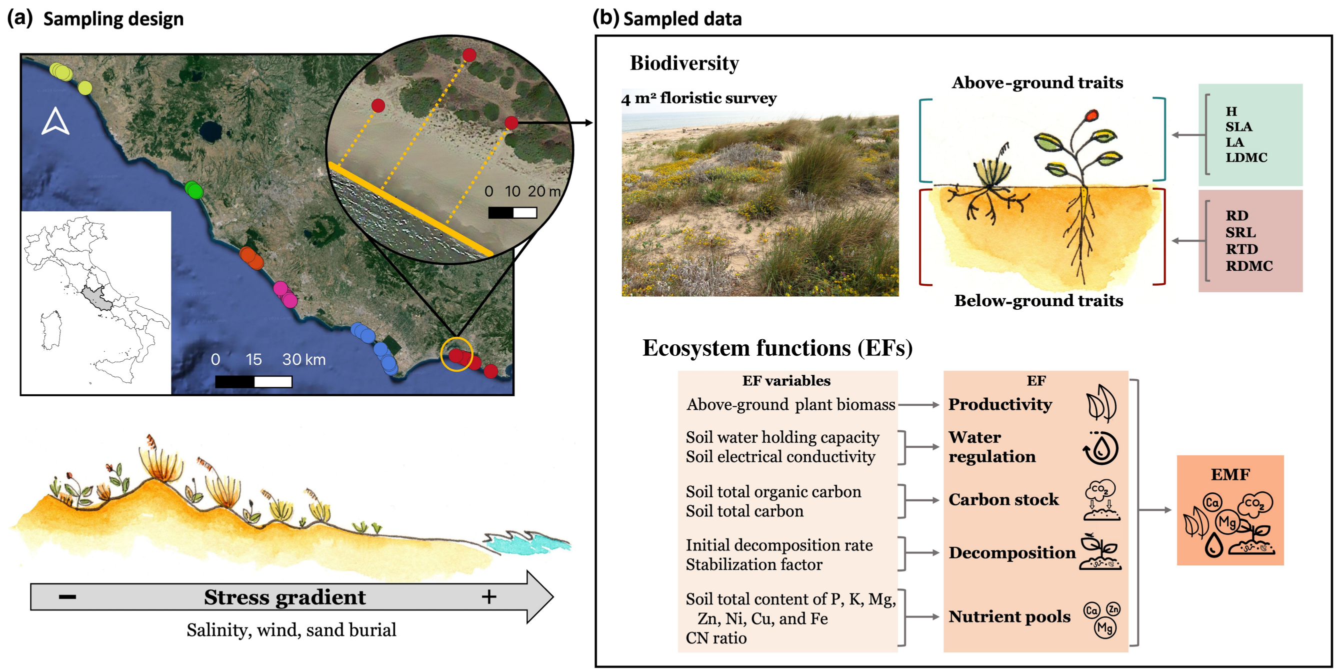

FIGURE 1 Conceptual figure illustrating the experimental design and listing the variables sampled. (a) The map shows the study area, where data were collected from 109 vegetation plots (represented by dots) distributed across six study sites (differentiated by dot colours). The inset shows plot distribution along the sea–inland environmental gradient of stress typical of coastal dunes. (b) Variables are measured at the plot scale to assess biodiversity and ecosystem functioning (EF). EMF, ecosystem multifunctionality; H, plant height; LA, leaf area; LDMC, leaf dry matter content; RD, root diameter; RDMC, root dry matter content; RTD, root tissue density; SLA, specific leaf area; SRL, specific root length.

zonation along the sea–inland gradient. Similarly, plots were also stratified by biodiversity to maximise the variation in biodiversity and to minimise the correlation between biodiversity and the sea–inland gradient and maintain a homogeneous distribution of taxonomic and FD along the gradient (Figure S1). Plots encompass all the herbaceous coastal communities characterising the coastal dune zonation, that is upper beaches, embryo dunes, shifting dunes and dune grasslands (Figure S2). In each plot, the number and percentage cover of all vascular plant species was recorded in May 2021, at the peak of the growing season. Species nomenclature followed the Portal to the Flora of Italy (http://dryades.units.it/floritaly/index.php).

In coastal dunes, the proximity to the sea is a good proxy of the environmental disturbance and stress running along the sea–inland gradient (Bazzichetto et al., 2016; Carboni et al., 2011), as communities situated closer to the sea experience greater levels of natural stresses and disturbances, including tidal storms, salt spray, wind and soil burial, as well as water and nutrients stress due to the high permeability of the sandy substrate. To represent this environmental gradient, we quantified distance to sea for each plot (Bazzichetto et al., 2016). This was measured in the field using a measuring tape, as the orthogonal distance from the shoreline (Figure 1a). As tidal variations along the Mediterranean Sea are relatively small, ranging between 0.2 and 1 m (Fenu et al., 2013), the effect of tides on sea proximity measurement is negligible.

2.2 | Plant traits

Functional trait data were available from previous studies carried out in the same study area (e.g. Bricca et al., 2023; Sperandii et al., 2021). We selected four above-ground and four below-ground effect traits (Table 1), namely plant height (H), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), root diameter (RD), specific root length (SRL), root tissue density (RTD) and root dry matter content (RDMC). These traits are linked to the functional strategies adopted by plants (Carmona et al., 2021; Díaz et al., 2016; Weigelt et al., 2021) and have been associated with several ecosystem processes and functions (see Table 1 for a description of the link between each trait and the EFs analysed; Bardgett et al., 2014; de Bello et al., 2010; Freschet, Roumet, et al., 2021; Lavorel & Garnier, 2002; Roumet et al., 2016). Prior to data analysis, trait values were log-transformed, as well as centred and scaled to mean 0 and standard deviation 1 (Májeková et al., 2016).

In each plot, we checked that at least 80% of the total plant cover was made up of species with trait information (Pakeman & Quested, 2007). While the set of above-ground trait data was sufficiently comprehensive for all sampled species, the below-ground set was not, such that we detected 16 plots (14.7%) where species below-ground trait information did not meet the 80% threshold. Therefore, to deal with missing trait data, we imputed

TABLE 1 Above-ground and below-ground traits analysed and their effect on ecosystem functioning as reported in the literature.

