Using revisitation data for predicting changes in ecosystem functioning across protected and non-protected coastal dunes

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ARTICLE IMPACT STATEMENT

Hindcasting ecosystem functions from historical vegetation data enables monitoring protection efficacy in preserving ecosystem functionality

KEYWORDS: BEF; biodiversity; ecosystem functioning; Resurvey; Natura 2000; protected areas; temporal changes; trait-based approach

ABSTRACT

Protected areas are generally designed to conserve biodiversity. However, how well they also contribute to maintaining ecosystem functions that plant diversity supports has rarely been explicitly tested, often due to the lack of historical ecosystem function data. Here, we used a trait-based approach to reconstruct past ecosystem functioning and examine changes in functions over the last 15 years in protected and unprotected coastal dune ecosystems, checking where functions remain stable over time. First, we resurveyed vegetation in quasi-permanent plots and measured in the present several ecosystem functions related to productivity, carbon, water, nutrient cycling, erosion control, and invasion resistance across six coastal dune sites in Central Italy. Second, using these data, we quantified Biodiversity-Ecosystem Function (BEF) relationships and employed them to hindcast past ecosystem functions based on historical vegetation surveys. Finally, as a case study, we applied this method to assess temporal changes in ecosystem functioning under three protection regimes: national protected areas (i.e. strict protection), Natura 2000 sites (loose protection), and non-protected areas. Productivity, carbon, and water regulation increased over time in non-protected areas, likely due to an expansion of ruderal and non-native species, that are usually more productive. Within Natura 2000 sites, communities showed a decrease in erosion control and invasion resistance potential, due to the loss of important dune-building species and the spread of non-natives. Only within national protected areas, ecosystem functions did not undergo significant temporal changes, and invasion resistance even increased. Our results suggest that in the study area ecosystem functioning remain stable over time only in areas under strict protection. More broadly, our study demonstrates the potential for using revisitation data in combination with locally estimated BEF relationships to hindcast past ecosystem functioning, providing a valuable tool for monitoring long-term functional changes in response to conservation measures.

INTRODUCTION

Monitoring ecosystem functions is critical for assessing the health and resilience of ecosystems and ensuring their ability to provide essential services to human societies. The post-2020 Global Biodiversity Framework (GBF) of the Convention on Biological Diversity (CBD) emphasizes not only the need to halt biodiversity loss but also to maintain and enhance ecosystem functions and services, as reflected in its goals and targets (CBD, 2022). Similarly, the United Nations Sustainable Development Goals (SDGs) highlight the importance of sustaining ecosystem integrity to support human well-being (UN, 2015). Despite these global commitments, measuring ecosystem functions presents significant challenges due to their

complex, multi-dimensional nature and the difficulty of obtaining long-term data. Many ecosystem processes operate at large spatial and temporal scales, requiring indirect methods or models to infer past dynamics. This limitation complicates the evaluation of conservation strategies, such as protected areas and restoration efforts, which should aim to preserve not only species diversity but also the ecological processes that sustain ecosystems. Without robust estimates of past ecosystem functions, it remains difficult to determine whether conservation actions have successfully maintained or restored functional integrity.

Worldwide biodiversity is undergoing an unprecedented decline, driven by factors such as habitat degradation, climate change, and the introduction of invasive species (IPBES, 2019). Given the strong relationship between Biodiversity and Ecosystem Functioning (also known as BEF relationship) found across a wide range of natural ecosystems (Hanisch et al., 2020; La Bella et al., 2024; Ratcliffe et al., 2017; Valencia et al., 2015), shifts in biodiversity can significantly alter ecosystem processes and functions. Nevertheless, while biodiversity changes have been widely documented, fewer studies have quantified the extent and direction in which functions are changing in natural ecosystems (Brauman et al., 2020). As ecosystem functions largely underpin the vital services provided by ecosystems to people (Garland et al., 2021; MEA, 2005), monitoring changes in ecosystem functioning is of crucial importance for human well-being.

To prevent further biodiversity loss and safeguard the last remaining intact natural areas, European countries have implemented national or international conservation measures (Heslenfeld et al., 2008), including the establishment of protected areas (CBD, 2022; UN, 2015). Although primarily conceived to reduce human-induced pressures on biodiversity (CBD, 2022), by conserving biodiversity protected areas also offer the opportunity to conserve the variety of ecosystem functions and processes that biodiversity supports. However, since most protected areas are not explicitly managed to maintain ecosystem functionality, their ability to counteract changes in ecosystem functions remain uncertain.

Overall, studies assessing temporal changes in ecosystem functioning in real-world ecosystems are scarce for several reasons (DeCock et al., 2023; Waldén et al., 2023; Williams et al., 2005). First, the interest in quantifying ecosystem functions in natural systems has only surged in recent years (Garland et al., 2021; van der Plas, 2019), and consequently, systematic data collection has just started, which has up to now prevented comparisons with past conditions (Kremen & Ostfeld, 2005; Meyer et al., 2015). Second, unlike biodiversity metrics, measuring ecosystem functions is challenging and methods are still highly debated (Byrnes et al., 2014; Garland et al., 2021; Manning et al., 2018; Meyer et al., 2015). In fact, while some

ecosystem functions can be quantified through direct, well-accepted indicators (e.g. biomass production), for other functions choosing the most appropriate indicator is less clear (e.g. water regulation) (Farnsworth et al., 2017; Garland et al., 2021; Jax, 2005). Moreover, measuring ecosystem functions is usually resource-intensive and time-consuming, requiring technical expertise and equipment which were until recently not widely accessible (Meyer et al., 2015). Consequently, reconstructing past data in order to track temporal changes in ecosystem functioning requires innovative solutions.

Plant functional traits are increasingly recognised as reliable predictors of several ecosystem functions and processes, such as productivity, carbon sequestration, and nutrient cycling (de Bello et al., 2010; Díaz et al., 2007; Funk et al., 2017; Lavorel & Garnier, 2002). As a result, plant traits are now routinely used in BEF research together with taxonomic diversity for quantifying the effect of species and communities on ecosystems. For example, species-rich communities dominated by fast-growing acquisitive plant species have been frequently associated to fast decomposition and biogeochemical cycles (Cornwell et al., 2008; Funk et al., 2017; Garnier et al., 2015; Lavorel & Garnier, 2002). Due to the strong BEF relationship, several trait-based approaches have been proposed to predict ecosystem functioning beyond the observed data, e.g. to larger datasets (Bodenhausen et al., 2023; Chen et al., 2023), or for predicting ecosystem functions under future scenarios of environmental change (Klumpp & Soussana, 2009; Madani et al., 2018; Quétier et al., 2007). BEF relationships can thus potentially also be used to hindcast past functioning levels using historical data, with even less uncertainty compared to e.g. forecasts based on many possible future scenarios. This potential application provides a chance to compare past and present ecosystem functions and, thus, to assess how ecosystems have responded to the last decades of global changes. As such, here we propose predictive modelling to reconstruct past ecosystem functions based on historical vegetation composition in order to track temporal changes in functioning, particularly in highly endangered ecosystems.

