RESEARCH ARTICLE

Land use determines Mediterranean ecosystems' multifunctionality more than plant richness or habitat composition

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Abstract

1. Local and landscape diversity loss, habitat fragmentation and land-use changes commonly co-occur and impair ecosystem multifunctionality, yet they are often studied in isolation. Therefore, we ignore the relative importance of these drivers of ecosystem change or whether or not they interact to determine ecosystem functioning.

2. We measured how changes in local (plant richness) and landscape (different land uses) diversity, land use (orchards, shrubland, pine, oak and mixed forests) and habitat sise, and their interactions, affected the functioning of Mediterranean ecosystems. At 49 plots, we measured 17 above- and below-ground functions, related to nutrient cycling, carbon sequestration and biotic interactions. Additionally, we generated different combinations of plots to compose artificial landscapes where multifunctionality and biodiversity conservation can be maximised, in order to aid land managers to preserve or design functional and diverse areas.

3. The relative importance of local and landscape attributes varied slightly depending on the target function, yet land use was by far the strongest predictor of most functions and multifunctionality above local plant biodiversity, habitat sise or landscape diversity. Oak and mixed forest were the most multifunctional land uses but were functionally wcomplemented by other land uses that maximised some individual functions.

4. The relative proportion of each land use within optimal landscapes varied if the target was biodiversity conservation (with an even dominance of land uses), carbon stocks or multifunctionality (highly dominated by native oak and mixed forests).

5. *Synthesis and applications*: Our results highlight the importance of remnant native forest to provide multiple ecosystem functions and the potential to restore them and complement these uses with sustainable agriculture. By merging landscape

and ecosystem approaches we provide specific numbers regarding the proportion that each land use should have in order to maximise biodiversity conservation and/or functioning in these charismatic environments.

1 | INTRODUCTION

Anthropogenic disturbances are altering natural ecosystems by reducing biodiversity at local and landscape levels, changing land uses and fragmenting landscapes, all known to impact ecosystem functioning (Cardinale et al., 2012; Liu et al., 2018; Mori et al., 2015). The strong and positive relationships between biodiversity and ecosystem functioning (BEF hereafter), often reported both in experiments and field observations, clearly suggest that local biodiversity loss hinders ecosystem functioning (Cardinale et al., 2012), and that this effect could extend to larger spatial scales (e.g. Hautier et al., 2017; Le Provost et al., 2023; Pasari et al., 2013). Habitat fragmentation also affects ecosystem functioning, with smaller and/or more isolated habitats showing alterations in critical biotic interactions, biomass production, or nutrient cycling (Haddad et al., 2015; Hertzog et al., 2019; Magrach et al., 2014). In addition to local biodiversity and habitat fragmentation, land use itself also drives important changes in ecosystem functioning. Sometimes these changes are wanted and obvious (e.g. maximise food production even at the expense of carbon sequestration or soil fertility when shifting forests to croplands; DeFries et al., 2004; Foley et al., 2005). Most of the times, however, the response of multiple functions to such land-use changes, particularly among natural or semi-natural vegetation types (e.g. forest to shrublands when fire frequency increases¸ conifer plantations or recruitment in former broadleaved forests) are much less understood (but see Hertzog et al., 2019; Moghli, Santana, Soliveres, et al., 2022; Neyret et al., 2023).

Habitat fragmentation, land-use changes and biodiversity loss, commonly co-occur and impair ecosystem multifunctionality, yet they are often studied in isolation. The former two are mostly studied by landscape ecology, which often ignores the effect of changes (including biotic composition or use intensity) *within* contrasting land uses and rarely measure multiple ecosystem functions on site (but see Neyret et al., 2023). These within-use variations are important, as contrasting intensities within a given land use (e.g. amount of fertiliser used in a grassland or cropland, type of management within a given forest type) can drastically affect ecosystem functioning (Allan et al., 2015; Felipe-Lucia et al., 2018). Analogously, the diversity of land uses across the landscape is also an important determinant of ecosystem functioning, as recently shown in grassland and agricultural landscapes (Tamburini et al., 2022; Wittwer et al., 2021). Different land uses can promote different ecosystem service "bundles" (e.g. Raudsepp-Hearne et al., 2010) and complement each

other if they promote different sets of functions (e.g. Alsterberg et al., 2017; Felipe-Lucia et al., 2014). In addition, different land-use types can facilitate each other's functioning through transfer of material and energy (e.g. carbon and nutrient fluxes between land-use or ecosystem types through animal movement [e.g. Gounand et al., 2018], crop yield aided by the presence of pollinators and pest-predators in surrounding habitats [e.g. Ricketts et al., 2004]). Thus, it is important to measure multiple functions as well as landscape habitat composition to properly evaluate the functional consequences of land-use changes (Stürck & Verburg, 2017).

On the other hand, BEF relationships are mostly studied within individual land-use types (commonly grasslands), but rarely *across* different land uses or landscape compositions. BEF studies often ignore landscape-level changes (reviewed in Liu et al., 2018), despite changes at this scale can be even more important for ecosystem functioning than those at the local scale (Zirbel et al., 2019). Indeed, land-use change is the main cause of habitat fragmentation (Van Dijk, 2003), which at the time is one of the strongest drivers of biodiversity loss (Haddad et al., 2015). Habitat fragmentation and local biodiversity loss can strongly interact to determine ecosystem functioning, as recently observed in forests or islands (Hertzog et al., 2019; Wardle & Zackrisson, 2005), although with contrasting results. Sometimes the functioning of smaller patches is more likely to decline after biodiversity loss than that in big patches (Hertzog et al., 2019), and sometimes the bigger patches are those more sensitive to biodiversity loss (Wardle & Zackrisson, 2005). Such BEF relationships may also depend on land use, again with contrasting findings in the literature; sometimes there are more positive BEF relationships in human-made than natural ecosystems (e.g. Felipe-Lucia & Comín, 2015), and sometimes BEF relationships remain consistent across different ecosystems (e.g. Fanin et al., 2018). Due to the likely interactions between biodiversity and landscape attributes and their unknown relative importance, studies simultaneously considering the effects of contrasting land uses, biodiversity levels within such land uses, and landscape configuration can be highly relevant for improving management at the landscape scale and to fully understand the consequences of these multiple co-occurring biotic changes (Le Provost et al., 2023).