Functional dimension	Trait (acronym and unit of measurement)	Effect	References
Above-ground	Plant height (H, m)	↑ Productivity, carbon stock and water regulation	Lavorel and Garnier (2002) de Bello et al. (2010)
	Leaf area (LA, cm^2)	↑ Productivity, decomposition, nutrients' mobilisation and water regulation	
	Specific leaf area (SLA, mm^2 mg^{-1})	↑ Productivity, decomposition and nutrients' mobilisation	
	Leaf dry matter content (LDMC, mg g^{-1})	↓ Decomposition and nutrients' mobilisation	
Below-ground	Root diameter (RT, mm)	↑ Productivity and carbon stock	Bardgett et al. (2014) Roumet et al. (2016) Freschet, Roumet, et al. (2021)
	Root tissue density (RTD, g cm^{-3})	↓ Decomposition, carbon and nutrient pools	
	Specific root length (SRL, m g^{-1})	↑ Carbon and nutrient pools	
	Root dry matter content (RDMC, g g^{-1})	↓ Decomposition, carbon and nutrient pools	

below-ground traits for 12 species (representing 18.5% of the total species sampled). Methods used for trait imputation are fully explained in Method S1. To ensure that imputation would not affect the overall results, we repeated all the statistical analysis excluding the 16 plots where species below-ground traits information did not meet the 80% threshold. The results obtained were qualitatively similar to those presented here in the main text (Figure S3).

2.3 | Ecosystem function variables

Concurrently with the floristic survey, in May 2021, in each plot we collected 19 ecosystem function variables related to the following 'supporting' services (Garland et al., 2021; Millennium Ecosystem Assessment, 2005): primary productivity, soil water regulation, soil carbon storage, decomposition and soil nutrient pools (Figure 1b; Table 2; Garland et al., 2021; Le Bagousse-Pinguet et al., 2019). To quantify soil variables, we collected 0.5 kg of soil (0–10 cm depth) at five different points around the centre of each plot. Soil samples were then air-dried for 1 week and sieved by a 2 mm mesh. A full description of the sampling method and soil analysis is found in Method S2.

2.4 | Data analysis

2.4.1 | Diversity metrics

Within each 4 m^2 plot, we computed different diversity metrics to quantify the taxonomic and functional structure of the community, including SR, above- and below-ground FD (FD_{above} and FD_{below}), and the CWM of each trait.

We measured SR as the total number of vascular plant species recorded and vegetation cover as the total plant percentage cover of the plot area. Total vegetation cover is expected to be particularly important in shaping ecosystem functioning in ecosystems where vegetation is sparse and a lot of ground is left bare, as is the case in coastal dunes. This is partly because plant communities with higher coverage likely influence plant–soil energy fluxes more through larger input of litter (Berdugo et al., 2017; Maestre et al., 2012). However, SR is inherently linked to vegetation cover, as the more individual plants there are in a plot the more likely they will be, by chance alone, to belong to different species (Aarssen, 1997; Huston, 1997). Thus, to remove the influence of the vegetation cover on SR, we fit a linear mixed model using SR as a response variable, vegetation cover as a fixed effect and study site as a random factor (Figure S4). We then used the residuals of this model as the value for SR, in order to investigate the effect of SR that is not related to plant cover.

As a proxy of trait complementarity, we assessed FD separately for above and below-ground functional traits. We first checked for the correlation between traits (Figures S5 and S6). Then, we computed a multi-trait dissimilarity matrix across all species using the 'gawdis' function (de Bello et al., 2021), which allows to group of correlated traits (Pearson $r > 0.7$). Finally, we employed the dissimilarity matrix to calculate the Rao quadratic entropy index ('melodic' function; de Bello et al., 2016) as a measure of above- and below-ground FD (respectively FD_{above} and FD_{below}). To capture the dominance of a particular set of traits and test the dominance effect, we computed for each plot the CWM of every selected trait using the 'functcomp' function (package FD; Laliberté et al., 2014). Indices of FD and CWM were weighted by species relative abundance as described in van der Plas et al. (2020) and Cadotte (2017).

TABLE 2 Variables used as ecosystem function indicators and corresponding methods.

Ecosystem functions	Variables	Measurement method
Primary productivity	Above-ground plant biomass	Weight of oven-dried plant biomass
Water regulation	Soil water holding capacity	Gravimetric method (Robertson et al., 1999)
	Soil electrical conductivity	Electrical conductivity metre
Carbon storage	Soil total organic carbon	Thermal-gradient analysis
	Soil total carbon	
Decomposition	Initial decomposition rate (*k*)	Tea Bag Index protocol (Keuskamp et al., 2013)
	Stabilisation factor (*S*)	
Nutrient pools	Soil total nitrogen[a]	Thermal-gradient analysis
	CN ratio	
	Soil total concentration of P, K, Mg, Mn,[a] Zn, Ni, Ca,[a] Cu, Cr[a] and Fe	Mehlich III method (Mehlich, 1984)

[a] Variables excluded due to high correlation with other ecosystem function variables (Pearson $r > 0.7$; Table S1).

Ultimately, rare species may also play a relevant role in ecosystem functioning (Dee et al., 2019; Gross et al., 2017; Le Bagousse-Pinguet et al., 2021; Wright et al., 2017); thus, we tested the effect of rarity on EMF. To classify species based on their rarity, we calculated the indices of species restrictedness (Ri) and functional uniqueness (Ui) proposed by Grenié et al. (2017). These two indices indicate whether a species is rare because of its low frequency at the regional scale (i.e. species restrictedness) or rather due to the uniqueness of its functional characteristics in the species pool (functional uniqueness; Violle et al., 2017).

2.4.2 | Ecosystem functioning and multifunctionality

For the analyses we only kept an uncorrelated set of 15 EF indicators (Table S1), namely above-ground biomass, soil electrical conductivity (EC), soil water holding capacity (WHC), initial decomposition rate (*k*), decomposition stabilisation factor (*S*), soil total organic carbon (TOC), soil total carbon (TC), C:N ratio and soil total concentration of P, K, Mg, Zn, Ni, Cu and Fe (Table 2). Ecosystem functioning was quantified using either all the EF variables to assess multifunctionality (EMF) or only a subset of them to separately assess primary productivity, decomposition, soil carbon stock, water regulation and nutrient pools (as shown in Table 2). We used the averaging approach to obtain ecosystem functioning estimates (Byrnes et al., 2014; Maestre et al., 2012). It consisted in computing the mean of the *Z*-scores values across the EF variables. It provides a straightforward measure of multifunctionality, which facilitates the interpretation of the average effect of biodiversity on ecosystem functions. Despite this advantage, the averaging approach has some limitations, for example it is unable to identify instances where one function is performing at a high level while another function is performing at a low level (Byrnes et al., 2014; Gamfeldt et al., 2008). Thus, to overcome this limitation and account for trade-offs between ecosystem functions, we computed multifunctionality also following the multiple-threshold approach (Byrnes et al., 2014; Le Bagousse-Pinguet et al., 2019), which allows estimating the level of diversity needed to perform high levels of multiple EFs simultaneously. This method consisted of counting, in each plot, the number of functions that reach a given performance threshold (20%, 40%, 60% and 80%) based on the highest value of each EF. The two approaches provided similar outcomes; thus, we present the results of the multiple-threshold analysis only in Figure S7.