Coastal dunes are very peculiar ecosystems, rich in highly specialized flora with an outstanding conservation value (Acosta et al., 2009; Van der Maarel, 2003). They also provide multiple essential services to society, e.g. coastal protection against the sea (Liquete et al., 2013) and recreational activities (Drius et al., 2019a). Despite their valuable features, coastal dunes are among the most threatened ecosystems in Europe, especially in the Mediterranean basin (Janssen et al., 2016; Prisco et al., 2020). High anthropogenic impact related to urban expansion and tourism as well as the spread of invasive alien species, have led to extensive degradation of coastal habitats and to biodiversity declines (Carboni et al., 2010; Defeo et al.,

2009; Drius, Bongiorni, et al., 2019; Malavasi et al., 2016; Schlacher et al., 2007). Still, the consequences of habitat degradation for the functioning of coastal dune ecosystems have been rarely quantified.

In this study, using coastal dunes as model system, we tackled two key objectives: (1) testing the predictive ability of biodiversity for hindcasting ecosystem functioning and assessing possible gains and losses in functions; (2) exploring the performance of different types of protected areas in maintaining the level of ecosystem functioning stable over time. Using a stepwise approach (Fig. 1), we first assessed BEF relationships in a subset of vegetation plots and estimated the predictive ability of biodiversity for hindcasting ecosystem functioning. Second, we applied the estimated BEF relationships to predict ecosystem functions of a large resurveying vegetation dataset as well as past ecosystem functioning levels based on historical vegetation data. Finally, we applied this method to a case study and explored temporal trends in ecosystem functioning under three different protection regimes: nationally designated strictly protected areas, sites belonging to the European Natura 2000 network (protected areas that allow a sustainable use of natural resources), and non-protected areas.

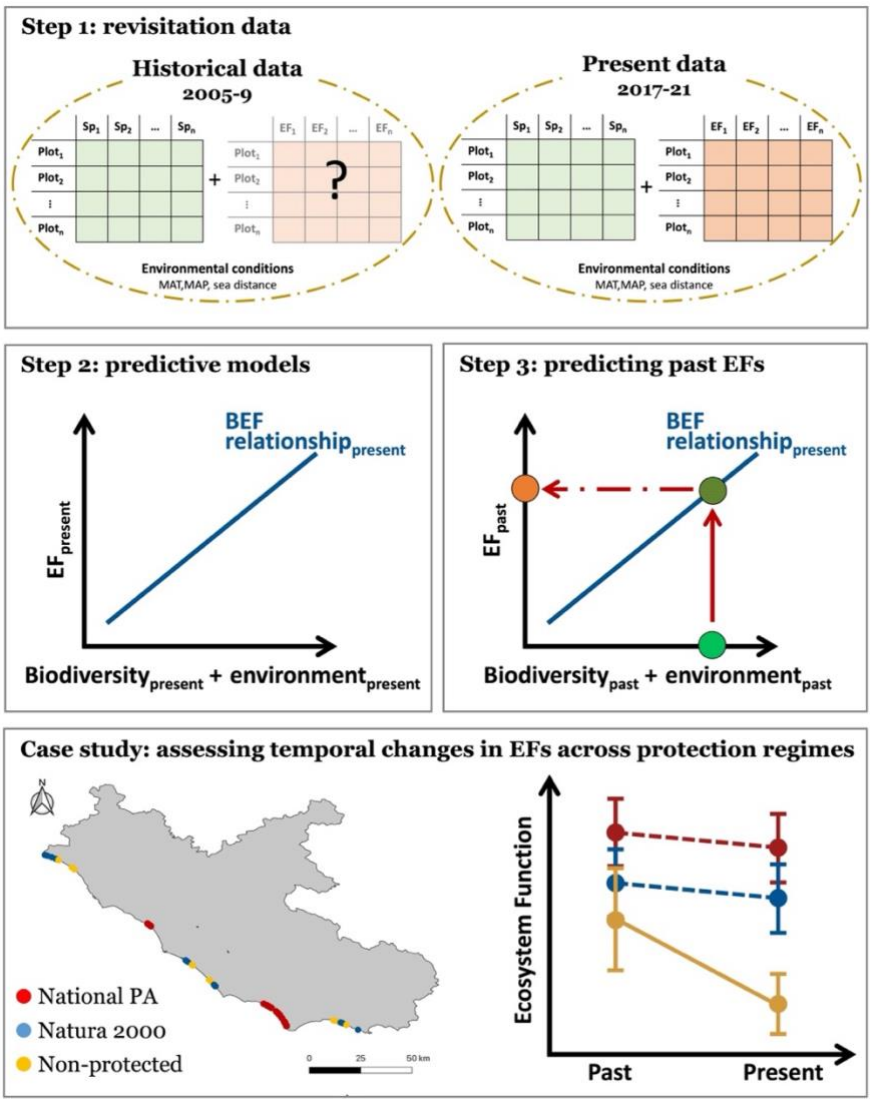


Figure 1 Workflow used to assess temporal changes in ecosystem functioning. **Step 1**: in 2021, we resurveyed vegetation in quasi-permanent plots and collected several ecosystem function variables. **Step 2**: using these data, we assessed BEF relationships and employed them to hindcast past ecosystem functioning based on historical vegetation surveys. **Step 3**: we assessed temporal changes in ecosystem functioning under different protection regimes, i.e. national protected areas (PA), Natura 2000 sites, and non-protected areas.

METHODS

Study area and protection status

The research was conducted on coastal dune ecosystems situated along the Tyrrhenian coast of Central Italy, specifically in the region Lazio, consisting of approximately 250 km of coast.

This geographical area falls within the Mediterranean climatic region and consists of Holocene sandy dunes forming a narrow stretch along the shoreline (Acosta et al., 2009).