Here we studied the response of the functioning of Mediterranean ecosystems to changes in local (plant species richness) and landscape (different land uses) diversity, land-use type (from orchards to mature forests, including shrublands and pine plantations) and habitat sise (proportion of such land use within a 500 m radius).

To provide a holistic view of the functioning of the ecosystem, we studied 17 functions, including aboveground biomass, biotic interactions (seed, insect and mammal predation rates), litter decomposition, water infiltration, nutrient cycling (enzymatic activities, N and P content), tree regeneration and carbon stocks (woody biomass and soil organic matter), and their collective response using a multifunctionality metric. We aimed to answer four main questions: (i) Which are the most important local and landscape-level drivers of ecosystem functioning? (ii) Does the relative importance of these different drivers depend on the function studied? (iii) Do these local and landscape drivers interact to determine the functioning of Mediterranean ecosystems? (iv) How similar are different land uses in the functions they provide? Additionally, our goal is designing landscapes combining different land uses where biodiversity conservation, carbon stocks or multifunctionality can be maximised, in order to aid land managers to preserve or design functional and diverse areas.

2 | MATERIALS AND METHODS

2.1 | Study area

The study took place in two Natural Parks: Carrascal de la Font Roja and Serra de Mariola, Alicante, in southeast Spain, (38°39′25″N 0°33′12″W, 2298 ha, 660–1340 m.a.s.l.; 38°43′59″N 0°33′17″W, 17257 ha, 640–1390 m.a.s.l., respectively, Figure S1). This area is characterised by a dry mesomediterranean climate, with an average annual temperature of 11°C and mean precipitation between 420 and 520 mm per year (https://en.climate-data.org/), and dominated by calcareous soils (Generalitat Valenciana, Conselleria d'Agricultura, Medi Ambient, Canvi Climàtic i Desenvolupament Rural, 2015). This area was managed during the last centuries, as other Mediterranean areas, for charcoal and wood extraction, urbanisation or forest fires (Blondel, 2006; Padilla et al., 2010), also afforestation with pine stands have been a usual practice over the past few decades (Pausas et al., 2004). Therefore, this area is characterised by a mixed landscape combining orchards (28.08%), shrublands (22.96%) and pine forests (22.46%), with mixed deciduous/evergreen (1.60%) and oak forests (18.44%) more rarely found, and often relegated to the least favourable sites (see also Figure S1).

2.2 | Study design

We selected a total of 49 plots within both Natural Parks (each plot was sampled once), 10 in each of the land-use types, except for mixed forest (where we took only nine due to access difficulties to this type of habitat). The median distance between plots was around 10 km (range 0.05–20 km). Plots sampled with the same land use were separated a least 1 km apart. The five land uses were: *Pinus halepensis* (pine) forest (*N* = 10), *Quercus rotundifolia* (oak) forest

(*N* = 10), shrublands dominated by *Cistus albidus*, *Thymus vulgaris*, *Stipa offneri* and *Brachypodium retusum* (*N* = 10), mixed (*Q. rotundifolia* and deciduous trees such as *Fraxinus ornus* and *Acer opalus* subsp. *granatense*) forests (*N* = 9) and tree orchards, mostly olive (*Olea europaea*) and almond (*Prunus dulcis*) crops (*N* = 10). We selected these plots to maximise variation in landscape features (diversity and sise) and local diversity (based upon local plant species richness). Fieldwork took place between June–July 2020 [June 10, 2020–July 8, 2020] and April–June 2021 [April 23, 2021–June 4, 2021] (25 and 24 sampled plots [half of each land-use type] sampled each year, respectively).

Plots were 5 × 5 m, geolocated and characterised in situ by land use (orchards, shrubland, pine forest, oak forest or mixed forest). In each plot, we placed 5 0.50 × 0.50 m quadrats (245 samples altogether) to perform vegetation and soil sampling (details below). Within each quadrat, we took a soil sample (0–10 cm depth), air-dried it in the laboratory and sieved (2 mm mesh) before further analyses (see below).

Our aim was to evaluate how changes in biodiversity and landscape attributes affect multifunctionality at local and landscape levels. To do so, we measured four landscape attributes aimed at summarising spatial heterogeneity, habitat quality (indicated by the different species richness levels within each land use), habitat fragmentation and land-use typology (see below). As response variables we assessed 17 ecosystem functions related to biotic interactions, nutrient cycling, carbon sequestration, water infiltration and plant productivity in each plot.

2.3 | Landscape and local attributes

We estimated three landscape attributes: habitat diversity and habitat richness (spatial heterogeneity), and habitat sise (habitat fragmentation). We evaluated the area surrounding each plot (500 m-radius circles with each plot as the centre) to obtain habitat diversity (Shannon index with the proportion of habitats in the 500 m circle), habitat richness (number of different habitat types around), and habitat sise (proportion of the same land-use type within the 500-m circle). We used this 500-m spatial scale as it was small enough to avoid overlapping areas between our sampling points, but still relevant to provide a measure of the landscape influence on ecosystem functioning (e.g. Couthouis et al., 2023; Moore et al., 2015; Perrot et al., 2021; but see Wittwer et al., 2021 for a larger scale). In any case, we also considered 1 km- instead of 500 m-radius circles and results remained qualitatively consistent (data not shown). To obtain these estimates, we used a detailed vegetation map available for the study area (Terrones et al., 2006) and the QGIS' (QGIS Madeira 3.4) buffer vector geoprocessing (GDAL). We dismissed habitat richness from further analyses, as it was highly correlated with habitat diversity (ρ = 0.80). We classified in situ the type of land use of each plot as local attribute, differing between orchards, shrubland, oak, pine and mixed forest. See Table 1 for average values of these attributes per land use.