2.4.3 | Replication statement

2.4.4 | Statistical analysis

The effect of biodiversity and of the environmental gradient (sea proximity) on ecosystem functioning was tested using linear mixed-effect models with the study site as a random factor. Prior to the analysis, we checked for multicollinearity between the predictors and excluded those with variance inflation factor (VIF) >3 (Zuur et al., 2010; Table S2). The final set of uncorrelated predictors tested were SR, total cover, FD_{above}, FD_{below}, H_{CWM}, SLA_{CWM}, $LDMC_{CWM}$, $RDMC_{CWM}$, RTD_{CWM} and proximity to the coastline (Figure S8). Total vegetation cover was also included as a predictor to account for the sparse structure of coastal dune vegetation, which is characterised by a high proportion of bare ground. Nevertheless, results without vegetation cover as a covariate were qualitatively similar (Figure S15). We also included sea proximity in interaction terms with the biodiversity variables to account for the potential impact of stress and disturbance on the BEF relationship. All predictors were centred and scaled to mean 0 and standard deviation 1 to compare parameter estimates. We ran a separate model for every set of ecosystem functions investigated as response variables, that is productivity, decomposition, soil carbon stock, water regulation, nutrient pools and ultimately multifunctionality. For each model, we applied a model selection procedure using the *MuMIn* R package (Barton & Barton, 2023) based on the Akaike information criterion selection (AIC <2) to obtain the best predictors of each response variable (Burnham & Anderson, 2002). Model residuals were visually inspected to ensure homoscedasticity and normality (Zuur et al., 2010). Productivity was log-transformed to meet normality. The R^2 of each model was calculated using the function 'model_performance' (*performance* R package; Lüdecke et al., 2021).

We assessed the relative importance of each predictor as drivers of each ecosystem function following Gross et al. (2017) and Le Bagousse-Pinguet et al. (2019, 2021). Specifically, for each model, we computed the relative importance as the ratio between the absolute values of the standardised regression coefficient of each predictor and the absolute sum of all standardised regression coefficients in the model. Values obtained were then scaled according to the R^2 of each model and expressed as percentage to indicate the relative importance of the predictor estimates over the total variance explained by the model. We summed up predictor relative importance to analyse the overall effect on ecosystem functioning of the following driver categories: (i) SR; (ii) total vegetation cover; (iii) complementarity of above-ground traits (i.e. the relative importance of FD_{above});

TABLE 3 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Plots	Plots	109 plots in six study sites
Species	Species	65 species sampled across 109 plots

(iv) complementarity of below-ground traits (i.e. the relative importance of FD_{below}); (v) dominance effect of above-ground traits (i.e. the summed relative importance of H_{CWM}, SLA_{CWM} and $LDMC_{CWM}$); (vi) dominance effect of above-ground traits (i.e. the summed relative importance of $RDMC_{CWM}$ and RTD_{CWM}); (vii) diversity-stress gradient interaction effect (i.e. the summed relative importance of the interaction between SR, FD_{below}, H_{CWM}, SLA_{CWM}, $LDMC_{CWM}$, $RDMC_{CWM}$, RTD_{CWM} and sea proximity); and (viii) and environmental stress effect (i.e. the relative importance of sea proximity).

We finally investigated how rare species influence EMF. First, we applied a linear mixed-effect model to quantify the effect of the presence of each single species on EMF. Specifically, we performed a model for each species (for a total of 65 species, Table 3), using species presence/absence as explanatory variable, multifunctionality as response variable and site as random effect. Then, from each model, we extracted the effect size (beta coefficient) of the species–EMF relationship as a measure of how strongly each species influences ecosystem functioning. Finally, we used this species–EMF relationship as response variable in two linear models to check whether (1) species restrictedness (Ri) or (2) functional uniqueness (Ui) influence how strongly species contribute to functioning. Species restrictedness was logit-transformed prior to the analysis to meet the model assumptions.

All data and statistical analyses were performed using R 4.3.1 (R Core Team, 2023).

3 | RESULTS

3.1 | Species and community composition

Across the surveyed plots, we found a total of 65 species (Table S3). Plot-level SR ranged from 2 to 14 species (mean = 7.09 ± 0.27, SD = 2.85), while the total vegetation cover spanned from 5% to 100% (mean = 55.4% ± 2.5%, SD = 25.97%). The upper beach (EUNIS classification N12) was dominated by *Cakile maritima* subsp. *maritima* and *Salsola kali*; in the shifting dunes (N14) the most abundant species were *Thinopyrum junceum*, *Anthemis maritima* subsp. *maritima* and *Pancratium maritimum*. In the interior dune grasslands (N16), *Silene colorata*, *Cutandia maritima* and *Lomelosia rutifolia* were prevalent.

3.2 | Biodiversity effects on ecosystem functioning

We found that total vegetation cover was the single strongest predictor of all EFs (average predictor relative importance = 8%, ranging from 0% to 14%; Figure 2a), with a positive effect on all functions except decomposition (Figures 3 and 4; Figures S9–S13). We also found an effect of SR, but it was weaker (average relative importance = 5%, ranging from 0% to 10%) and less consistent across functions, in particular for productivity which decreased with SR (Figure 3; Figure S9).

From a functional trait perspective, dominance effects were generally stronger than trait complementarity (Figure 2a). On average, dominance effects (assessed as the sum of the relative importance of each traits' CWM) explained 15% (1%–26%) of the variance across ecosystem functions, compared with 8% (3%–16%) of trait complementarity (Figure 2a). Moreover, we identified a specific combination of traits promoting all ecosystem functions (Figure 3), specifically tall species (high H_{CWM}), with acquisitive leaves (high SLA_{CWM} but low $LDMC_{CWM}$) and conservative roots (high $RDMC_{CWM}$ and RTD_{CWM}). By contrast, trait complementarity had a lower effect on most EFs (8%), which were weakly or not influenced by FD_{above} and even decreased with FD_{below} (Figures 2 and 3).