For determining the protection status, we acquired spatial data related to the World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM), from the "Protected Planet" data portal (UNEP-WCMC and IUCN, 2025). We consider three categories of protection: nationally designated protected areas, including both national parks and natural reserves (hereafter national protected areas); sites belonging to the Natura 2000 network, under Habitat Directive 92/43/EEC and Bird Directive 79/409/EC, which, compared to national protected areas allow a sustainable, albeit limited, use of nature (e.g., controlled dune stabilization or regulated tourism; Dudley, 2008; EC, 2025; Tsiafouli et al., 2013); and areas without any legal protection status.

Historical and revisitation data

We used an Italian database of coastal dune vegetation resurveying ("RanVegDunes" dataset included in "ReSurveyEurope"; Knollová et al., 2024) consisting in 286 quasi-permanent random plots (4 m^2) for the study area. These plots were uniformly distributed across six study sites (Fig. S1) covering all herbaceous habitats of the coastal vegetation zonation along the sea-inland gradient in central Italy, i.e. the upper beach, embryo dunes, shifting dunes, and dune grasslands (see Sperandii et al., 2019 for a description of the habitats). Overall, plot fall within two national protected areas, five Natura 2000 sites, and six non protected areas (Fig. 1; Table S1). Plots were historically surveyed between 2005-2009 (historical data) and then revisited between 2017-2021 (revisitation data), thus after a period of 10-15 years. In each plot, sampling consisted in recording the number and percentage cover of all vascular plant species during the peak of the growing season (between April and May). Sampling method was consistent between historical survey and revisitation (see Sperandii et al., 2019 for details about the resurveying protocol). We classified species into natives and non-natives following (Galasso et al., 2024).

Plant traits

We compiled functional trait data from local databases incorporated into TRY (Kattge et al., 2020), aggregating plant traits measured within the study area of Central Italy. Specifically, we chose four aboveground and four belowground traits: plant height (H; measured in m), leaf area (LA; measured in cm2), specific leaf area (SLA; measured in mm2/mg), leaf dry matter content (LDMC, measured in mg/g), root diameter (RD; measured in mm), specific root length

(SRL; measured in m/g), root tissue density (RTD; measured in g/cm3), and root dry matter content (RDMC; measured in g/g). These traits are associated with the leaf and roots economic spectra (Carmona et al., 2021; Díaz et al., 2016), and are known to be related to several ecosystem processes and functions (Bardgett et al., 2014; de Bello et al., 2010; Freschet et al., 2021; Lavorel & Garnier, 2002; Roumet et al., 2016), including on coastal dunes (La Bella et al., 2023, 2024). Trait values were averaged across individuals by species, then log-transformed, centred, and scaled (Májeková et al., 2016).

Environmental conditions

To account for climatic variability potentially affecting changes in vegetation between the two sampling periods, we obtained mean annual temperature (MAT) and mean annual precipitation (MAP) of each plot from CHELSA, a high-resolution (30 arcs, ∼1 km) global database of climate data (Karger et al., 2021). Moreover, in coastal dunes, the distance from the sea is associated with varying environmental disturbance and stress along the sea-inland gradient (Carboni et al., 2011). This means that communities situated closer to the sea are exposed to increased levels of natural stresses and disturbances, such as tidal storms, salt spray, wind, soil burial, as well as water and nutrient stress due to the high permeability of the sandy substrate. To represent this environmental gradient, we use the shortest distance between each plot and the shoreline (hereafter sea distance) as a proxy (Bazzichetto et al., 2016; La Bella et al., 2023). The shorelines of 2006 and 2017 were obtained through photointerpretation from satellite images in a QGIS environment (Version 3.28). We used the shoreline of 2006 for historical plots and the shoreline of 2017 for revisitation plots to quantify sea distance as the shortest Euclidean distance of each plot from the shoreline.

BEF subset

From the compiled vegetation dataset, we randomly extracted a subset of 100 plots to collect data related to plant biodiversity and ecosystem functioning (hereafter, BEF subset). For this subset, in spring-summer season of 2021, we repeated the floristic survey (as explained above) and concurrently collected ecosystem function variables related to supporting and regulating services (Garland et al., 2021; MEA, 2005). Supporting services were primary productivity, soil water regulation, soil carbon stock, soil nutrients cycling, and decomposition, while as regulating service we assessed erosion control and invasion resistance (Table 1). Aboveground plant biomass was used as a proxy of primary productivity. Decomposition was estimated following the Tea Bag Index protocol (Keuskamp et al., 2013). Water regulation, carbon stock,

and nutrient cycling were quantified from soil samples collected in each plot. A full description of the sampling and analysis of these ecosystem functions can be found in Supplementary Methods S1.

In coastal dunes, erosion control is mainly operated by rhizomatous geophyte grasses that, through a dense root network, entrap sandy sediments and stabilize the dune. For this function, rhizomatous geophyte grasses are commonly referred to as dune-building or engineering species (Durán & Moore, 2013; Levin et al., 2008; Stallins, 2005). Here we used the total cumulative cover of the dune-building grasses *Calamagrostis arenaria*, *Thinopyrum junceum*, and *Sporobolus virginicus*, as a measure of the erosion control function. Invasion resistance was assessed as 100% minus the cumulative percent cover of the most abundant non-native species in the study area (Cascone et al., 2021), i.e. *Carpobrotus edulis*, *Carpobrotus acinaciformis*, *Agave americana subsp. americana*, and *Yucca gloriosa* (Balvanera et al., 2006; Quijas et al., 2010). Thus, higher values indicate greater resistance to invasion and lower cover of non-natives, while lower values indicate lower resistance to invasion. Since erosion control and invasion resistance measures are based on vegetation data, unlike the supporting functions, there was no need to make predictions for the past values, but we used historical vegetation records for quantifying past erosion control and invasion resistance potential.

Table 1 Variables and methods used to measure ecosystem functions.

