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Research article

Trade-offs among restored ecosystem functions are context-dependent in Mediterranean-type regions

Sebastian Fiedler[1,2,3,4], **Michael P. Perring**[5,6], **José A. Monteiro**[1,7], **Cristina Branquinho**[8], **Oksana Buzhdygan**[1], **Lohengrin A. Cavieres**[9], **Elsa E. Cleland**[10], **Jordi Cortina-Segarra**[11], **José M. Grünzweig**[12], **Jennifer A. Holm**[13], **Katja Irob**[1,12], **Trevor F. Keenan**[14,15], **Melanie Köbel**[8], **Fernando T. Maestre**[16], **Jörn Pagel**[17,18], **Natalia Rodríguez-Ramírez**[19,20], **Paloma Ruiz-Benito**[21,22], **Frank M. Schurr**[17,18], **Efrat Sheffer**[12], **Enrique Valencia**[23] and **Britta Tietjen**[1,24]

[1]Freie Universität Berlin, Theoretical Ecology, Institute of Biology, Berlin, Germany
[2]Department of Ecological Modelling, University Bayreuth, Bayreuth, Germany
[3]Department of Ecosystem Modeling, University of Göttingen, Göttingen, Germany
[4]Department of Plant Ecology, Technische Universität Berlin, Berlin, Germany
[5]UKCEH (UK Centre for Ecology and Hydrology), Environment Centre Wales, Bangor, UK
[6]The UWA Institute of Agriculture, The University of Western Australia, Perth, WA, Australia
[7]Statistical Office Basel-Stadt, Basel, Switzerland
[8]cE3c – Centre for Ecology, Evolution and Environmental Changes & CHANGE – Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal
[9]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción and Institute of Ecology and Biodiversity (IEB), Concepción, Chile
[10]Ecology, Behavior & Evolution Department, University of California, San Diego, La Jolla, CA, USA
[11]Department of Ecology and IMEM, University of Alicante, Alicante, Spain
[12]Institute of Plant Sciences and Genetics in Agriculture, Faculty of Agriculture, Food and Environment, the Hebrew University of Jerusalem, Rehovot, Israel
[13]Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
[14]Earth and Environmental Sciences Area, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
[15]Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, USA
[16]Environmental Sciences and Engineering, Biological and Environmental Science and Engineering 34 Division, King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia
[17]Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany
[18]KomBioTa – Center for Biodiversity and Integrative Taxonomy, University of Hohenheim & State Museum of Natural History, Stuttgart, Germany
[19]IMBE, Aix Marseille Université, Avignon Université, Marseille, France
[20]Office Français de la Biodiversité (OFB), Vincennes, France
[21]Universidad de Alcalá, Grupo de Ecología y Restauración Forestal, Departamento de Ciencias de la Vida, Alcalá de Henares, Spain
[22]Universidad de Alcalá, Grupo de Investigación en Teledetección Ambiental, Departamento de Geología, Geografía y Medio Ambiente, Alcalá de Henares, Spain
[23]Departamento de Biodiversidad, Ecología y Evolución, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, Madrid, Spain
[24]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Correspondence: Sebastian Fiedler (sebastian.fiedler@tu-berlin.de)

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Global biodiversity hotspots, including Mediterranean-type ecosystems worldwide, are highly threatened by global change that alters biodiversity, ecosystem functions, and services. Some restoration activities enhance ecosystem functions by reintroducing plant species based on known relationships between plant traits and ecosystem processes. Achieving multiple functions across different site conditions, however, requires understanding how abiotic factors like climate and soil, along with plant assemblages, influence ecosystem functions, including their trade-offs and synergies. We used the ModEST ecosystem simulation model, which integrates carbon, water, and nutrient processes with plant traits, to assess the relationships between restored plant assemblages and ecosystem functions in Mediterranean-type climates and soils. We investigated whether maximised carbon increment, water use efficiency, and nitrogen use efficiency, along with their trade-offs and synergies, varied across different abiotic contexts. Further, we asked whether assemblages that maximised functions varied across environments and among these functions. We found that maximised ecosystem carbon increment and nitrogen use efficiency occurred under moist, warm conditions, while water use efficiency peaked under drier conditions. Generally, the assemblage that maximised one function differed from those for other maximised functions. Synergies were rare, except between water and nitrogen use efficiencies in loam soils across most climates. Trade-offs among maximised functions were common, varying in strength with abiotic context and plant assemblages, and were more pronounced in sandy loam soils compared to clay-rich soils. Our findings suggest that due to variation in abiotic conditions within and across Mediterranean-type regions at the global scale, site-specific plant assemblages are required to maximise ecosystem functions. Thus, lessons from a single site cannot be transferred to another site, even where the same plant functional types are available for restoration. Our simulation results offer valuable insights into potential ecosystem performance under specific abiotic conditions following restoration with particular plant functional types, thereby informing local restoration efforts.

Keywords: biotic and abiotic context, ecosystem functioning, ecosystem restoration, Mediterranean-type ecosystems (MTEs), process-based simulation modelling, trade-offs and synergies

Introduction

Worldwide, multiple global change factors such as land use and climate change have led to degraded ecosystems, biodiversity loss, and a decline in the provision of ecosystem services people rely on for their well-being (IPBES 2019). One way to mitigate these negative impacts is through the restoration of degraded lands in order to recover their ecosystem functioning and service provisioning (Bullock et al. 2011, Gann et al. 2019).