TABLE 1 Mean, maximum and minimum of considered predictors: habitat sise (proportion of the same land-use type as the plot within the 500-m circle), habitat diversity (Shannon index with the proportion of habitats in the 500m circle) and plant species richness of each plot, per land use.

Land use	Habitat sise mean	Maximum habitat sise	Minimum habitat sise	Habitat diversity mean	Maximum habitat diversity	Minimum habitat diversity	Plant species richness	Maximum plant species richness	Minimum plant species richness
Orchards	54.46	80	13.56	0.94	1.38	0.50	101	30	4
Mixed forest	10.24	44.85	0.00	0.91	1.42	0.49	55	15	3
Oak forest	33.96	76.27	0.00	1.05	1.40	0.69	52	26	4
Pine forest	38.91	56.71	8.28	1.16	1.36	0.84	82	22	6
Shrubland	16.88	46.50	0.00	0.98	1.43	0.21	65	25	8

2.4 | Biodiversity

At each plot, we estimated plant and bird richness (Table 1). Plant richness was evaluated as the number of different plant species found in the 5m×5m plot, whereas bird richness was estimated through 15′ point-counts, where we recorded each bird species heard or seen (Bibby et al., 1992). These point-counts took place between 7:00 and 11:00 in the morning, avoiding adverse weather conditions such as wind or rain, and were randomly distributed among plots and land uses, to avoid biasing our results. Point-counts detect animals at spatial scales larger than our plots sise (100-m radius circles, on average; Ralph et al., 1995). However, the area where we sampled each plot that was covered by the same land-use was generally larger than this distance. Hence, we can assume that, if detected, birds use this type of habitat.

2.5 | Ecosystem functions

At each plot, we measured 17 functions, either field or laboratory-based. We measured in the field (1) aboveground (herbaceous, shrub and tree) plant biomass, (2) litter decomposition rate, (3) regeneration capacity (species richness of tree seedlings recruiting, highly correlated with their abundance), (4) mouse predation, (5) seed predation, (6) caterpillar predation, (7) herbivory and pathogens´ damage, and three indices obtained from the landscape functional analysis (Tongway & Hindley, 2004; visual evaluation of 11 soil surface indicators including plant cover, litter depth, soil erosion, aggregate stability, etc., see Table S1 for further details), which are combined to produce indices of: (8) nutrient cycling, (9) resistance to soil erosion [stability], and (10) runoff capture. In addition, we also measured in the laboratory (11) infiltration capacity, (12) field capacity, (13) soil organic matter, (14) beta-glucosidase and (15) acid phosphatase enzymatic activities, (16) available phosphorous, and (17) nitrogen ($NH_4^+ + NO_3^-$) content. These variables are related to nutrient cycling (2, 8, 14–17; Keuskamp et al., 2013; Maestre et al., 2012), biotic interactions (4–7; Castro et al., 1999; García et al., 2021; Jactel et al., 2021), water regulation (9–12; Tongway & Hindley, 2004), carbon stocks (1, 13; Flombaum & Sala, 2007) and forest regeneration (3; Gil-Tena et al., 2019; Van Der Plas et al., 2016; see Table S1 for full details and rationale).

We standardised each individual function to a common scale to avoid a higher influence of those functions with larger units. This was done according to the following formula: $STD = (X - X_{min})/(X_{max} - X_{min})$; where STD is the standardised function and X, X_{min} and X_{max} are the value of target function at a given plot, its minimum and maximum value across all plots, respectively. Then, we computed Spearman correlation coefficients for all pairs of ecosystem functions and removed from further analyses those offering redundant information ($\rho > 0.7$ with others; Table S1). We then used the remaining functions to calculate a unique multifunctionality metric (MF) per plot using the averaging method. It is important to note that, when calculating multifunctionality, we

did not assign negative values to any function (e.g. seed predation or herbivory), regardless of the implications for management. We just assumed faster rates of matter and energy transference as high functioning (i.e. ecosystem *function* multifunctionality as opposed to ecosystem *service* multifunctionality; see Manning et al., 2018 for a review). We checked alternative multifunctionality measures, such as weighted average organised by groups of functions related to ecosystems services of interest, and also following the multiple thresholds approach (Byrnes et al., 2014). First, we grouped functions into five ecosystem services: climate regulation (biomass and soil organic matter), forest regeneration (regeneration capacity, seed predation*-1), nutrient cycling (beta-glucosidase and acid phosphatase enzymatic activities, available phosphorous, dissolved inorganic nitrogen and litter decomposition rate), water regulation (stability, infiltration/run off index, infiltration capacity, field capacity) and pest control (mouse predation, caterpillar predation, herbivory*-1 and pathogens *-1). We calculated the average of the standardised values for the functions forming each service, and then average these service-values to produce a multifunctionality index. That way we provide the same weight to all services of interest, regardless of the number of indicators used to measure them (see Maestre et al., 2022 for a related approach). For the multiple threshold approach, and considering we have multiple potential drivers, we chose to focus only on three contrasting threshold levels (50%, 70% and 90%), which provide a sufficient description of potential trade-offs in between the supply of different functions (see Soliveres et al., 2016 for a related approach). All these multifunctionality indices were all highly correlated and rendered the same conclusions as the results presented here (Figure S2).

2.6 | Statistical analysis

We wanted to evaluate which were the most important local and landscape-level drivers of ecosystem functioning, and if the relative importance of these different drivers (the % of variance explained by them) depends on the function studied. To do so, those variables that did not have a normal distribution were log-transformed to approximate it. Otherwise, if variables did not get normal distribution after transformation, we kept untransformed data. The only exception was regeneration capacity whose distribution fit better with negative binomial, and for which negative binomial regressions were applied. Then, we fitted linear models using each individual function, as well as the overall multifunctionality metric as response variables and local and landscape attributes (plant richness, land use, habitat diversity and habitat sise) as predictors. Since the effect of local plant richness can be modulated by both habitat sise and land use, and the latter two can also interact with each other to determine ecosystem functioning (see Section 1), we considered interactions between these predictors in our models. The model structure was: Function or MF~Plant richness * (Land use+Habitat sise+Habitat diversity)+Land use * Habitat sise+Year.