Category	Ecosystem functions	Variables	Measurement method
Supporting	Primary productivity	Aboveground plant biomass	Weight of oven-dried plant biomass
	Water regulation	Soil water holding capacity (WHC)	Gravimetric method (Robertson et al., 1999)
		Soil electrical conductivity (EC)	Electrical conductivity meter
	Carbon stock	Soil total organic carbon (TOC) Soil total carbon (TC)	Thermal-gradient analysis
	Nutrient cycling	Soil total nitrogen (TN) CN ratio	Thermal-gradient analysis

		Soil total content of P, K, Mg, Zn, Ni, Cu, and Fe	Mehlich III method (Mehlich, 1984)
	Decomposition	Initial decomposition rate (K) Stabilisation factor (S)	Tea Bag Index protocol (Keuskamp et al., 2013)
Regulating	Erosion control	Total cover of dune-building grasses: *Calamagrostis arenaria, Thinopyrum junceum,* and *Sporobolus virginicus* (Durán & Moore, 2013; Levin et al., 2008; Stallins, 2005)	
	Invasion resistance	100 minus the cumulative percent cover of non-native species (*Carpobrotus edulis, Carpobrotus acinaciformis, Agave americana subsp. americana,* and *Yucca gloriosa;* Balvanera et al., 2006; Quijas et al., 2010)	

Biodiversity and ecosystem functioning metrics calculation

Our approach assumes that past trait-environment relationships have remained stable over time, but this may not always hold, particularly in ecosystems that have undergone significant anthropogenic or climatic changes. Consequently, although the original resurveying database included 286 plots (each visited twice), we only hindcasted ecosystem functions in plots where environmental conditions were expected to have remained relatively stable over time, minimizing the risk of violating this assumption. In particular, we excluded plots: (1) in which vegetation disappeared at time of the resurvey due to anthropogenization or coastal erosion (n = 50); (2) belonging to the drift lines' annual vegetation (n = 21), due to their ephemeral nature (Maun, 2009); (3) where species with trait information did not account for at least 80 % of the total vegetation (n = 8) (Májeková et al., 2016); (4) where environmental conditions and biodiversity measures were out of the prediction range to avoid extrapolation (n = 25). Although plots where vegetation disappeared may provide interesting insights over the consequences of habitat loss, in this study we chose not to consider them in the analysis due to the unfeasibility of assigning reliable values of ecosystem functions. The final dataset consisted of 203 plots with two repeated measures each, located either inside national protected areas (n = 69) and Natura 2000 sites (n = 89), or in non-protected areas (n = 45).

Biodiversity metrics

In each plot, we calculated several diversity metrics for historical and revisitation data. In particular, we assessed both taxonomic and functional aspects of the community, including

species richness, total vegetation cover, above- and below-ground functional diversity (FD_{above} and FD_{below}), and the Community-Weighted Mean (CWM) of each trait.

Species richness was quantified as the total count of recorded species, while total vegetation cover as the cumulative percentage of plant cover within the plot area. Since species richness and vegetation cover are generally highly correlated (Aarssen, 1997), but species richness is known to influence functioning independently of total vegetation cover (Hooper et al., 2005) we fit a linear mixed model using species richness as a response variable, vegetation cover as a fixed effect, and study site as a random factor. Then, the residuals from this model were used as the adjusted species richness value, to represent the effect of species richness that is independent of vegetation cover (La Bella et al., 2024). For clarity, we will refer to this adjusted species richness as simply species richness (SR) throughout the text.

Functional diversity was measured separately for above and belowground traits. We first generated a multi-trait dissimilarity matrix across all species ("gawdis" function; de Bello et al., 2021) and then calculated the Rao quadratic entropy index ("melodic" function; de Bello et al., 2016) to quantify above- and belowground functional diversity (FD_{above} and FD_{below}). For each trait, the community-weighted mean (CWM) was computed using the "functcomp" function (package FD; Laliberté et al., 2014).

Ecosystem functioning

Ecosystem functions assessed using more than one variable (see Table 1), i.e. water regulation, soil carbon stock, nutrient cycling, and decomposition were quantified using the averaging approach (Byrnes et al., 2014; Maestre et al., 2012). This method calculates the mean of the Z-score values across the EF variables, providing a straightforward composite measure of an ecosystem function.

Statistical analysis

Predictive models for ecosystem functions

While erosion control and invasion resistance were calculated based on historical vegetation data, information over productivity, carbon stock, water regulation, nutrient cycling, and decomposition were not available for part of the resurveying dataset (i.e. that part not included in the BEF subset) and for all historical surveys. Thus, using both random forest (randomforest package; Breiman et al., 2018) and linear mixed-effect models ("lmer" function, lme4 package; Bates et al., 2014), we fit current BEF relationships based on the data of the BEF subset. Separate models were fit for each ecosystem function considered as response variable, i.e.

productivity, soil carbon stock, water regulation, nutrient cycling, and decomposition. In each model, biodiversity and environmental variables were used as predictors. Before conducting the analysis, we assessed multicollinearity among predictors and excluded those with a Variance Inflation Factor (VIF) exceeding 3 (Zuur et al., 2010). The final predictors included the adjusted SR, total vegetation cover, FD_{above}, FD_{below}, H_{CWM}, SLA_{CWM}, $LDMC_{CWM}$, $RDMC_{CWM}$, RTD_{CWM}, sea distance, and MAT. Additionally, in the mixed-effect models, we incorporated the study site as a random factor and the statistical interaction between sea distance and the biodiversity variables to address potential impacts of stress and disturbance on the BEF relationships (La Bella et al., 2024). For each response variable, we applied a model averaging approach using the "dredge" function (MuMIn R package; Barton & Barton, 2023) based on Akaike Information Criterion ($\Delta AIC < 3$; Burnham & Anderson, 2002; Richards, 2005) to identify the best predictors. Model residuals underwent visual inspection to ensure homoscedasticity and normality (Zuur et al., 2010). Productivity was log-transformed to meet the normality assumptions.

Cross-validation

We used leave-one-out cross-validation (LOOCV) to assess the predictive power of the selected models related to supporting ecosystem functions (Yates et al., 2023). It consisted in randomly leaving out from the model training set one plot per run, which was used as testing set to predict the ecosystem function variable starting from the plant community and environmental data. However, since within each site plots where moderately close to each other due to the narrow spatial conformation of Mediterranean coastal dunes, we applied the B-LOOCV proposed by Ploton et al. (2020) to account for spatial autocorrelation. This method leaves out from the training set the testing plot and all its neighbours included within a spatial buffer. We tested several exclusion buffer sizes, with radius ranging between 0 m and 500 m with intervals of 50 m. This spatial extent has been previously advised for Mediterranean costal dunes (Malavasi et al., 2018). The procedure was repeated 1000 times for each ecosystem function model. For each iteration, the model predictive performance was quantified using several goodness-of-prediction statistics: Pearson correlation between observed and predicted values (Pearson r); root mean squared error (RMSE); and mean absolute error (MAE). Response variables were scaled and centred (mean = 0 and standard deviation = 1) before the cross validation in order to obtain standardized and comparable measures of the predictive performance (i.e. not influenced by the unit scale). We then calculated the mean and standard deviation of each statistical metric, grouped by buffer size to evaluate if the model predictive

accuracy was affected by spatial autocorrelation. The model performance was consistent across sizes of exclusion buffer (Fig. S2), indicating low spatial dependence between training and test sets. Linear models and random forest performance was qualitatively similar (see Table 2 for linear models and Table S2 for random forest), thus we kept only mixed-effect models for predictions.