3.3 | Effects of above- versus below-ground functional traits on ecosystem functioning

We found that root traits influenced ecosystem functioning, explaining some of the variation in ecosystem functioning that was not captured by above-ground traits. Overall, the effect of below-ground traits was on average comparable to that of above-ground traits (Figure 2b). Specifically, the average importance of below-ground traits (assessed as the sum of each below-ground traits' CWM and FD_{below} relative importance) across all ecosystem functions was 10% (ranging from 3% to 22%) compared with 14% (1% to 21%) of above-ground traits. Variation in productivity, carbon stock and nutrient pools were equally influenced by above and below-ground traits (their relative importance was, respectively, 21% and 22% of the total variance explained for productivity, 19% and 15% for carbon stock, 11% and 8% for nutrient pools; Figure 2b). On the contrary, variation in water regulation and multifunctionality were mostly driven by above-ground traits (relative importance of 15% above-ground traits compared with 6% and 5% of below-ground traits, respectively), while decomposition was mostly influenced by below-ground traits (relative importance of 1% of above-ground traits and 3% of below-ground traits; Figure 2b), although the total variance explained by this model was anyway low.

3.4 | The effect of stress and disturbance on BEF relationships

Overall, stress and disturbance associated with the sea–inland gradient modify BEF relationships (Figure S14). In particular, we found strong negative interactions of the proximity to the sea on the effects of SR on nutrient pools and EMF, in the sense that SR had a positive effect on EF only far from the sea while this effect decreased as stress and disturbance increased (Figures 3 and 5; Figure S13). Similarly, the positive effect of $RDMC_{CWM}$ on water regulation, nutrient pools and multifunctionality, as well as of $LMDC_{CWM}$ on carbon sequestration, and of SLA_{CWM} on decomposition, decreased along the sea–inland gradient as stress increased (Figures 3 and 5; Figures S10–S13).

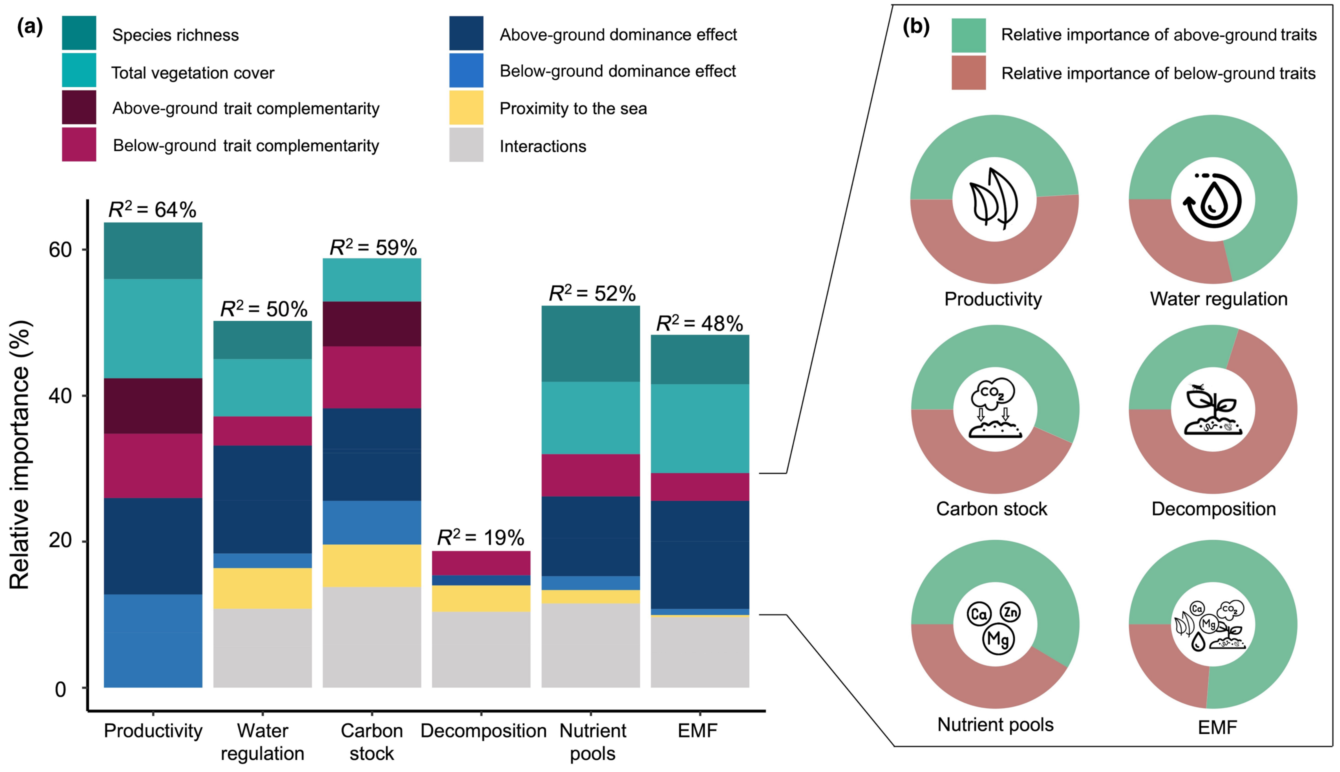

FIGURE 2 Relative importance of the effect of plant diversity and the environmental gradient on individual ecosystem functions and multifunctionality. (a) The relative importance is expressed as % of the total variance explained (model R^2) by each predictor in the models and is based on the absolute values of their standardised regression coefficients. Above- and below-ground trait complementarity refer respectively to the effects of $\mathrm{FD}_{\mathrm{above}}$ and $\mathrm{FD}_{\mathrm{below}}$ (in dark and light purple). The above-ground dominance effect (in dark blue) is the summed effect of the above-ground traits $\mathrm{H}_{\mathrm{CWM}}$, $\mathrm{SLA}_{\mathrm{CWM}}$ and $\mathrm{LDMC}_{\mathrm{CWM}}$, while the below-ground dominance effect (in light blue) is the summed effect of the below-ground traits $\mathrm{RDMC}_{\mathrm{CWM}}$ and $\mathrm{RTD}_{\mathrm{CWM}}$. Proximity to the sea effect (in yellow) includes the effect of sea distance and of the interactions. (b) Donut plots comparing the overall relative importance of above- and below-ground traits (respectively in green and brown). The two groups consist of the summed variance explained by both FD and CWM indices of above- or below-ground traits separately. CWM, community-weighted mean; EMF, ecosystem multifunctionality; FD, functional diversity; H, plant height; LDMC, leaf dry matter content; RDMC, root dry matter content; RTD, root tissue density; SLA, specific leaf area.