Ecosystem restoration towards improved ecosystem functioning can be achieved by introducing plant species that are selected based on known links between functional traits and desired ecosystem functions and services (Funk et al. 2008, Laughlin 2014, Carlucci et al. 2020). Ecosystem functioning is also affected by abiotic conditions, both directly and indirectly, i.e. by filtering which species persist in a local environment (Funk et al. 2017, Yuan et al. 2020). Biotic and abiotic factors can therefore not be considered independently when quantifying the ecosystem functions supplied by restored ecosystems. For example, temperature directly alters the ecosystem function of litter decomposition, as it affects the decomposition rate (Rustad et al. 2001), but can also indirectly affect this function through filtering which species persist in a plant assemblage and their associated litter quality (Sariyildiz et al. 2005, LeRoy et al. 2014). Quantification is further complicated by the fact that changes in two or more abiotic factors can occur simultaneously, leading to interactive effects on ecosystem functioning (Xu et al. 2013). For example, increased soil nitrogen content can raise the evaporative demand of a plant assemblage by stimulating plant growth, potentially intensifying drought's negative impact on biomass production (Meyer-Grünefeldt et al. 2015).

Furthermore, if restoration aims to enhance multiple ecosystem functions simultaneously (Zavaleta et al. 2010), the trade-offs and synergies among functions must be accounted for (Bennett et al. 2009). These trade-offs and synergies arise from complex interrelationships between co-varying plant traits and multiple abiotic factors that affect ecosystem functions differently (de Bello et al. 2010, Lavorel and Grigulis 2012, Cebrián-Piqueras et al. 2021). Importantly, the potential for trade-offs and synergies may vary across abiotic conditions, leading to context-dependent relationships among ecosystem functions and associated ecosystem services (Biel et al. 2017). For example, water-use efficiency (WUE) tends to be negatively related with growth rates (Angert et al. 2007, Wang et al. 2013), leading to a trade-off between the ecosystem services of water conservation and carbon sequestration. The strength of this trade-off is potentially greater in arid climates where WUE is assumed to be higher (Huxman et al. 2004). Given this potential context dependence, it is not clear whether evidence gained from single sites can be transferred to different abiotic contexts, specifically for relationships between plant traits and ecosystem functions, and among functions (Fiedler et al. 2021). This strongly limits our ability to translate existing knowledge into restoration practices.

Here, using a simulation modelling approach, we aimed to evaluate if trade-offs and synergies among multiple restored ecosystem functions differ across a range of environmental contexts. We hypothesised that the abiotic (soil and climate) environmental context determines the plant functional trait composition that can persist and co-exist in restored plant assemblages where both direct (abiotic context) and indirect (plant-trait influenced) pathways determine trade-offs and synergies among multiple ecosystem functions. By analysing our model, we aim to develop a general understanding of trait–environment–ecosystem function relationships that single-site studies cannot achieve.

We illustrate our approach for Mediterranean-type ecosystems (MTEs), which are global biodiversity hotspots (Myers et al. 2000) as they cover only approximately 2% of the global land surface but host nearly 20% of the world's plant diversity (with very high levels of endemicity) and face serious threats such as desertification, erosion, salinisation, and changes in nutrient availability (Cowling et al. 1996, Médail and Quézel 1997, Hobbs 1998, Vallejo et al. 2001). Kottek et al. (2006) identified five Mediterranean-type regions using an updated Köppen–Geiger climate classification (Csa and Csb): North America (mostly California), South America (mostly central Chile), south Eurasia/North Africa (mostly the Mediterranean Basin), South Africa and southwest Australia. Although these ecosystems are found across a great range of variation in topography, geology, and soils (Vallejo et al. 2012), they share a set of common climate features, that is, cool wet winters and warm dry summers (Köppen 1900). This results in assemblages and organisms displaying similar structures and processes (Cody and Mooney 1978). Therefore, MTEs can serve as an ideal study system for assessing the generality of the links between restored plant functional traits and ecosystem functions, as well as trade-offs among them across different environmental contexts.

We focused on three functions related to carbon, water, and nitrogen pools that are of particular interest when restoring water- and nutrient-limited MTEs (Luo et al. 2020). These functions are 'ecosystem carbon increment' (ECI), which is linked to the ecosystem service of carbon sequestration, 'ecosystem water use efficiency' (WUE), which can indicate how an ecosystem may respond to drought (Yu et al. 2017), and 'ecosystem nitrogen use efficiency' (NUE), as an indicator of nutrient supply (Congreves et al. 2021). We assessed how these functions and relationships among them are affected by different assemblages of woody plant functional types (PFTs) that can be introduced in restoration initiatives in MTEs (Pausas et al. 2004, Perring et al. 2012). We combined empirical data with the ModEST ecosystem model (Fiedler et al. 2021), which links water and nutrient cycling to the life cycle of individual woody plants. These plants are grouped into six PFTs typical of MTEs worldwide. The model considers how water and nutrient cycling and plant assemblages are influenced by abiotic conditions representative of MTEs.