We later simplified this model by using multiple model inference by applying the function "dredge", from MuMIn package. In a nutshell, multiple model inference fits all the possible models from a given initial model structure (i.e. models containing all possible combinations of predictors previously specified) to obtain the Akaike information criteria (AIC) of each model. The model with the lowest value of AIC is considered the most parsimonious, and those with AIC difference respect to the most parsimonious of ≤2 are considered equally well suited. This procedure allowed us to simplify our modelling framework; selecting a set of the most relevant predictors (i.e. those included at least in one of the models) for each function and multifunctionality. We calculated the Variance Inflation Factors (VIF) to confirm that we did not have any multicollinearity issues (all VIFs <5; Table S2). We also used "SimulateResiduals" function from the DHARMa package (Hartig, 2022) to check if our models fulfilled assumptions of normality, lack of over/under-dispersion and existence of influential points (Table S3). These later tests pointed that the models fitted for mouse predation failed to fulfil normality of residuals. Since no transformation fixed this problem, we keep the model results but interpret these results cautiously considering this limitation. To evaluate the relative importance of each one of our predictors, we performed a variance partitioning (evaluating the relative percentage of R^2 explained by each predictor) using the function "calc.imp" from R package "relaimpo" (Grömping, 2006). For this latter analysis, we used linear models fitted with the individual predictors and the interactions selected from the multiple model inference explained above. Additionally, we ranked the importance of all predictors including interactions for each function and multifunctionality, graphing the respective average standardised effect sise across those models in which the predictor was significant and the number of models in which each predictor was significant (Figure S3).

We also wanted to test if functions provided in each land use were complementary. To do so we estimated Euclidean's dissimilarity index (as implemented in the "vegan" package, function "vegdist"), between every pair of land uses and with itself (average across all possible plot pairs) as a measure of β-multifunctionality, where the value of each function was considered as the "species´ abundance" at each plot (see Hautier et al., 2017; Mori et al., 2018; Pasari et al., 2013; Van Der Plas et al., 2016 for related approaches). Hence, higher values of this metric indicate that the functions provided by two different land uses are less similar and therefore that these land uses are more complementary in the functions they promote collectively. Lower β-multifunctionality values, in turn, indicate that two land uses are relatively redundant in terms of the functions they support. High β-multifunctionality values could also occur under low complementarity if a given land use provided all functions at high levels and the other one would provide none. However, this was not our case (see Section 3 below), and therefore in our study high β-multifunctionality values reflect high functional complementarity between land uses. In order to aid the interpretation of these results, we also calculated differences between land uses in the levels provided for the multifunctionality

metric, by using ANOVAs with land use as the sole factor and Tukey's post-hoc tests to tease apart significant different between our five land-use categories.

Finally, we complemented our analysis by designing landscape compositions with different proportion of land uses that could maximise biodiversity conservation (higher richness of plants [including recruitments] and birds), or carbon stocks (carbon storage in soils and vegetation). In addition to plant and bird richness, we also considered the richness of young tree recruitments (forest regeneration function) in the biodiversity conservation scenario, due to the strong limitation of new forest recruits in the area, and their interest in conservation and management (Natural Park's staff, pers. comm.). Habitat provision for plants and animals and carbon capture (related to the two landscape scenarios presented above), are among the top services prioritised by local stakeholders (Silva et al., 2021) and government agencies (PATFOR, 2018) and are also top priorities in the natural parks where we worked according to several conversations with Natural Parks' staff. We also produced a third "multifunctionality" scenario, maximising all processes simultaneously. The latter may not be necessarily related to a desired state by society (as it includes for example, high levels of herbivory or seed predation; details for each individual function in Figure S4). Nevertheless, our multifunctionality index was highly correlated to the more service-oriented one (the "ecosystem service bundles" explained above; $\rho = 0.74$; Figure S2) and thus could be of interest from a management perspective. For the multifunctionality scenario, we used the average of functions across the five plots composing the landscape. For carbon stocks, we used the average of belowground (soil organic matter) and aboveground (biomass) carbon stocks. For the biodiversity scenario, we considered Gamma diversity across each combination of five plots. We seek for those combinations of land uses that maximises each one of our three management scenarios (see Neyret et al., 2023 for similar approach). To do this, we built 1,906,884 artificial landscapes, each one with a random combination of 5 of our plots, considering all possible combinations. From these, we took the best 100 combinations, and quantified the average proportion of each land-use type. Then, we performed χ^2 tests to identify which of these land uses were over- or underrepresented in each case. To assess this, we assumed that the null expectation is an even distribution of 20% cover of each land use (our "expected" values). To aid interpretation of these results, we repeated the same procedure with every individual ecosystem function. We used R version 4.2.1 (R Core Team, 2022) and RStudio 2022.12.0.353 (Posit Team, 2022) to perform all the analyses. Fieldwork was performed in a protected area (Carrascal de la Font Roja and Serra de Mariola Natura Parks) with permission granted to do so from the Conselleria d'agricultura, desenvolupament rural, emergència climàtica i transició ecològica (Generalitat Valenciana, Spain).

3 | RESULTS

Land use was by far the most important predictor of multifunctionality and of many individual functions, explaining, together with plant richness and habitat sise, 44% of the variance in our multifunctionality metric (Table S2, Figure 1, Figure S3). Mixed and oak forests were the land uses with the highest multifunctionality, but also those showing more similarities to the functions they favoured (β-multifunctionality = 1.37; Figure 2). Orchards, in turn, were the least multifunctional land use (Figure 3), but also the one showing more complementarity with all other land uses in the functions it favoured (mainly litter decomposition and aboveground biomass) and the highest heterogeneity across the 10 plots sampled (Figure 2). We observed positive BEF relationships in three out of five land uses, with the most positive one (and the only statistically significant) observed in orchards (Figure S5).