3.5 | The effect of rare species on multifunctionality

As concerns species rarity, the contribution of species to multifunctionality (EMF) increased with their restrictedness (estimate = 0.18, $p < 0.001$). However, this relationship did not hold for functional uniqueness, since more functionally unique species contributed less to EMF (i.e. negative relation of species-EMF contribution with uniqueness, estimate = −4.32, $p < 0.05$, Figure 6).

4 | DISCUSSION

The past decades have seen major progress in acknowledging that biodiversity promotes ecosystem functioning, but the mechanisms by which biodiversity operates in natural ecosystems are still not fully understood (Dee et al., 2023; Duffy, 2009; Lepš, 2004; van der Plas, 2019). Our study uses Mediterranean coastal dunes as model systems to unravel the drivers of the diversity–functioning relationship in plant communities exposed to a natural gradient of stress. We found that below-ground traits are important drivers of ecosystem functioning, explaining a portion of variation not related to above-ground traits. The dominance effect was overall stronger and ecosystem functions were higher in species-rich communities with a specific functional structure, that is composed of tall species with a balance between an acquisitive functional strategy in the above-ground (i.e. high SLA and low LDMC) and a conservative one in the below-ground (i.e. high RDMC and RTD). However, the effect of species diversity and dominant functional traits on multiple ecosystem functions decreased along the sea–inland gradient as stress increased, indicating that stress can reduce the ability of biodiversity to support single ecosystem functions as much as multifunctionality. Additionally, we showed that rare species play a key role in promoting multifunctionality in natural ecosystems, and the underlying reasons need to be investigated further.

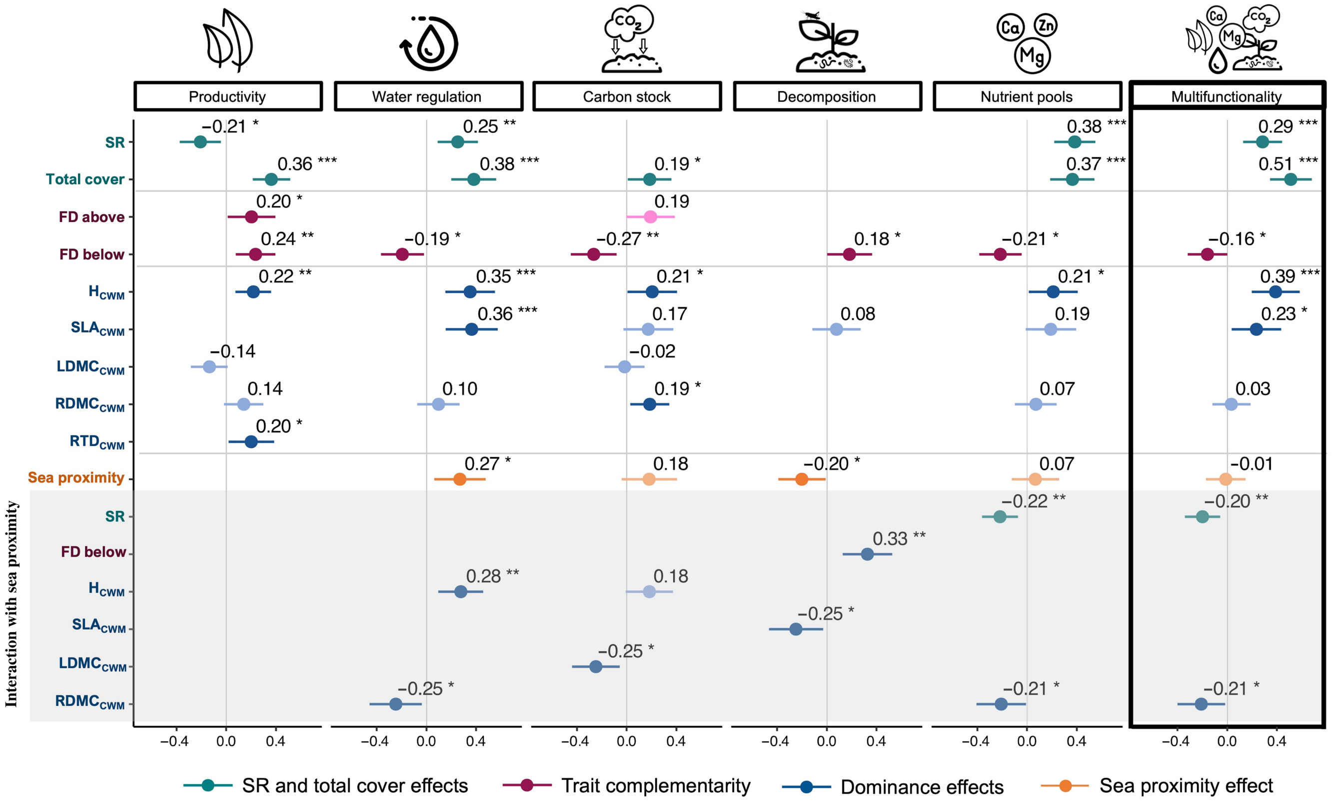

FIGURE 3 Estimate plots showing the effect of biodiversity and the environmental gradient on individual ecosystem functions and multifunctionality. Each column refers to the final linear model after model selection. Dots indicate the standard regression coefficients of each model predictors while lines the associated 95% confidence intervals. Standard regression coefficients and significance are shown next to each dot. Coefficients' significance indicated as follows: $p < 1$–0.05, *$p < 0.05$–0.01, **$p < 0.01$–0.001 and ***$p < 0.001$. Significant coefficients are shown in full colours, while non-significant ones in transparency. The grey band at the bottom refers to the interaction coefficients which describe how the effect of the biodiversity metrics on ecosystem functions varies along the sea–inland gradient. A negative effect size would indicate, for example that the effect of SR on EMF decreases in proximity to the sea. CWM, community-weighted mean; FD, functional diversity; H, plant height; LDMC, leaf dry matter content; RDMC, root dry matter content; SLA, specific leaf area; SR, species richness.