By simulating these dynamics, we estimated ecosystem functions provided by various restored PFT assemblages in different abiotic contexts. This allowed us to identify links between PFT traits and ecosystem functions, as well as trade-offs and synergies among functions in different MTE abiotic conditions. Specifically, we asked the following questions:

1) How do maximised values of restored ecosystem functions vary across the climatic and edaphic range in Mediterranean-type regions, given the same available pool of woody PFTs for restoration?
2) What are the relationships among restored ecosystem functions, i.e. synergies or trade-offs, and do these relationships vary in different abiotic contexts?
3) How are these context-dependencies shaped by shifts in the functional composition of restored PFT assemblages?

Material and methods

We used the spatially explicit and trait-based simulation model ModEST (modelling ecosystem services based on traits, Fiedler et al. 2021) to determine the context-dependency of the links between restored plant assemblages and ecosystem functions, and the trade-offs among these functions (Fig. 1 for an overview of our approach and the model). We parameterised the model for six woody PFTs typical for MTEs, representing potential plant species for restoration. We ran the model for various abiotic conditions (i.e. different climatic conditions and soil textures) found in MTEs globally. By using a full-factorial design of these abiotic conditions and different PFT combinations ranging from monocultures to the full PFT pool, we assessed whether the links of plant traits to the provision of the three ecosystem functions and their relationships (e.g. trade-offs or synergies) are context-dependent; that is, if they vary with abiotic conditions and PFT assemblages (Fig. 1).

Model description

ModEST simulates daily coupled dynamics of soil water, soil nitrogen, and carbon, as well as biomass of individual competing woody plants (Fig. 1, Simulation model setup). ModEST has been developed and successfully validated for a site in southwest Australia (Fiedler et al. 2021) but can be run for various abiotic conditions (i.e. different soil textures and climatic conditions) and for different woody plant species or PFTs.

The modelled landscape is divided into 5 × 5 m grid cells and two soil layers to allow within-landscape environmental variation. Individual plants are positioned continuously across the landscape. For each plant, daily dynamics of below- and aboveground carbon and nitrogen pools and structural components (e.g. height, crown area) are simulated. Key processes include CO_2 uptake and water loss by transpiration, nitrogen uptake, photosynthesis, respiration, carbon and nitrogen allocation, dispersal, establishment, and mortality. These processes are driven by abiotic conditions (air and soil temperature, photosynthetically active radiation, water, and nitrogen availability) and modified by functional trait values, specific to a given PFT (Supporting information). For each grid cell and soil layer, daily dynamics of soil water, organic matter, nitrate, and ammonium are calculated. Soil water dynamics are influenced by precipitation, surface water redistribution, infiltration, vertical fluxes, and evaporation, all of which depend on soil texture (Supporting information). Nutrient processes are driven by atmospheric nitrogen deposition and plant residues, which decompose into soil organic matter, then into ammonium and nitrate. These nutrients are

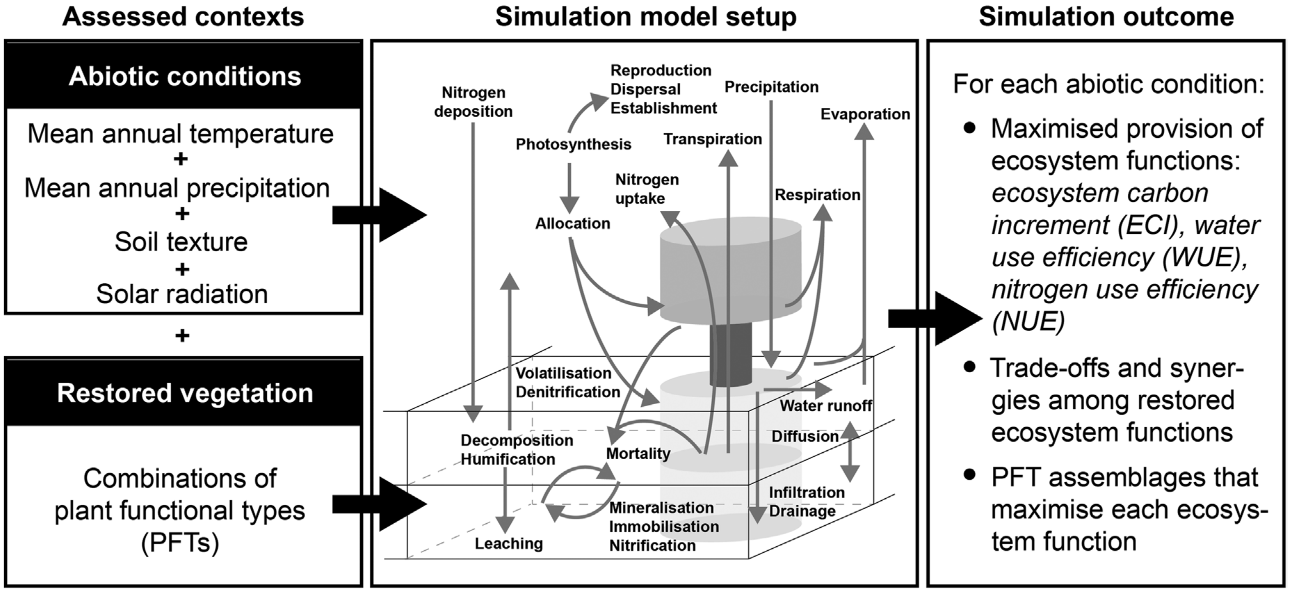

Figure 1. Conceptual structure of the study. Shown are the assessed context dependency of restoration in a full-factorial design (left panel) by using the simulation model ModEST (centre panel, adapted from Fiedler et al. 2021) and evaluated simulation outcomes of the model (right panel).