We finally selected only the BEF models that showed a satisfactory predictive ability (e.g. Pearson $r > 0.5$) and implemented to predict the ecosystems functions of the whole resurveying dataset in both time periods, i.e. historical and revisitation data.

Temporal changes in ecosystem functioning across different protection regimes

We evaluated differences in temporal changes in ecosystem functioning in communities under different protection regimes using linear mixed-effect models ("lmer" function, lme4 package; Bates et al., 2014). Ecosystem functions were analysed separately and used as separate response variables. Time, protection status, and their interaction were used as fixed effects. The "Time" variable consisted in two levels, i.e. past and present; while protection status had three levels, i.e. national protected areas, Natura 2000 sites, and non-protected areas. Study site and plot identity nested in study site were included as random factors to account for the temporal repeated measure in each plot and for the spatial dependence of plots within sites. We performed a Moran's test to verify for any remaining spatial autocorrelation of the residuals of each model ("moran.test" function, spdep package; Bivand et al., 2015) which revealed no spatial autocorrelation (Table S3). Finally, Tukey's post hoc tests were used to assess the significance of temporal trends in the three classes of protection (emmeans package; Lenth, 2022). We consider non-significant changes as an effective conservation outcome of the protection regime. Since species related to invasion or erosion control are present in some plots, we analysed temporal trends in invasion resistance or erosion control only in plots were non-native or dune-building species where present in at least one period. For each model, residuals were visually inspected to ensure assumptions of homoscedasticity and normality (Zuur et al., 2010). The model for invasion resistance and erosion control did not meet the assumption of normality, so we applied generalised linear mixed-effect models (glmmTMB package; Brooks et al., 2017) with beta distribution. Prior to the analysis, we transformed the response variables to avoid extremes of 0 and 1 (response variable value/100 × (number of observations − 1) + 0.01)/number of observations; Cribari-Neto & Zeileis, 2010). We then used diagnostic plots of the DHARMa package (Hartig, 2017) and tested the model for uniformity, dispersion, and homoscedasticity.

To account for uncertainty in the predicted past ecosystem functions, we propagated uncertainty from fixed effects, random effects, and residual variance. We first obtained 1000 samples of the model's coefficients using the "sim" function (arm package; Gelman et al., 2015). For each set of simulated coefficients, we computed the predicted values of the modelled functions and added normally distributed residual noise with standard deviation equal to the model's residual standard deviation (function "sigma"), to account for unexplained variability. Then, to propagate the uncertainty we fit the above-mentioned mixed-effect models testing temporal change in ecosystem functions across different protection levels for each set of simulated predictions (n = 1000), generating a distribution of results that incorporates the three sources of uncertainty, i.e. from fixed effects, random effects, and residual variance. Finally, we extracted the mean values and assessed the significance of temporal changes for each protection level using confidence intervals (Fig. S4).

RESULTS

Predictive models for ecosystem functions

The models of productivity, water regulation, carbon stock, and nutrient cycling showed a satisfactory predictive ability (Pearson $r > 0.5$; Table 2). Among these, the model for productivity had the highest predictive ability (Pearson $r = 0.8$). In contrast, the model for decomposition performed poorly (Pearson $r < 0.5$; Table 2) with plant diversity, community composition, and environmental conditions only explaining around 20 % of variation (R^2). Consequently, we did not perform predictions and further analysis for decomposition.

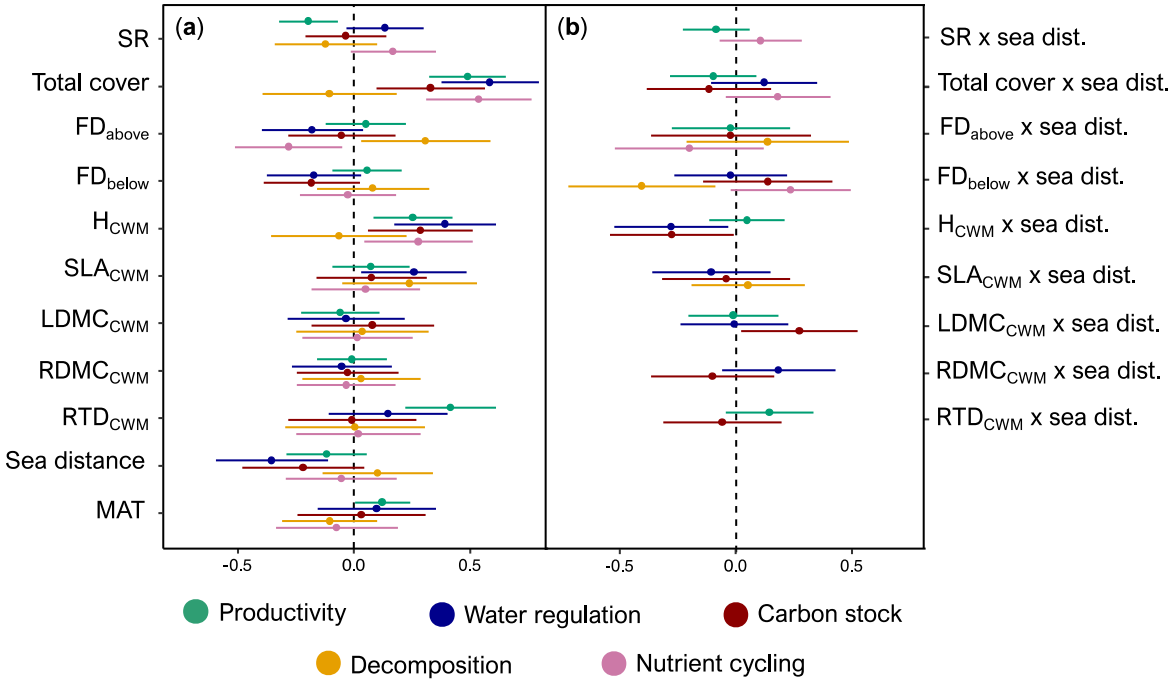
Table 2 Predictive models of ecosystem functions. The table show the goodness-of-prediction of each model evaluated with several statistics, i.e. Pearson *r*, RMSE, and MAE. "Model" column indicates whether the final model after model selection consisted in a linear model ("lm") or a linear mixed-effect model ("lmer"). Adjusted R^2 and conditional R^2 are provided for each model. Pearson *r* is the correlation between observed and predicted values. RMSE stand for root-mean-square error while MAE for mean absolute error.