4.1 | Ecosystem functioning is promoted by dominant functional traits

Understanding how biodiversity simultaneously influences multiple ecosystem functions in natural ecosystems is one of the main challenges in ecology. In our study system, single ecosystem functions and multifunctionality were generally higher in communities dominated by some specific functional traits (i.e. dominance effect) rather than in communities with high FD (i.e. trait complementarity). This result is consistent with current literature studying several ecosystem functions in dryland ecosystems (Gross et al., 2017; Le Bagousse-Pinguet et al., 2019), temperate forests and grasslands (Chollet et al., 2014; van der Plas, 2019), but contrasts with the emerging evidence that multifunctionality is rather more strongly supported by FD (Tang et al., 2023; Valencia et al., 2015; van der Plas, 2019). A possible explanation for this inconsistency is that, while other studies found that every individual ecosystem function is influenced by a particular set of species and traits (Valencia et al., 2015; van der Plas, 2019), here, on the contrary, we identified the same type of community functional structure increasing all ecosystem functions and, ultimately, multifunctionality. In particular, we found greater ecosystem functioning in species-rich communities with high vegetation cover and dominated by tall species with a trade-off between acquisitive leaves and conservative roots, such as *Calamagrostis arenaria* subsp. *arundinacea* and *Helichrysum stoechas*. Moreover, this study primarily focused on 'supporting' ecosystem functions (Garland et al., 2021). Consequently, the observed biodiversity effect may not necessarily extend to other aspects of ecosystem functioning. In fact, recent studies have shown that maintaining the functioning of coastal dunes stable over time rather requires the conservation of slow-growing and long-living perennial species (La Bella et al., 2023).

Noteworthy, productivity was the only function that was quantitatively equally influenced by dominance effect and trait complementarity. Moreover, contrary to other functions, SR had a negative effect on productivity. This result warns against generalisations when studying the effect of diversity on ecosystem functioning, especially since productivity is often used as a proxy for other functions (Baert et al., 2018; Hulvey et al., 2013; Lopatin et al., 2019), but here we showed that it can be influenced by aspects of biodiversity that contrast with the other functions.

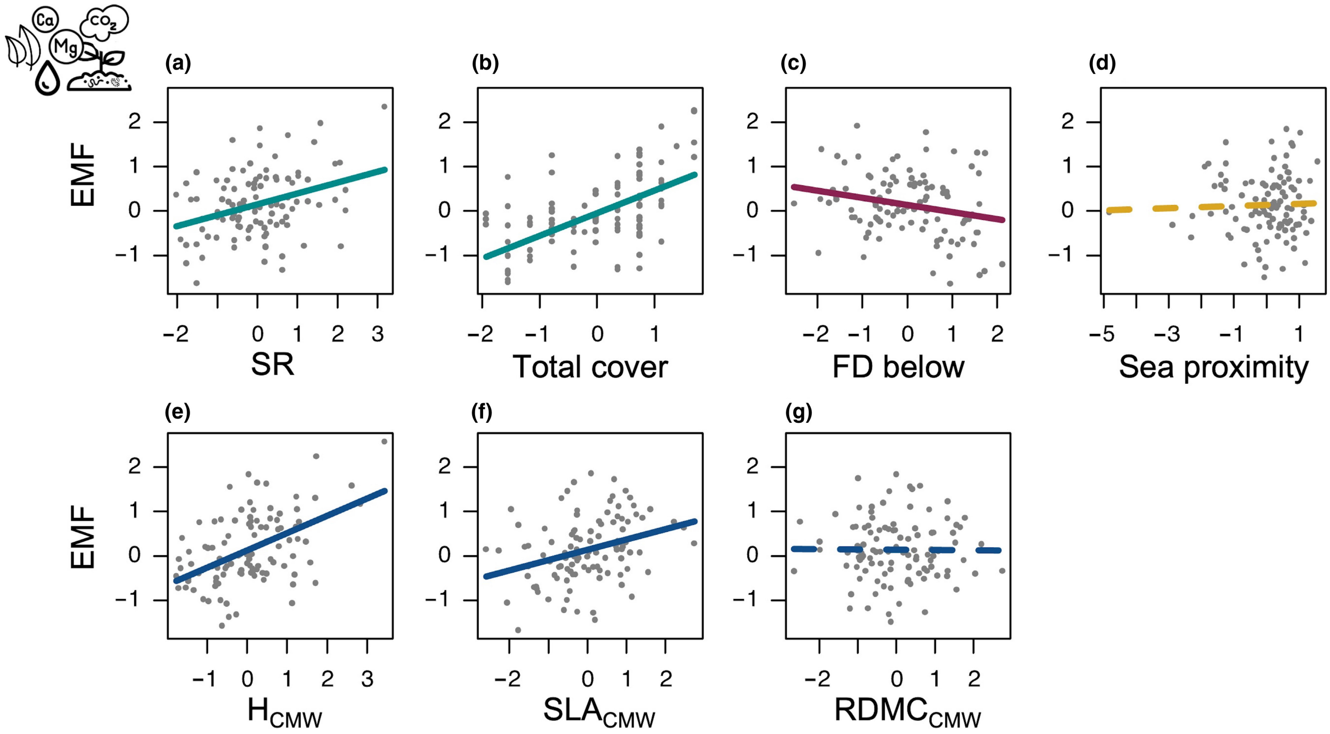

FIGURE 4 Effect of (a) species richness (SR), (b) total cover, (c) below-ground functional diversity (FD below), (d) sea proximity, (e) the CWMs of plant height (H_{CWM}), (f) specific leaf area (SLA_{CWM}) (g) and root dry matter content ($RDMC_{CWM}$) on ecosystem multifunctionality (EMF). Each point represents a plant community sampled within a 4 m^2 plot. Continuous regression lines refer to significant relationships between the two variables while dotted lines to non-significant relationships detected through mixed-effect linear models. CWM, community-weighted mean.