taken up by plants or lost through volatilization, denitrification, and leaching, influenced by soil temperature, water, texture, and plant residue C:N ratio. Fire was excluded as a factor due to the focus on short-term dynamics, assuming fire exclusion after planting, similar to the Ridgefield restoration experiment in southwest Australia (Perring et al. 2012). Full model details are available in Fiedler et al. (2021) and cited publications.

Simulation experiments

We aimed to understand the context-dependency in trade-offs and synergies among ecosystem functions. To do so, we systematically simulated ModEST for a broad set of potential abiotic conditions found across MTEs worldwide (Fig. 2), and for different biotic conditions, i.e. plant communities assembled from six potential Mediterranean-type PFTs available for restoration (Fig. 3). Herein, we refer to these restored communities of one or more PFTs as ‘PFT assemblages’, where each PFT is characterised by a particular combination of trait values. In other words, there is no intra-PFT variation in trait values in our simulations. We used a full-factorial simulation design combining all possible initial PFT assemblages (63 restoration scenarios, see ‘Restoration scenarios’) with a range of abiotic conditions found in these regions including mean annual temperature, precipitation, solar radiation, and different soil textures (1320 abiotic condition scenarios, see ‘Climate and soil texture scenarios’). This resulted in a total amount of 83 160 scenarios (63 PFT assemblages × 1320 abiotic condition combinations). Each scenario was run on a fire-excluded landscape of 50 × 50 m for 100 years, to achieve a quasi-stationary state, and was repeated ten times to account for stochasticity in the spatial initialization of plant individuals, weather input (see ‘Climate and soil texture scenarios’), and the plant dispersal process of ModEST (for details see model description in Fiedler et al. 2021).

Climate and soil texture scenarios

To cover a wide spectrum of abiotic conditions of the MTEs world-wide and within each Mediterranean-type region, we combined different observed soil textures, latitudes, mean annual temperatures (MATs), and mean annual precipitations (MAPs) in a full factorial setup. We simulated four, most common, soil textures of Mediterranean-type regions (Fig. 2d), i.e. clay loam, loam, sandy clay loam, and sandy loam (soil parameters in the Supporting information). MTEs are found in latitudes between 30 and 50° north and south, impacting annual solar radiation dynamics and thus potential evapotranspiration (Fig. 2a). We therefore conducted simulations at set latitudes of 30, 40, or 50° and calculated corresponding values for solar radiation based on Tietjen et al. (2009). Scenario ranges for MAP and MAT across the five Mediterranean-type regions were obtained from monthly modelled climate data with a spatial resolution of 0.5° × 0.5° (1901–2019, Harris et al. 2020). Here, we took the 25–75th percentiles of MAP (200–1200 mm in steps of 100 mm: 11 values) and MAT (8–17°C in steps of 1°C: 10 values) across all regions to define the limits of our scenario ranges for MAP and MAT (Fig. 2b–c). By encompassing this overall climatic range, we ensure that the variability within each Mediterranean-type region is also adequately represented, as shown later in results figures.

For each simulation replicate, we generated 100 years of daily precipitation according to the respective climate scenario after Köchy (2006) as well as daily mean, and minimum