EFs	Model	Adjusted/ conditional R^2	Pearson *r*	RMSE	MAE
Productivity	lm	0.719	0.833	0.548	0.450
Water regulation	lmer	0.554	0.574	0.767	0.654

Carbon stock	lmer	0.610	0.624	0.709	0.592
Nutrient cycling	lmer	0.573	0.529	0.855	0.698
Decomposition	lm	0.197	0.201	1.014	0.794

Across the models, total vegetation cover and H_{CWM} were the most important predictors of ecosystem functioning (Fig. 2a), showing a general positive effect across all functions except decomposition. Species richness and the diversity in above and belowground functional traits, also contributed to ecosystem functioning, but their effect was less consistent: water regulation and nutrient cycling were generally higher in communities with high species richness but low functional diversity; in contrast, productivity increased with functional diversity rather than with species richness. Ecosystem functioning was also overall promoted by tall species (high H_{CWM}) with high values of SLA_{CWM}. Beside SLA and H, the other traits did no show consistent effects across the modelled functions. Finally, sea distance was a predictor for all functions. We detected a negative direct effect, indicating that close to the sea ecosystem functions are generally higher. Moreover, we also tested the interaction between biodiversity metrics and sea distance, and we found that many biodiversity effects vary along the sea-inland environmental gradient (Fig. 2b; for further details see La Bella et al., 2024).

Figure 2 Results of the predictive models. Dots indicate the standard regression coefficients of each model predictors while lines the associated 95% confidence intervals. Panel (**a**) show the direct effects of biodiversity and environmental conditions on ecosystem functioning. Panel (**b**) 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 e.g. that the effect of SR on EF decreases as sea distance increases. SR, species richness; FD, functional diversity; H, height; SLA, specific leaf area; LDMC, leaf dry matter content; RDMC, root dry matter content; RTD, root tissue density; MAT, mean annual temperature; sea dist., sea distance.



Temporal changes in ecosystem functioning across different protection regimes

We identified temporal changes in all ecosystem functions. However, these changes were not consistent across different protection regimes. Specifically, in non-protected areas, productivity, water regulation, and carbon stock increased over time (respectively: estimate = 0.393, P = 0.003; estimate = 0.481, P = 0.001; estimate = 0.495, P =0.001; Fig. 3a-c) while nutrient cycling and invasion resistance decreased (respectively: estimate = -0.250, P = 0.029; estimate = -0.721, P < 0.001; Fig. 3d and f). Inside Natura 2000 sites, water regulation increased (estimate = 0.202, P = 0.032; Fig 3b) while nutrient cycling, erosion control, and invasion resistance decreased over time (respectively: estimate = -0.177, P = 0.008; estimate = - 0.838, P < 0.001; estimate = -0.444, P < 0.001; Fig 3d-f). In contrast, within national protected areas most functions remained stable over time, although there were positive trends in carbon stock (estimate = 0.282, P = 0.018; Fig 3c) and invasion resistance (estimate = 0.722, P < 0.001; Fig. 3e).

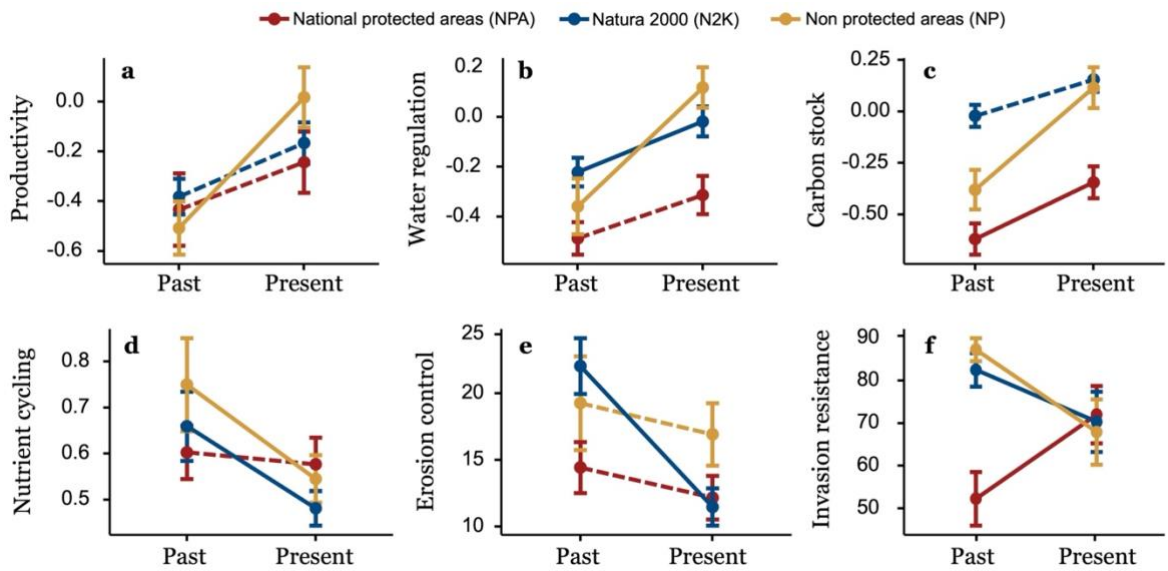


Figure 3 Temporal changes in ecosystem functions. Dots indicate the mean values and lines the associated standard errors. Continuous lines refer to significant changes, while dotted lines to non-significant.

DISCUSSION

In this study, we proposed a new application of revisitation studies in combination with locally estimated BEF relationships to trace back past ecosystem functions and assess how these have changed over the last 10-15 years under different regimes of protection. Specifically, in this section, we first discuss the ability of biodiversity to predict ecosystem functioning in coastal dunes as well as the effectiveness of using BEF relationships to hindcast past ecosystem functioning. Then, through a case study, we highlight the relevance for conservation of our approach by proposing a possible implementation, i.e. monitoring how ecosystem functioning has changed in the context of ongoing global changes as well as the performance of different protection regimes in counteracting these temporal changes in the study area.