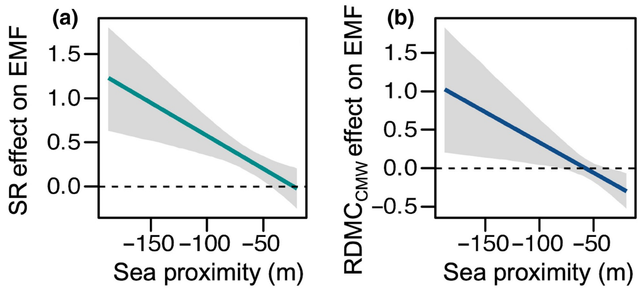

FIGURE 5 Interaction plots showing how the biodiversity effect on multifunctionality varies along the sea–inland gradient. Specifically, the graphs show how the effect of (a) species richness (SR) and (b) the CWM of root dry matter content ($RDMC_{CWM}$) on multifunctionality varies with proximity to the sea. On the *y*-axis, values greater than zero indicate a positive biodiversity and ecosystem functioning relationship, while values lower than zero a negative relationship. Continuous lines represent the interaction coefficient. Grey bands are the 95% confidence interval indicating the uncertainty area of the interactions. CWM, community-weighted mean; EMF, ecosystem multifunctionality.

4.2 | Below-ground functional traits matter for multiple ecosystem functions and their effect cannot be inferred by above-ground traits

One of the major knowledge gaps in the BEF research lies in the role played by below-ground traits (Freschet, Roumet, et al., 2021; Laliberté, 2017; van der Plas et al., 2020). Specifically, it remains unclear whether the effect of below-ground traits on ecosystem functioning can be inferred by above-ground traits. Here, we found that below-ground traits do not mirror the effects exerted by above-ground traits, but independently influence ecosystem functioning. Results show that below-ground traits explain a portion of the variation in ecosystem functions that is not captured by above-ground traits. Moreover, the effect of root traits was quantitatively comparable to that of above-ground traits, and for decomposition was even higher. These findings are in line with recent studies that showed a lack of coordination between above and below-ground traits in several ecosystems including coastal dunes (Bricca et al., 2023; Carmona et al., 2021; Ciccarelli et al., 2023; but see Weigelt et al., 2021). To our knowledge, this is the first attempt to explicitly test and compare the relative contribution of below-ground traits and above-ground ones, highlighting that below-ground traits influence multiple ecosystem functions as much as above-ground traits. As a result, above-ground traits cannot be used as a surrogate and below-ground traits should be routinely considered for predicting ecosystem functioning.

Specifically, on the above-ground side, in line with the literature, we found that communities dominated by tall species with high SLA and low LDMC overall increased ecosystem functioning (Garnier et al., 2004, 2015; Quétier et al., 2007). This functional composition refers to fast-growing and acquisitive leaf strategy (Díaz et al., 2016; Reich, 2014), that is species that strategically concentrate energies for a fast nutrient acquisition and are associated with, for example

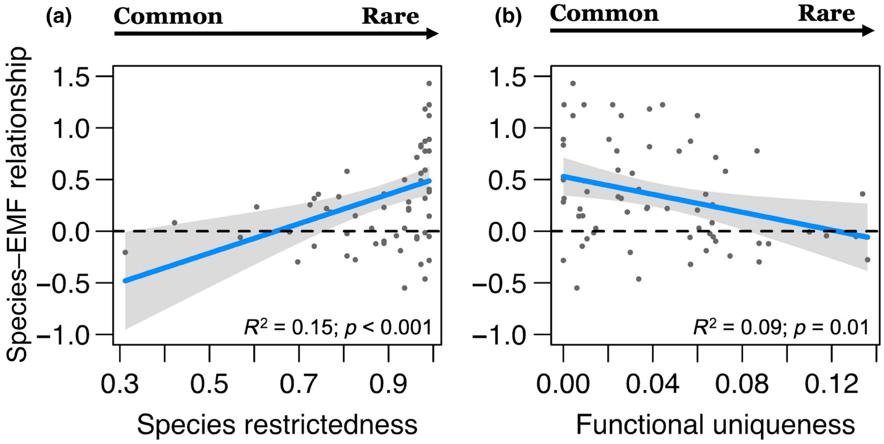

FIGURE 6 Effect of rarity on multifunctionality (EMF) for (a) species restrictedness and (b) functional uniqueness. The *y*-axes show the relationship between the presence of each species sampled and multifunctionality. Values higher than 0 indicate a positive relationship while values lower than 0 negative. Lines refer to the average response of the species–multifunctionality (EMF) relationship to the rarity index and each dot indicates a species. The figure shows the original data of species restrictedness while it was logit-transformed to approximate normality for the statistical analysis. EMF, ecosystem multifunctionality.

thin leaves, large photosynthetic area and high photosynthetic rate. Acquisitive leaves have been frequently related to high productivity, rapid tissue turnover and decomposition, and large litter input which in turn promote fast nutrient mobilisation and availability in the soil (Cornwell et al., 2008; De Deyn et al., 2008; Fortunel et al., 2009; Funk et al., 2017; Garnier et al., 2015). Interestingly, plant height had a strong positive effect across different ecosystem functions. This could be attributed, at least in part, to the buffering effect of canopy height on local microclimate (Guimarães-Steinicke et al., 2021). Tall plants can mitigate the harsh environmental condition of coastal dunes (e.g. by cooling surface temperatures via shading, increasing soil humidity and providing protection from wind), thereby facilitating the growth and survival of other species (Wright & Francia, 2024). In this way, taller canopies can enhance biodiversity and ecosystem functions such as productivity, water regulation, carbon capture and nutrient cycling (Beugnon et al., 2024; Boisvenue & Running, 2006; Novick et al., 2024). On the below-ground side, we found that species with conservative roots (e.g. *Thinopyrum junceum* and *Achillea maritima* subsp. *maritima*), characterised by high RDMC, overall enhanced the functioning of coastal dune ecosystems. In addition, and exclusively for decomposition, we found a positive effect of below-ground FD, which was probably related to a greater diversity in the soil microbial community (Bardgett et al., 2014; Freschet et al., 2018). On the contrary, below-ground FD had a negative effect on all the other ecosystem functions, confirming that a dominant slow-growing and conservative root structure is needed for sustaining ecosystem processes and functions (Le Bagousse-Pinguet et al., 2019). Conservative root—that is roots implemented for nutrient conservation, thus rich in lignin and recalcitrant compounds—have been previously associated either with slow decomposition and thus low amount of nutrients in the soil (Klumpp & Soussana, 2009; Lavorel et al., 2007), or with higher decomposition and nutrient pools, thanks to the greater association with arbuscular mycorrhizal fungi (Eissenstat et al., 2015; Jo et al., 2016; Kong et al., 2014). These contrasting patterns call for more research to clarify how below-ground traits influence decomposition and nutrient cycling, for example by analysing the effect of root traits related to the fungal 'collaboration' gradient (Bergmann et al., 2020). As concerns soil carbon accumulation and water regulation, which are often related (Freschet et al., 2018), previous studies found that they are promoted by a trade-off between high productivity and slow decomposition, thus by communities that supply the system with large quantities of litter (high carbon input) but slow decomposing (low carbon output) (De Deyn et al., 2008; Schulze, 2006). Accordingly, we found that soil carbon stock and water regulation were higher in communities composed by either: fast-growing acquisitive traits in the above-ground, which ensures higher biomass input in the system; and slow-growing below-ground traits, which produce a more recalcitrant litter that slowly decomposes (Cornwell et al., 2008; De Deyn et al., 2008; Fortunel et al., 2009).