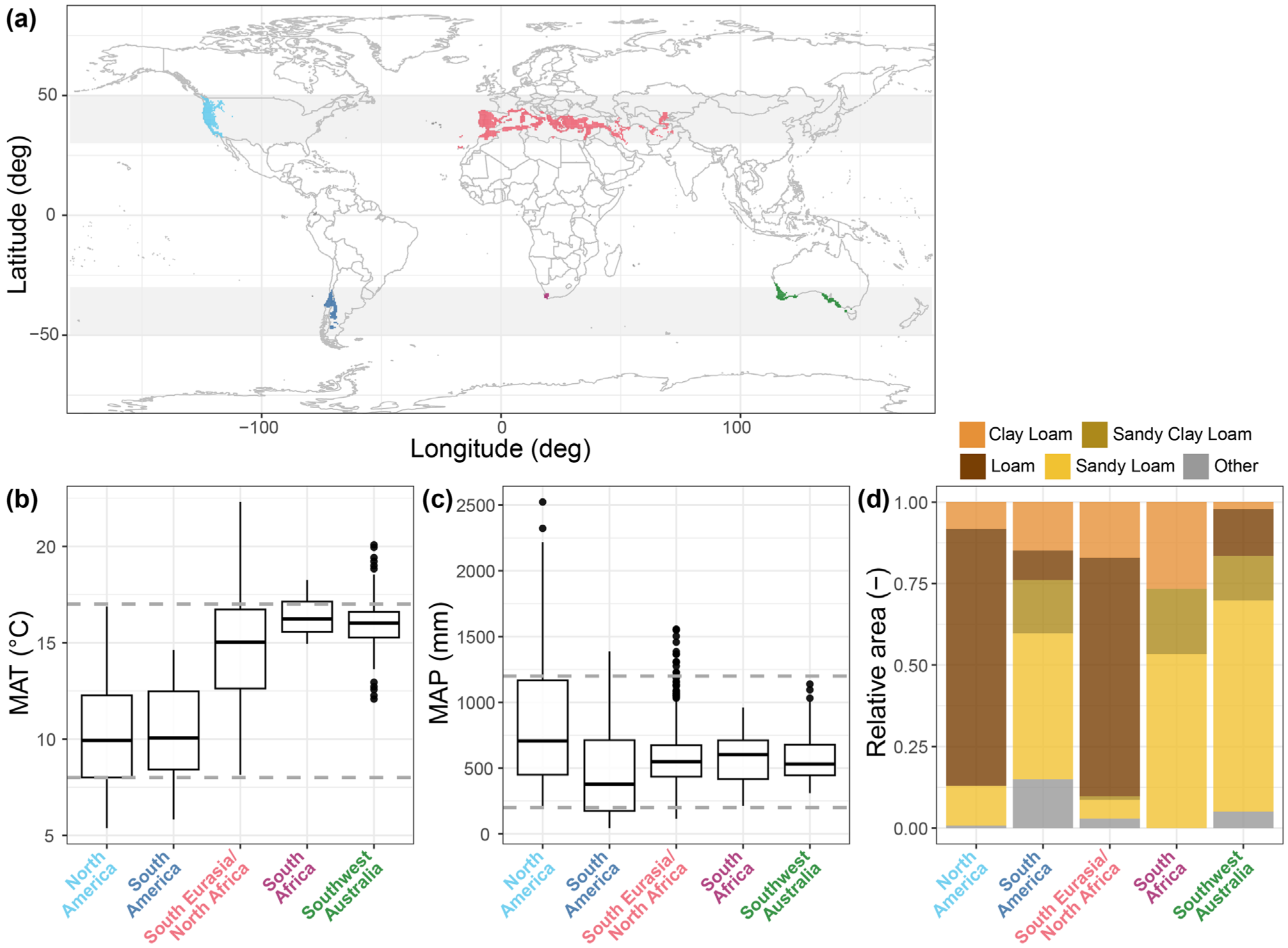

Figure 2. Overview of Mediterranean-type ecosystems (MTEs) world-wide. Shown are (a) global distribution of MTEs (Csa and Csb, Kottek et al. 2006) and simulated range of latitudes (grey shaded areas), as well as abiotic conditions found at each of the five Mediterranean-type regions (bottom), i.e. (b) mean annual temperature (MAT, 1901–2019, Harris et al. 2020) and simulated range (dashed lines), (c) mean annual precipitation (MAP, 1901–2019, Harris et al. 2020) and simulated range (dashed lines), and (d) observed proportion of soil textures in each region, all of which were simulated, except 'other' (Koirala 2012).

and maximum temperature following Tietjen et al. (2009). For each MAP scenario, annual precipitation varied randomly over the simulation period, with probabilities derived from monthly 0.5° × 0.5° gridded data spanning 1901–2019 (Harris et al. 2020). Daily rainfall was generated using monthly patterns of daily rainfall variation based on 0.5° × 0.5° gridded daily data from 1991 to 2020 (NOAA 2020b). Similarly, for each MAT scenario, daily temperatures were generated using gridded minimum and maximum temperature data at 0.5° × 0.5° resolution for the period 1991–2020 (NOAA 2020a).

Restoration scenarios

For each abiotic condition, we simulated all possible PFT combinations from a pool of six Mediterranean-type PFTs (Fig. 3): five evergreen PFTs and one deciduous PFT (PFT 4). The five evergreen PFTs are characterised as follows: PFT 1 has high SLA and leaf nitrogen; PFT 2 features very small, lightweight leaves and a low SLA; PFT 3 is a nitrogen fixer; PFT 5 has low stomatal conductance, and photosynthetic rate; and PFT 6 has a low SLA but broader, heavier, and nitrogen-rich leaves.

Our simulations ranged from monocultures, where only one PFT is simulated, to assemblages initially comprising the full PFT pool with all six PFTs present, resulting in a total of 63 distinct simulated PFT assemblages. This approach allowed us to capture a wide range of functional diversities and trait compositions to evaluate their effects on restored ecosystem functioning.