The relative importance of local and landscape attributes varied depending on the target function, which at the same time showed a contrasting level of responsiveness to our local and landscape predictors (from ca. 1% vs. 68% of the variance explained for dissolved inorganic Nitrogen vs stability, respectively). Although land use still predominated overall, other drivers became relevant for some specific functions (Figure 1, Table S2, Figure S3). Habitat sise and diversity were important to determine carbon stocks (soil organic matter), water infiltration and functions related with predation (seed and caterpillar predation). Plant richness, in turn, was an important predictor for soil organic matter (which together with stability was the function with a higher R^2, over 60% of the variance explained), and for some of the biotic interactions evaluated (seed predation, herbivory; Figure 1, Table S2). We found that land use interacted significantly with plant richness to determine stability and betaglucosidase enzymatic activity. Land-use x habitat sise interactions, in turn strongly affected infiltration capacity (Table S2). Larger plant richness reduced beta glucosidase enzymatic activity and stability, but this negative effect was only evident in forests (oak, mixed and pine forest) and not in other land uses. However, larger habitats promoted infiltration capacity in natural land uses (oak forest, pine forest and shrubland).

The simulations of landscape mixtures maximising each of the three management scenarios (multifunctionality, biodiversity conservation, and carbon stocks) exhibited remarkable differences on the cover of each land-use type. If the aim was to maximise biodiversity conservation, orchards (19.6%), oak forest (42.6%) and mixed forest (32.4%) predominated. For maximum carbon stocks, oak and mixed forests (43.4% and 30.4%, respectively), were the land uses to favour, which were also similar to those needed to maximise multifunctionality (oak [58.6%] and mixed [33.8%] forests; Figure 4). Considering each individual function separately rendered qualitatively similar results, oak and mixed forest were generally overrepresented in 11 out of the 16 optimal landscapes (13 functions and 3 management scenarios), and orchards and shrublands were generally under-represented in the optimal landscape compositions (Figure S4).

4 | DISCUSSION

Biodiversity loss, landscape homogenisation and fragmentation, and land-use change are widespread and co-occurring anthropogenic
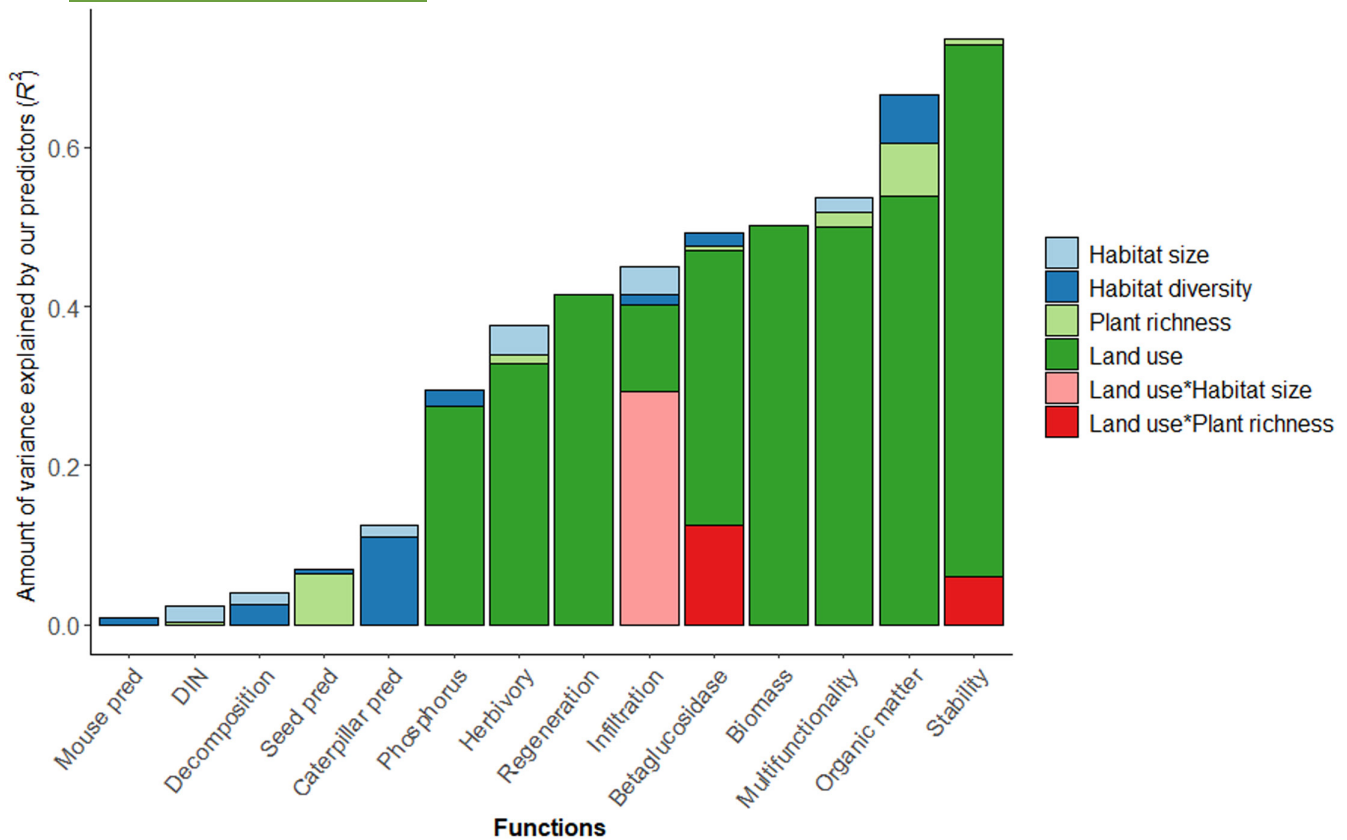
FIGURE 1 Relative importance of local and landscape drivers on the variance explained for the individual functions. The sise of the column shows the amount of variance explained by our predictors (R^2) for each individual function. Values were estimated using "calc.relimp" from linear models. (see Table S1 for detailed description of each function, and S2 for full results). DIN: Dissolved Inorganic Nitrogen.