4.3 | Environmental stress impacts the biodiversity effect on ecosystem functioning

Assessing the influence of the environmental conditions on ecosystem functioning has become a central focus over the last decades in the face of increasing environmental changes and biodiversity loss (van der Plas, 2019; Wardle, 2016). Studying how the BEF relationship varies along gradients of stress could aid in tackling this issue. Overall, we found that the effect of SR and CWMs decreased along the stress gradient, highlighting the context-dependency of BEF relationships. Previous attempts to clarify the influence of increasing stress conditions on ecosystem functioning have resulted in both increasing (Dee et al., 2019; Hong et al., 2022; Isbell et al., 2011; Mouillot et al., 2013; Spohn et al., 2023) and decreasing (Baert et al., 2018; De Boeck et al., 2008; Steudel et al., 2012) effects on the BEF relationship.

One possible explanation of these contrasting patterns lies in stress intensity, in line with Baert et al. (2018) who found that the BEF relationship can change unimodally along environmental stress gradients. Specifically, biodiversity effects can be positive at low levels of environmental pressures, suggesting an initial resistance of species-rich communities driven by the rising of some stress-tolerant species or by higher expression of niche complementarity (Hodapp et al., 2016; Steudel et al., 2012). However, when stress persists and increases enough to strongly limit population growth across species, then the biodiversity effect collapses (negative relationship; Baert et al., 2018). Accordingly, if only analysing the BEF relationship across conditions of mild-to-moderate stress intensity, we are likely to detect an increasing biodiversity effect, but moderate-to-high stress conditions, as in our study system, actually produce a decline in the biodiversity effect. By applying a space-for-time framework (Pickett, 1989), our results therefore suggest that in natural ecosystems the potential long-term impact of ongoing environmental changes may weaken BEF relationships even more than previously anticipated. For example, in coastal dunes, climate change is expected to cause sea level rise and extensive coastal erosion, which will increase plant communities' exposure to stress such as salinity, wind and sedimentation. Consequently, our findings suggest that in these systems, as well as others characterised by strong environmental or land-use gradients, biodiversity may not be able to buffer the impacts of ongoing environmental changes on ecosystem functioning.

4.4 | Rare species promote EMF

Rare species are likely more vulnerable to future environmental changes (Foden et al., 2019; Sodhi et al., 2009), underscoring the need to understand their role for the functioning of ecosystems. In our study, we found that rare species, that is species that are regionally sparse and locally not abundant, tended to increase EMF. This result can be explained by the positive relationship between SR and ecosystem functioning: indeed, species-rich communities are likely to embrace a larger number of rare species than species-poor communities. Consequently, increasing SR also increases the number of rare species, which can generate positive interspecific interactions (mutualism and facilitation) that enhance ecosystem functioning (Dee et al., 2019; Wright et al., 2017). However, in contrast with previous studies, suggesting that rare species can influence ecosystem functioning disproportionally by displaying some unique functional traits important for the ecosystem (Gross et al., 2017; Le Bagousse-Pinguet et al., 2021); in this study, the effect was not mediated by rare functional traits, as rare species exhibited a combination of traits similar to more common species. Furthermore, we found that the presence of species bearing rare traits decreases multifunctionality, thus reinforcing the idea that ecosystem functioning is enhanced by certain common traits within the community. This result is in line with our findings that increasing FD does not necessarily contribute to multifunctionality. Overall, these findings highlight that rare species influence ecosystem functioning despite their low abundance and the importance of conserving rare species in addition to highly functioning species.

5 | CONCLUSIONS

The present study aimed to clarify how biodiversity influences the functioning of natural ecosystems exposed to an intense gradient of natural stress. Overall, our findings underline that simultaneously maintaining multiple ecosystem functions requires the conservation of specific functional strategies in addition to high SR and rare species. On the contrary, we warn over the potential impact that ongoing environmental changes could have on natural ecosystems, by decreasing the ability of biodiversity to sustain ecosystem functioning. Finally, although we missed some key root-related traits (e.g. root exudates or mycorrhizal fungi) potentially influencing plant–soil processes, this study ultimately highlights the importance of considering overlooked root traits in addition to the well-studied above-ground traits and emphasises the need to further investigate the effect of below-ground traits on ecosystem functioning. Indeed, a better understanding of root-functioning relationships would significantly improve our ability to predict the impacts of biodiversity loss on ecosystem functioning.

AUTHOR CONTRIBUTIONS

ATRA, MC and GLB conceived and designed the study. GLB collected the data. AB, DC, and AS contributed to the data. MM helped with the soil analyses. ATRA, MC, TJ and GLB analysed and interpreted the data. GLB wrote the first draft of the manuscript. All authors made significant contributions to the manuscript and approved it for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.24659154 (La Bella et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Relationship between diversity indices and sea proximity.
Figure S2. Sea proximity as a proxy of the coastal dune zonation.
Figure S3. Sensitivity analyses without trait imputation.
Figure S4. Regression between species richness and total vegetation cover.
Figure S5. Principal Component Analysis of above-ground traits.
Figure S6. Principal Component Analysis of below-ground traits.
Figure S7. Multiple-threshold approach for quantifying multifunctionality.
Figure S8. Pairwise correlation between predictors.
Figure S9. Biodiversity effect on productivity.
Figure S10. Biodiversity and environmental effect on water regulation.
Figure S11. Biodiversity and environmental effect on carbon stock.
Figure S12. Biodiversity and environmental effect on decomposition.
Figure S13. Biodiversity and environmental effect on nutrient pools.
Figure S14. Interaction between sea proximity and biodiversity effects.
Figure S15. Sensitivity analyses without vegetation cover.
Table S1. Correlation matrix between ecosystem function variables.
Table S2. Variance inflation factor test.
Table S3. Species list.
Method S1. Ecosystem function variables: sampling and soil analysis.
Method S2. Trait imputation.

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