We identified representative PFTs through a cluster analysis of all shrubs and tree taxa observations from the TRY database within the Mediterranean climate region (Kattge et al. 2020) based on similarities of ten plant traits (Supporting information). First, numeric traits were standardised, and missing data were imputed using additional sources and the Random Forest-based *missForest* method in R (Stekhoven and Buhlmann 2012). We then calculated a Gower distance

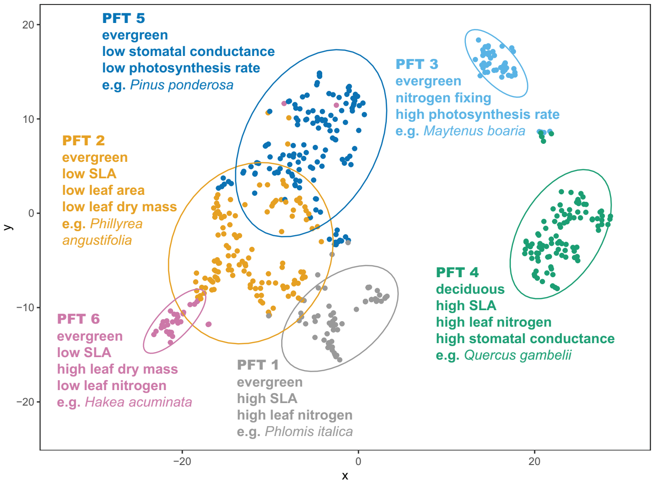

Figure 3. Classifications of six woody plant functional types (PFTs) in Mediterranean-type ecosystems (MTEs) as a result of a cluster analysis based on traits for each species. Two-dimensional visualisation of the multidimensional Gower distances between trait data is based on the t-distributed stochastic neighbour embedding (t-SNE) method (R package 'Rtsne', Krijthe 2015). Clustering into PFTs is based on partitioning the Gower distance data into six clusters around medoids (partitioning around medoids [PAM]). Per PFT one representative plant species is given whose trait values are close to the median trait values of the given PFT cluster. SLA is an abbreviation for specific leaf area. A full description of the PFT classification and the parameterisation of these PFTs for ModEST can be found in the Supporting information. A full list of species, their PFT assignment, and trait values can be found in Fiedler et al. (2025).

matrix to measure pairwise trait dissimilarities and performed clustering using the *pam* function from the R package 'cluster' (Maechler et al. 2021). The optimal number of clusters was determined using the 'NBclust' package (Charrad et al. 2014). Based on this, we categorised the species into six distinct PFTs which we then implemented in ModEST (see the Supporting information for further details).

For each of the 63 simulated PFT assemblages, a total of 300 young individuals of the respective PFTs were positioned with a plant height of 50 cm into a 50 × 50 m landscape with 2 m distance to neighbouring individuals. Except for monocultures, PFT identity was assigned randomly to the positioned individuals in the landscape with an equal share of each included PFT, e.g. for assemblages initially simulated with three PFTs, 100 individuals of each PFT were placed at random in the landscape.

By simulating combinations of the six PFTs, we focus on the average trait values of each PFT, representing a broader pool of species with inherent trait variation. This allowed us to assess how general plant strategies could influence ecosystem functioning across diverse abiotic conditions, and we contend this provides insights that are applicable across all MTEs. We chose this PFT-based approach over species-level assessments because species are often highly site-specific and/or restricted to one continent, whereas our study aimed to address broader, functional, patterns relevant to the suite of MTEs. In future, incorporating trait variability within each PFT could enhance our understanding of how this variability, along with differences across PFTs, influences ecosystem functional responses under different abiotic contexts.

Evaluation of simulation outcomes

In the following, we describe evaluations conducted for each research question separately. All data analyses were performed in R ver. 4.0.3 (www.r-project.org).

Restored provision of ecosystem functions across abiotic contexts

For each combination of abiotic conditions (i.e. MAP, MAT, latitude, soil texture) and initial PFT assemblage we first calculated the mean provision of ecosystem functions and the mean total biomass of each PFT within the simulation run, for the years 90–100, repeating the simulation ten times. We focused on the provision of three ecosystem functions, namely 'total ecosystem carbon increment' (ECI, unit: t × ha^{-1} × $year^{-1}$) as the sum of the annual plant and soil carbon increment, 'ecosystem water use efficiency' (WUE, unit: g × l^{-1} × $year^{-1}$) as the ratio between annual net primary productivity (NPP) and annual precipitation per m^2, and 'ecosystem nitrogen use efficiency' (NUE, unit: kgNPP × m^{-2} × gN^{-1} × m^{-3}) as the ratio between annual NPP per m^2 and annual mean soil available nitrogen per m^3.

For each combination of abiotic conditions, we then determined, separately for each ecosystem function, the PFT assemblage (out of the 63 possible simulated PFT assemblages) that maximised the respective function.

Relationships among restored functions across abiotic contexts

To determine trade-offs and synergies among ecosystem functions we plotted pairwise relationships across two focal ecosystem functions for all 63 PFT assemblages. Then, we explored the similarity in the delivery of a target function when compared to the maximised delivery of another function. In essence, we aimed to determine whether a particular PFT assemblage could achieve maximum values for two functions within a specific abiotic context, or if there were differences among the restored assemblages yielding maximised functioning. Overall, our goal was to assess whether such synergies or trade-offs among functions and PFT assemblages that maximised ecosystem functions varied across different abiotic contexts.

To investigate this objective, we examined relationships at five combinations of temperature and precipitation (within the overall abiotic space) across soil types and latitudes. Given initial findings that soils with the lowest amount of clay in the scenarios modelled here (i.e. sandy loam) displayed contrasting results to those with more clay (i.e. loam, clay loam, sandy clay loam), and limited effects of latitude, we focus our presentation on loam and sandy loam soil types at 40° latitude; full results can be found in the Supporting information. These two soil types are also the most common across Mediterranean-type climate regions (Fig. 2d).