pressures with known implications for conservation and ecosystem functioning (Cardinale et al., 2012; Haddad et al., 2015; Isbell et al., 2017). By studying their influence simultaneously, we found that although these drivers often interact and influence each other, land use was the main predictor of multifunctionality and of most individual functions, over and above local biodiversity, habitat sise or landscape diversity (Table S2). This agrees with previous comparisons on the influence of local biodiversity versus other factors, showing that the positive BEF relationships often observed locally can be overridden by the even larger effects of landscape (Hertzog et al., 2019; Zirbel et al., 2019) or environmental (Wardle, 2002) factors, in our case covered by contrasting land uses (but see Mori et al., 2015). Generally, changes in land use are considered one of the most important drivers of biodiversity loss (Newbold et al., 2015; Sala et al., 2000) and affect important ecosystems processes such as the global carbon cycle (Foley et al., 2005). Our study extends those findings to the multiple ecosystem functions humans rely upon, and show that remnants of native well-conserved vegetation (in our case oak and mixed forests) are of particular importance in the supply of these functions.

Millennia of anthropogenic management in the Mediterranean Basin, and particularly the extensive deforestation occurred during the 1950s and 60s for charcoal, food and fibre production in our study area, have relegated remnant native forests to the least

favourable sites (steepest and least accessible slopes, shallowest soils). Despite this, our results show that oak and mixed forests are still the most multifunctional land uses and clearly support the importance of conserving these remnant and diverse forest patches in order to maintain ecosystem functioning (see also Arroyo-Rodríguez et al., 2020; Ding et al., 2021; Gamfeldt et al., 2013). In parallel, these results suggest strong potential for the restoration of more favourable habitats (e.g. abandoned orchards with deeper soils) with this vegetation, which could importantly enhance carbon stocks and multifunctionality overall, well above those registered for the most commonly used conifer (*Pinus halepensis*) plantations (see differences in Figure 3). Although beyond the scope of our study, oak and mixed forests are also less vulnerable to wildfires than pine forests or shrublands; hence, increasing their coverage within the landscape could also enhance resilience to such disturbances in the future (e.g. Moghli, Santana, Baeza, et al., 2022; Pausas et al., 2004). Reintroducing these native forests in more favourable habitats could also enhance colonisation of new tree individuals in these stagnating ecosystems, the recruitment of which is limited by current climatic conditions or overgrazing (reviewed in Gil-Tena et al., 2019) and a concern for land managers in the driest parts of the distribution of these tree species (Natural Park's staff, pers. comm.).

Conversely, orchards were the least multifunctional land use, at least for the functions we considered in this study, which left out
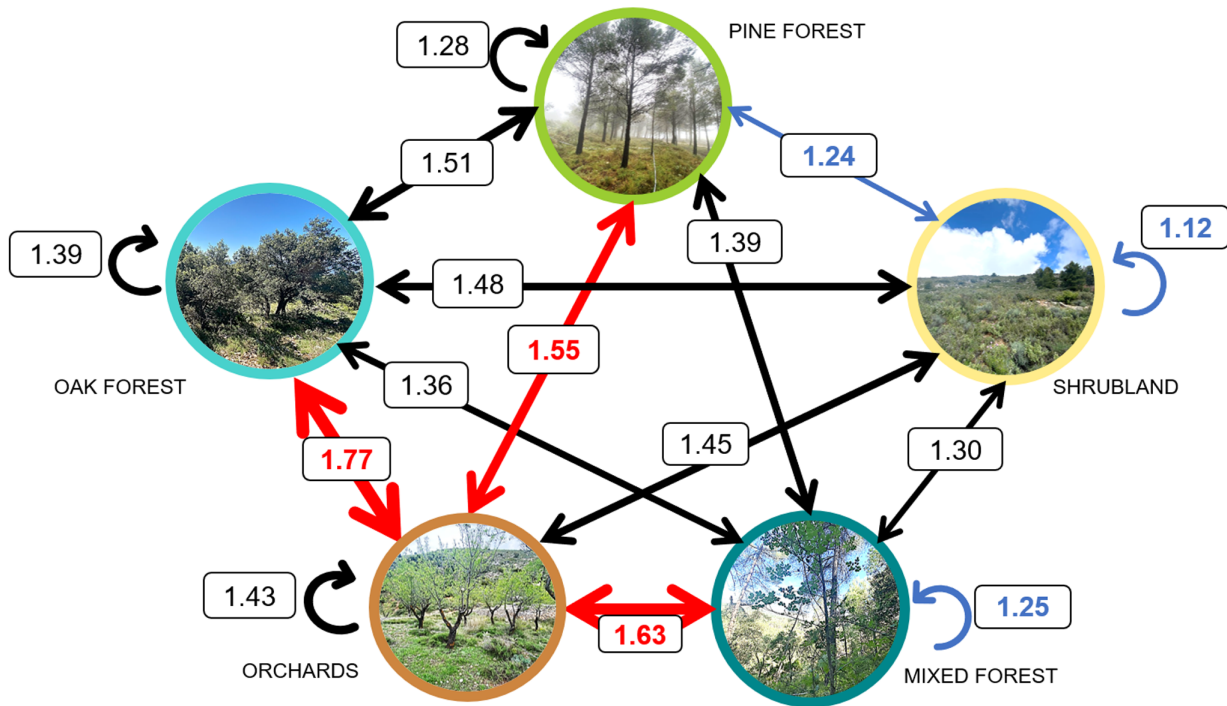
Habitat	Aboveground biomass	Decomposition rate	Infiltration capacity	Organic matter	Regeneration capacity	Herbivory	Mouse predation	Caterpillar predation	Seed predation	Beta-glucosidase	PO$_4$	Nitrogen	Stability
Orchards	0.44	0.41	0.25	0.06	0.01	0.49	0.16	0.20	0.34	0.25	0.58	0.21	0.27
Shrubland	0.01	0.32	0.52	0.35	0.03	0.66	0.28	0.34	0.39	0.43	0.32	0.36	0.58
Pine forest	0.28	0.36	0.54	0.38	0.24	0.30	0.49	0.20	0.36	0.35	0.25	0.22	0.71
Oak forest	0.30	0.31	0.48	0.70	0.49	0.47	0.31	0.24	0.57	0.63	0.61	0.46	0.78
Mixed forest	0.19	0.35	0.54	0.69	0.22	0.25	0.13	0.35	0.31	0.59	0.65	0.27	0.83