Biodiversity as predictor of past ecosystem functioning

In this study, we tested the ability of plant diversity and community composition to model several ecosystem functions in coastal dunes, such as productivity, water regulation, carbon stocks, nutrient cycling, and decomposition. Since BEF relationships are often highly context dependent (Jucker et al., 2016; La Bella et al., 2024; Ratcliffe et al., 2017; Spohn et al., 2023), our models also include environmental conditions and how these interact with the effect of plant diversity and community composition on ecosystem functioning. Including the environmental context is necessary to properly model BEF relationships, and it improves the

predictive power of biodiversity (Díaz et al., 2007; La Bella et al., 2023, 2024; Lavorel et al., 2011; Van Der Plas et al., 2020). Here, we found that plant diversity, community composition, and environmental conditions can effectively predict most ecosystem functions analysed, except decomposition. Among all functions, productivity was the one that was best predicted. This result is in line with the strong plant-productivity relationship found in a wide range of natural ecosystems (Duffy et al., 2017; Garnier et al., 2015; van der Plas, 2019). On the other hand, the predictive ability of our models for carbon stock, water regulation, and nutrient cycling was lower compared to productivity, but still sufficient to make meaningful predictions. In contrast, the relationship with decomposition was very weak. Plants should influence decomposition through the type and quantity of litter produced (Cornwell et al., 2008; Srivastava et al., 2009). However, in this study the effect of plant diversity, community composition, and environmental conditions on decomposition was limited, only 20 %, compared to other studies that reach up to 60 % of variation explained (Oliveira et al., 2019; Scherer-Lorenzen, 2008). In our system, there might be some other factors, not considered here, more important for decomposition. As recently suggested, including soil microbes, fungi, and mycorrhiza, might increase our ability to predict decomposition (Fujii et al., 2017; Van Der Heijden et al., 2008).

Trait-based predictive frameworks are currently predominantly employed for spatial predictions, involving the mapping of ecosystem functions and services (Chen et al., 2023; Lavorel et al., 2011), or for forecasting ecosystem functions under future scenarios of climate and land-use change (Green et al., 2022; Klumpp & Soussana, 2009; Lamarque et al., 2014; Madani et al., 2018; Quétier et al., 2007). However, their use for hindcasting the past remained up to date unexplored. In this study, we proposed and validated a novel application of trait-based predictive models for reconstructing past ecosystem functions based on historical vegetation records. Similar to future global change predictions, one of the objectives of predicting the past is to compare it with present ecological features. These comparisons can provide essential information that goes beyond biodiversity patterns, thus guiding more accurate conservation actions (Green et al., 2022). By bridging this gap, our study provides a novel framework that can be extended to other ecosystems with available historical vegetation data, offering new opportunities to assess long-term ecosystem dynamics to address the CBD and the UN sustainable development goals. Our method can be particularly relevant, especially considering the recent surge in resurvey studies of the past years, e.g. ReSurveyEurope (Knollová et al., 2024), ReSurveyDunes (Acosta et al., 2025), BioTIME (http://biotime.st-andrews.ac.uk), or VESTA (Świerkosz & Reczyńska, 2022).

Limitations of hindcasting ecosystem functions

While our study demonstrates the potential of using revisitation data and BEF relationships for hindcasting past ecosystem functions, some limitations should be acknowledged. First, the availability and quality of historical vegetation data pose a constraint. Vegetation resurvey datasets often vary in taxonomic resolution, accuracy of plot re-location, operator, and sampling methodologies, introducing potential biases in reconstructing past functional composition. Second, our approach assumes that past trait-environment relationships have remained stable over time, but this may not always hold, particularly in ecosystems that have undergone significant anthropogenic or climatic changes. To overcome this issue and ensure reliable predictions, in this study we focused on a subset of the original revisitation dataset and 30 % of the vegetation plots were not analysed. Specifically, we excluded plots where predicting ecosystem functions with sufficient accuracy was not feasible, such as highly variable or ephemeral habitats, plots lost due to anthropogenic changes or coastal erosion, and those with environmental conditions or biodiversity values outside the models' prediction range (see Methods section for details). Additionally, while plant diversity, community composition, and environmental conditions explain a significant proportion of variation in ecosystem functions, other unmeasured factors, such as microbial communities and climate fluctuations, may also play critical roles, as emerged in our study with processes like decomposition. Finally, while our models integrate environmental conditions, they may not fully capture the complex interactions and feedback among multiple ecosystem components. To address this, we propagated uncertainty in the predicted ecosystem functions using a simulation-based approach, incorporating variability from model parameters and unexplained residuals. This method enhances the robustness of our estimates, yet the inherent limitations of predictive modelling remain. Future applications of this framework would benefit from incorporating additional biotic and abiotic predictors to further refine predictive accuracy and broaden the applicability of hindcasting approaches across different ecosystems.

Case study: Temporal changes in ecosystem functioning across different protection regimes

One of the main arguments for biodiversity conservation relies on the ability of biodiversity to support ecosystem functioning (Balvanera et al., 2006). However, although many BEF study found a positive relationship between biodiversity and ecosystem functioning (Le Bagousse-Pinguet et al., 2019; Maestre et al., 2012; van der Plas, 2019), our findings suggest that BEF relationships can be more much more complex. We observed that biodiversity can have

positive, negative or even no effects on ecosystem functioning, depending on the ecosystem function analysed and the environmental conditions. In this light, conserving biodiversity may not necessary ensure also the conservation of ecosystem functioning (O'Connor et al., 2021). Here, as a case study, we applied our hindcasting approach to tackle this question by comparing temporal changes in ecosystem functions under three different protection regimes, i.e. national protected areas, Natura 2000 sites, and non-protected areas. This analysis illustrates how our method can be a useful tool for conservation and long-term ecological monitoring, providing valuable insights into the consequences of vegetation changes on ecosystem functioning.