PFT assemblages that maximise ecosystem functions across abiotic contexts

To characterise the composition of the PFT assemblages that maximised ecosystem functions, we calculated the mean biomass of each PFT present in that assemblage. Where trade-offs exist between maximised values of two restored functions within a given environment, the relationship must be driven by the different plant assemblages as the abiotic environment is otherwise constant. Where relationships between functions differ across abiotic contexts, this is driven by a combination of direct (abiotic) effects and indirect (plant trait-mediated) effects. In some circumstances, the same plant assemblages may be present in different abiotic conditions, such that any difference in relationships between the maximised provision of two functions must be driven by the abiotic condition alone. When interpreting results, we considered these properties, as well as the relevance of a given abiotic condition to the conditions observed in Mediterranean-type regions worldwide.

Results

Variation in maximised ecosystem functioning across abiotic contexts

We found that maximised ECI, WUE, and NUE differed strongly between different soils and climatic conditions (Fig. 4, Supporting information), while the effect of solar radiation was minimal (Supporting information). Furthermore, ecosystem function patterns across the climate space were similar on clay-rich soils (i.e. clay loam, loam, and sandy clay loam) compared to those on sandy loam (Supporting information).

Maximised ECI was highest for warm-moist conditions, which are rarely found in MTE regions. It was lowest for cold-moist conditions, typical of North America. ECI was generally higher for loam, which is rare in South Africa compared to sandy loam, which is found across all regions (Fig. 4). Maximised WUE was highest for dry conditions, typical of South America, lowest for warm-moist conditions, and generally higher for sandy loam compared to loam soil types. Maximised NUE was highest for warm-moist conditions, lowest for cold-moist and warm-dry conditions, which are rare across regions, and was generally higher for loam compared to sandy loam soil types.

Synergies and trade-offs among functions in the different abiotic contexts

Across all simulated PFT assemblages (from monocultures to the full PFT pool), we generally found a positive correlation (i.e. synergy) between functions except for WUE and NUE on sandy loam soils (Fig. 5, see the general positive relationships among functions). The reason for the synergy, however, is that the general performance of the assemblage (e.g. the number of surviving plants and their biomass) is dependent on its initial composition, and numerous PFT assemblages show low performance, including local extinction from the simulated landscape (Fig. 6).

When maximising individual functions under a given abiotic condition (as shown in Fig. 4), trade-offs with the other maximised functions were common (Fig. 5, large dots). This means that the PFT assemblage providing the maximal value of one function does not simultaneously maximise another function (Fig. 5, two same-coloured large dots representing two different PFT assemblages that maximised functions with the direction and length of the dashed line representing the magnitude of the trade-off). These trade-offs were, in general, strongest and more common on sandy loam soil textures. In particular, trade-offs between maximised WUE and NUE greatly increased from loam to sandy loam under all climatic conditions except for cold-wet conditions (Fig. 5, bottom panel with longer dashed lines representing stronger trade-offs). These cold-wet conditions are mostly found in North America (Supporting information). Trade-offs between maximised ECI and WUE also increased from loam to sandy loam (Fig. 5, top panel) but only for cold-dry conditions, common across North and South America (Supporting information) and in warm-dry conditions, mostly found in South Africa (Supporting information). The greatest trade-off between maximised ECI and NUE was found for warm-wet and sandy loam conditions (Fig. 5, right centre panel, brown dashed line).

Nevertheless, under some conditions synergies were also observed, either if two functions were maximised by the same PFT assemblage (strong synergy, Fig. 5, single large dot per abiotic condition representing the same assemblage maximising both functions at the same time) or if two distinct PFT assemblages only slightly differed in their maximised provision of both functions (weaker synergy, Fig. 5, very short dashed lines between two same-coloured dots representing different assemblages but only slight differences in the maximised provision of the functions). These synergies mostly occurred between maximised WUE and NUE on loamy soils for all climatic conditions except the cold-wet climate; this cold-wet climate is poorly represented across most MTEs except those in North America (Supporting information).

The underlying PFT assemblages providing maximised ecosystem functions in different abiotic contexts

For each abiotic condition and for each ecosystem function we assessed the plant assemblage providing the maximised function value. We found that all simulated PFTs played a role in maximising ecosystem functions when considering the full range of investigated abiotic conditions (Fig. 6, Supporting information). However, the functional diversity of PFT assemblages maximising individual functions,