FIGURE 2 Dissimilarity indices between the functions favoured by each land use, calculated using Euclidean's distance. Higher numbers mean more dissimilarity in the functions provided between any given pair of land uses. The sise of the number and the arrows are proportional to the number. Red and blue values and lines were the three maximum and minimum values respectively. The table shows the mean standardised (0–1) values for each function and land use ($N=9$–10).
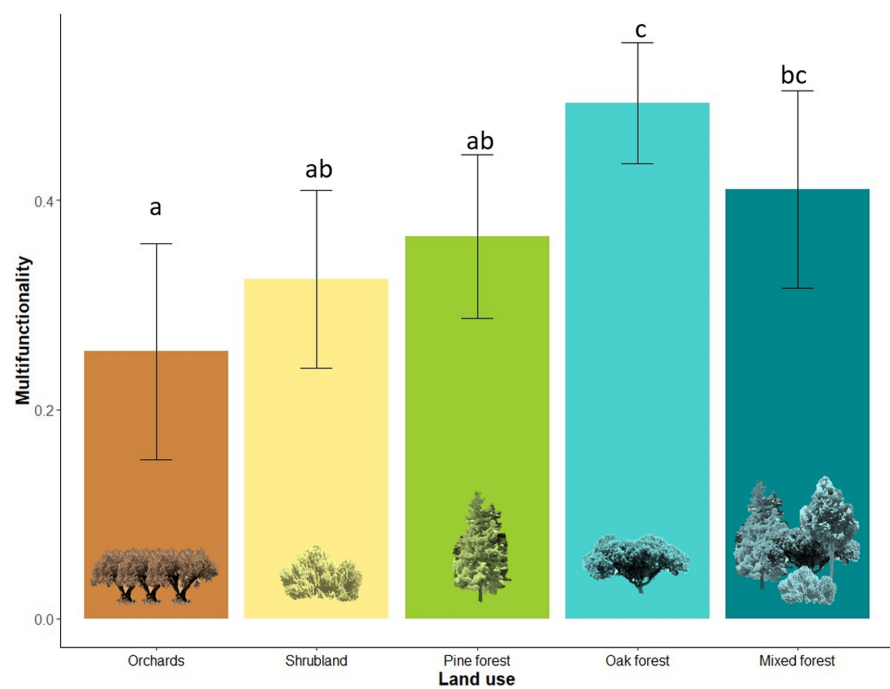

FIGURE 3 Mean (+/− SE; $N=9$–10) multifunctionality in each type of land use. Different letters show significant differences between land-use types (results from pots-hoc test).
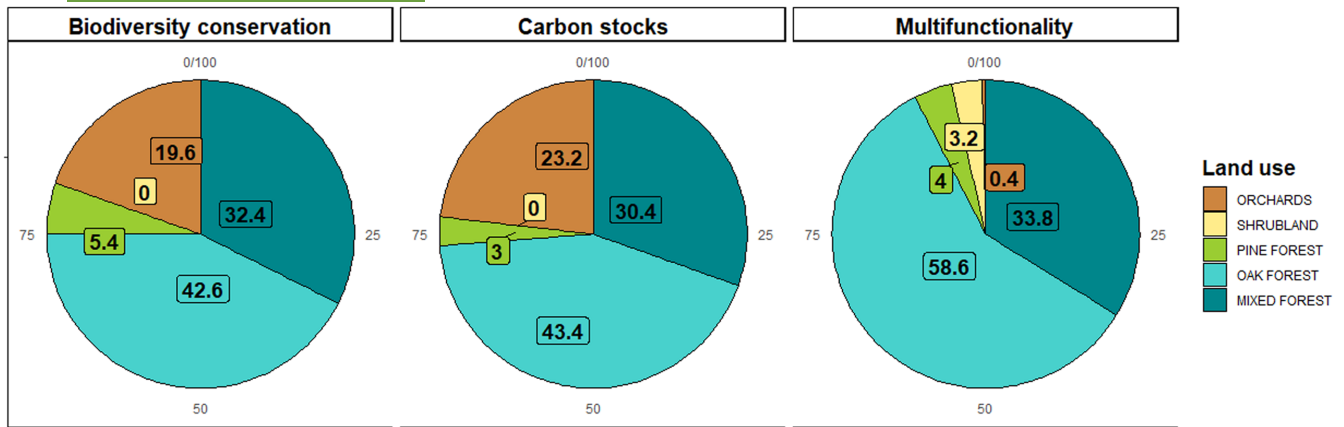
FIGURE 4 Proportion of each land use in landscapes maximising biodiversity conservation, carbon stocks or multifunctionality. These proportions were estimated as the average of the 100 highest values obtained from 1,906,884 artificial landscapes built from five randomly chosen plots from the 49 sampled in the different land uses. The three management scenarios were built according to: biodiversity conservation (bird richness, plant richness and tree recruitment richness), carbon stocks (aboveground plant biomass and soil organic matter) and multifunctionality (average of the 13 non-correlated individual functions; see Table S1).