In the study area, significant vegetation changes have been observed over the last 10-15 years both inside and outside Natura 2000 sites (Sperandii et al., 2020). As a result, we detected also marked temporal changes in ecosystem functions within non-protected areas and Natura 2000 sites, while national protected areas remained relatively stable. Specifically, we found that, within non-protected areas and Natura 2000 sites, most ecosystem function underwent temporal changes with a general increase of productivity, carbon stock, and water regulation and a decline in nutrient cycling, invasion resistance, and erosion control. These patterns align with vegetation changes observed over the last decades in Italian coastal dunes (Del Vecchio et al., 2015, 2016), including in our study area (Sperandii et al., 2020), where fast-growing ruderal and non-native species have replaced typical coastal dune species as well as dune-building species responsible of erosion control. Fast-growing ruderal and non-native plant species are often linked to enhanced productivity and biogeochemical cycles (Liao et al., 2008; Marzialetti et al., 2025; Rout & Callaway, 2009; Simberloff, 2011; Wilsey et al., 2023), due to their rapid growth and competitive traits, e.g. high SLA and plant height. However, while ruderal and non-native species might temporarily enhance certain functions, their spread could come at the cost of long-term ecosystem stability and biodiversity conservation (Del Vecchio et al., 2015; La Bella et al., 2023; Sperandii et al., 2019). Together, all these changes suggest that current management and conservation strategies within these Natura 2000 sites may not be sufficient to prevent the decline of ecosystem functioning or, as showed by Sperandii et al. (2020), of biodiversity. These findings question the efficacy of the existing set of Natura 2000 sites of our study area to counteract pressures such as tourism, urban expansion, or climate change-driven disturbances, as observed also by other studies (Bricca et al., 2024; Ricci et al., 2023; Tsiafouli et al., 2013).

Within national protected areas most ecosystem functions remained stable over time and invasion resistance even increased. These results are encouraging, because they suggest that the national protected areas considered here have been effectively planned and managed to

accomplish the maintenance of well-functioning ecosystems, even in highly threatened ecosystems like coastal dunes. Our findings support previous research suggesting that stricter conservation policies can enhance ecosystem functions and services (Lecina-Diaz et al., 2019). However, results in the literature are mixed. Some studies have found no significant differences in ecosystem functioning between Natura 2000 sites and non-protected areas (Olmo et al., 2025), while others have even reported higher levels of ecosystem functioning in Natura 2000 sites compared to strictly protected areas (Castro et al., 2015). This variety of results suggests that there may not be a universal trend across protection regimes and that the ecosystem functioning across different types of protected areas could depend on multiple factors, such as the specific functions analysed or local management practices.

The contrasting outcomes between national protected areas and Natura 2000 network can be attributed to their differences in objectives and management. The primary goal of the Natura 2000 network is ensuring the long-term maintenance of Europe's endangered species and habitats at "favourable conservation status" (Commission, 2009). On the other hand, although aims can vary depending on national legislations and policies (Barnes et al., 2017), national protected areas cover a wider range of objectives, ranging from the conservation of biodiversity, ecosystems, and landscapes, to the maintenance of natural processes (CBD, 2022). Still, the biggest differences rely on the management. In contrast to national protected areas, Natura 2000 sites may not implement adaptive management plans or lack dedicated funding and personnel, preventing the accomplishment of adequate conservation measures (Hochkirch et al., 2013; Kati et al., 2015; Maes et al., 2013). In coastal dunes, conservation measures that have proven effective include limiting trampling by fencing areas or constructing wooden walkways (Acosta et al., 2013; Prisco et al., 2021), controlling and eradicating invasive species (Lazzaro et al., 2020), and restrictions on mechanical cleaning of the beach (Battisti et al., 2023; Roig et al., 2009).

We should note that in coastal dune ecosystems, supporting services such as productivity, water regulation, and nutrient cycling, are relatively low compared to other habitats (Van Der Biest et al., 2017). Their primary ecosystem services are linked to erosion control, invasion resistance, and habitat provisioning for biodiversity (Drius et al., 2019a, 2019b; Liquete et al., 2013). Consequently, in these ecosystems higher functioning may not necessarily translate into more valuable services to human societies, and selected key functions should be prioritised by conservation actions. Our findings indicate that non-protected coastal dunes are shifting toward more productive ecosystems, with the risk of losing their key characteristics in the near future. On the other hand, Natura 2000 sites are not effectively protecting dune-building species

responsible for dune stability, resulting thereby in the loss of erosion control potential, and not contrasting the expansion of non-native species. In contrast, the promising trend observed within national protected areas provides optimistic signals that intensive conservation efforts can preserve the functionality of highly vulnerable ecosystems such as coastal dunes.

Finally, it is important to remember that this work is not intended to assess the overall success of different protection regimes but rather to examine how revisitation data can be used to monitor changes in ecosystem functioning within an existing network of protected areas. Here, we provide insights into the dynamics of ecosystem functioning, highlighting the potential of the hindcasting approach proposed for monitoring and conservation purposes. However, as the number of sites included in this study is relatively limited, the findings from these specific locations should be generalized with caution. However, as the number of sites included in this study is relatively limited, the findings from these specific locations should be generalized with caution.

Final remarks

Although most revisitation studies primarily focused on quantifying how biodiversity is changing in response to global changes, they also offer a unique opportunity to evaluate temporal trends in the ecosystem functions that biodiversity supports. However, historical vegetation data commonly lack direct measurements of ecosystem processes. Here, we proposed an innovative practical solution for overcoming this data gap in revisitation data, namely predicting past ecosystem functions using BEF relationships assessed in the present. Reconstructing past ecosystem functioning in the context of resurveying studies allows us to jointly assess temporal changes in biodiversity as well as ecosystem functioning and, consequently, to acquire a more holistic understanding of the repercussions of global changes on natural ecosystems. In this light, we demonstrated a possible application and the relevance for conservation of this approach by quantifying how ecosystem functioning has changed over the last 15 years in protected and unprotected coastal dunes.

Many conservation efforts currently focus on preserving individual species or habitats, often neglecting crucial functions and services that ecosystems provide, which are also important goals and targets in the post-2020 global biodiversity framework. Here, we showed that designing protected areas for conserving biodiversity can also have positive effects on the maintenance of ecosystem functions. Still, the mere designation of a protected area does not guarantee conservation success, as evidenced by the functioning decline observed in the Natura 2000 sites examined in this study. Preserving well-functioning coastal dune ecosystems may

instead require rigorous conservation measures, like those carried out in national protected areas. This uncertainty highlights the need to monitor within protected areas not only biodiversity but also trends in ecosystems functioning, ensuring that conservation efforts effectively maintain ecosystem integrity and resilience over time.

AUTHOR CONTRIBUTIONS

GLB, ATRA, and MC conceived and designed the study. GLB collected the data, led the statistical analysis, and wrote the first draft of the manuscript. All authors contributed to results interpretation, made significant contributions to the manuscript, and approved it for publication**.**

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