some important processes such as food production or wildfire regulation, in which croplands could offer much higher levels of functioning. Nevertheless, our results are in line with previous studies highlighting that fertiliser application, pesticide use and mechanical disturbance on orchards reduce biodiversity and impairs the functioning of agricultural landscapes (de Graaff et al., 2019; Flynn et al., 2009). Interestingly, the relationship between biodiversity and functioning within orchards was the strongest and most positive in our study (Figure S5), as observed in other human-made ecosystems (e.g. Felipe-Lucia et al., 2014; Yin et al., 2019). Biodiversity in these agricultural systems relates to management intensity (e.g. Allan et al., 2014). Hence, the strongest BEF relationships we observed in orchards show strong potential for sustainable management practices in these ecosystems to improve multiple functions simultaneously (Allan et al., 2015; Foley et al., 2005; Rallings et al., 2019), where fostering and conserving biodiversity may be even more beneficial than in less anthropogenic ecosystems. Indeed, taken collectively, the biodiversity×land use interactions we found, together with those previously shown in the literature (Felipe-Lucia et al., 2014; Hertzog et al., 2019; Wardle & Zackrisson, 2005) suggests that biodiversity conservation may be particularly important in those habitats showing overall lower functioning levels, regardless of their proportion in the landscape, land-use type or degree of anthropogenic pressure. The latter suggests that, in addition to the level of species richness or the type of function considered (reviewed in Cardinale et al., 2012; Hagan et al., 2021; Van der Plas, 2019), we should take into account the average level of functioning a given habitat or land use has, in order to predict the strength of its BEF relationships. In other words, in addition to the X-axis (biodiversity), we should be able to better predict BEF relationships if we also focus on the Y-axis (the functioning itself) and expect less positive BEF relationships in ecosystems already showing high levels of functioning.

While land use was the most important predictor explaining overall multifunctionality in our sites, we also found a high degree

of functional complementarity among land uses (Figure 2). Oak and mixed forest provided the highest levels of functioning, but they also fostered similar functions, which were complemented by those provided by orchards. This result suggests that different land uses may complement each other to provide multiple functions at the same time (Alsterberg et al., 2017; DeFries et al., 2004; Neyret et al., 2023). The fact that different functions are co-determined by different local and landscape attributes (Figure 1, Table S2) may partly explain this complementarity. Beta-diversity positive effects on functioning are explained because different species provide different functions in different sites, and because dissimilarity in species composition may enhance movement of organisms and resources in between sites (e.g. Hautier et al., 2017; Mori et al., 2015; Van Der Plas et al., 2016). Similarly, different land uses can promote different functions across the landscape (Neyret et al., 2023; Stürck & Verburg, 2017), and diverse landscapes can also enhance movement of organisms and resources in between land uses. For example, bird species that contribute largely to pest control or seed dispersal (García et al., 2021), often nest in forests but prefer to forage on shrublands and orchards. Thus, having these different land uses next to each other could favour both biodiversity conservation and bird-related ecosystem processes. Perhaps, this is the reason why habitat diversity was a good predictor in our two predation's functions (caterpillar and seed predation), because these functions imply movement of organisms and resources.

Considering this complementarity in between land uses, we generated landscapes by mixing different plots aiming at maximisation of three different scenarios: biodiversity conservation, carbon stocks and multifunctionality overall. There is strong support to the benefits of the mosaic of land uses characterising Mediterranean landscapes for biodiversity conservation and functioning (reviewed in Aurelle et al., 2022; Blondel, 2006; Naveh, 1998). However, to the best of our knowledge no previous study has placed concrete numbers about the relative coverage of different land uses within

this Mediterranean mosaic. Our results suggest that oak and mixed forests should cover a large proportion (~90%) of the landscape, far more than what they cover now, in order to maximise multifunctionality (Figure 4). This figure will, of course, depend on the functions and attributes of interest for landscape managers, and can be much lower in other ecological or cultural contexts (Neyret et al., 2023). In fact, our results showed a lower proportion of these forest types if we want to prioritise carbon stocks or biodiversity conservation (Figure 4). Under the former scenarios, oak and mixed forests were still important, but orchards were also of strong interest for these management scenarios. The slow-growing, long-aged tree crops as olive trees, like most sampled orchards in our study, could contribute to accumulate woody mass in Mediterranean landscapes (Brunori et al., 2017) and, if well-managed, can function as a biodiversity reservoir in these environments (Rey et al., 2019) and elsewhere (e.g. Neyret et al., 2023). Thus, if orchards and crops are managed sustainably, the potential trade-offs between food production (which we did not measure in this study), biodiversity conservation, and other ecosystem services of interest could be promoted simultaneously (see Muller et al., 2017; Wittwer et al., 2021 for more detailed discussions on the topic). Our study revealed that land use is the most important driver of multifunctionality above local plant biodiversity, habitat sise, or landscape diversity. Our results highlight the crucial role of remnant native forests to provide multiple ecosystem functions and the potential to restore them in more favourable environments that the ones they are currently relegated too. In addition to remnant native forests, we highlight the interest of orchards and the strong and positive biodiversity-relationships they hold, which suggest that biodiversity conservation may hold the greatest benefits for functioning in human-made or less productive environments. Finally, our study highlights that preserving a diverse array of land uses may help maximising the provision of different functions in landscapes, as they complement each other. Supporting the interest to keep a mosaic of land uses in Mediterranean landscapes, we were also able to provide specific numbers regarding the proportion each of these land uses should have in order to maximise biodiversity conservation and/or functioning in these charismatic environments.

AUTHOR CONTRIBUTIONS

Santiago Soliveres designed the study. Paula Lopezosa, Santiago Soliveres and Soraya Constán-Nava conducted field and lab work. Lluís Serra identified plant species. Paula Lopezosa curated and analysed the data, with assistance of Miguel Berdugo and Santiago Soliveres. Paula Lopezosa wrote the first draft of the manuscript, and all authors contributed revisions.

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CONFLICT OF INTEREST STATEMENT

The author(s) declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available on Figshare https://figshare.com/s/d2f47ee34c 44285c9d24: (Lopezosa, 2023).

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SUPPORTING INFORMATION

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

Table S1. Measured functions and used methodology.

Table S2. Results of the linear models performed for each function as response variable.

Table S3. Results from model assumptions evaluation.

Figure S1. Detailed map from study area.

Figure S2. Relative importance of landscape and local attributes explaining the variance of bundles of Ecosystems Services and Threshold Multifunctionality.

Figure S3. Importance of each predictor (and their interactions) across different functions.

Figure S4. Representation of biodiversity-functioning relationships for each land use type.

Figure S5. χ^2 results. The over- or underrepresentation of each land use in order to maximize each function and scenario.