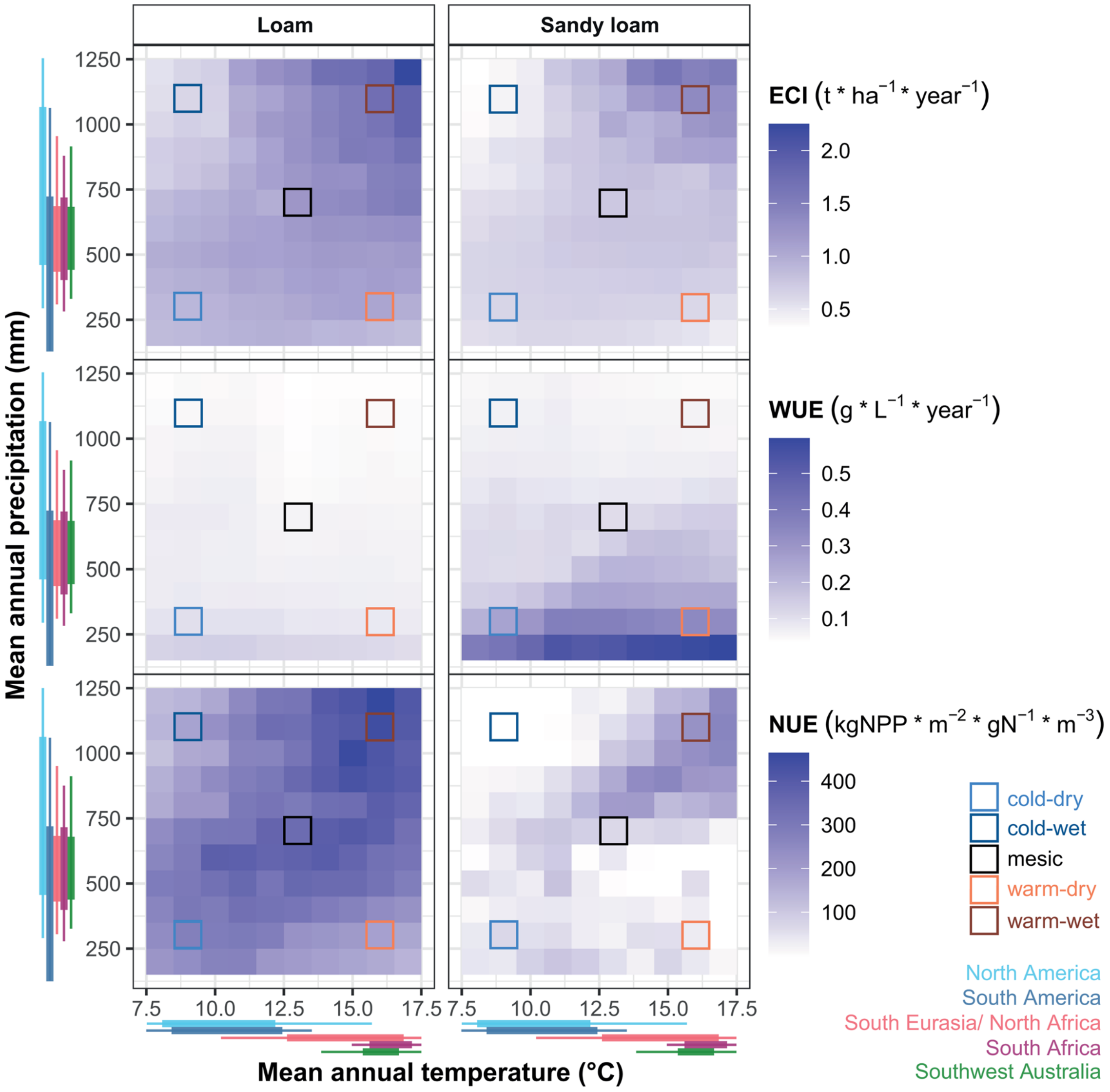

Figure 4. Maximised ecosystem functioning across planted plant functional type (PFT) assemblages for each abiotic condition. For each combination of mean annual precipitation (y-axis), mean annual temperature (x-axis), and soil texture (columns) we show maximised ecosystem carbon increment (ECI, top), ecosystem water use efficiency (WUE, centre), and ecosystem nitrogen use efficiency (NUE, bottom) across the restoration scenarios. Shown is mean functioning over the simulation years 90 to 100 and ten model replicates. Results are given for the two most common soil textures across Mediterranean-type ecosystems (MTEs) and for solar radiation at 40° latitude (results for all simulated abiotic conditions can be seen in the Supporting information). Coloured lines represent climatic ranges (thick line: 25–75th percentile, thin line: 5–95th percentile whenever in the focal range of 200–1200 mm for mean annual precipitation and 8–17°C for mean annual temperature) of each of the Mediterranean-type climatic regions (c.f. Fig. 2). Coloured bordered squares highlight the focal climatic conditions shown in Fig. 5.

or all functions simultaneously, was generally low, with greater diversity observed primarily under wetter conditions (Supporting information). This means that, in general, a low number of PFTs are responsible for maximising functions.

PFT assemblages that maximised individual ecosystem functions, or all three focal functions simultaneously, generally differed across abiotic conditions (Fig. 6, Supporting information). However, across environmental contexts PFT 1 (high specific leaf areas [SLA] and leaf nitrogen) as well as PFT 6 (low SLA and leaf nitrogen, and high leaf dry mass) were the most dominant groups in most of the assemblages that maximised ecosystem functions. When considering sandy loam soils, for maximising ECI (Fig. 6 left column), PFT 1 was dominant for drier and cold-wet conditions. In contrast, on the same sandy loam soil, PFT 2 (low SLA, leaf area, leaf dry mass) and PFT 4 (deciduous and high SLA, leaf nitrogen, stomatal conductance) were dominant for warm-wet conditions, and PFT 6 was always present except for some warm-wet and warm-dry conditions. For maximising WUE, PFT 1 was dominant across all climatic conditions,

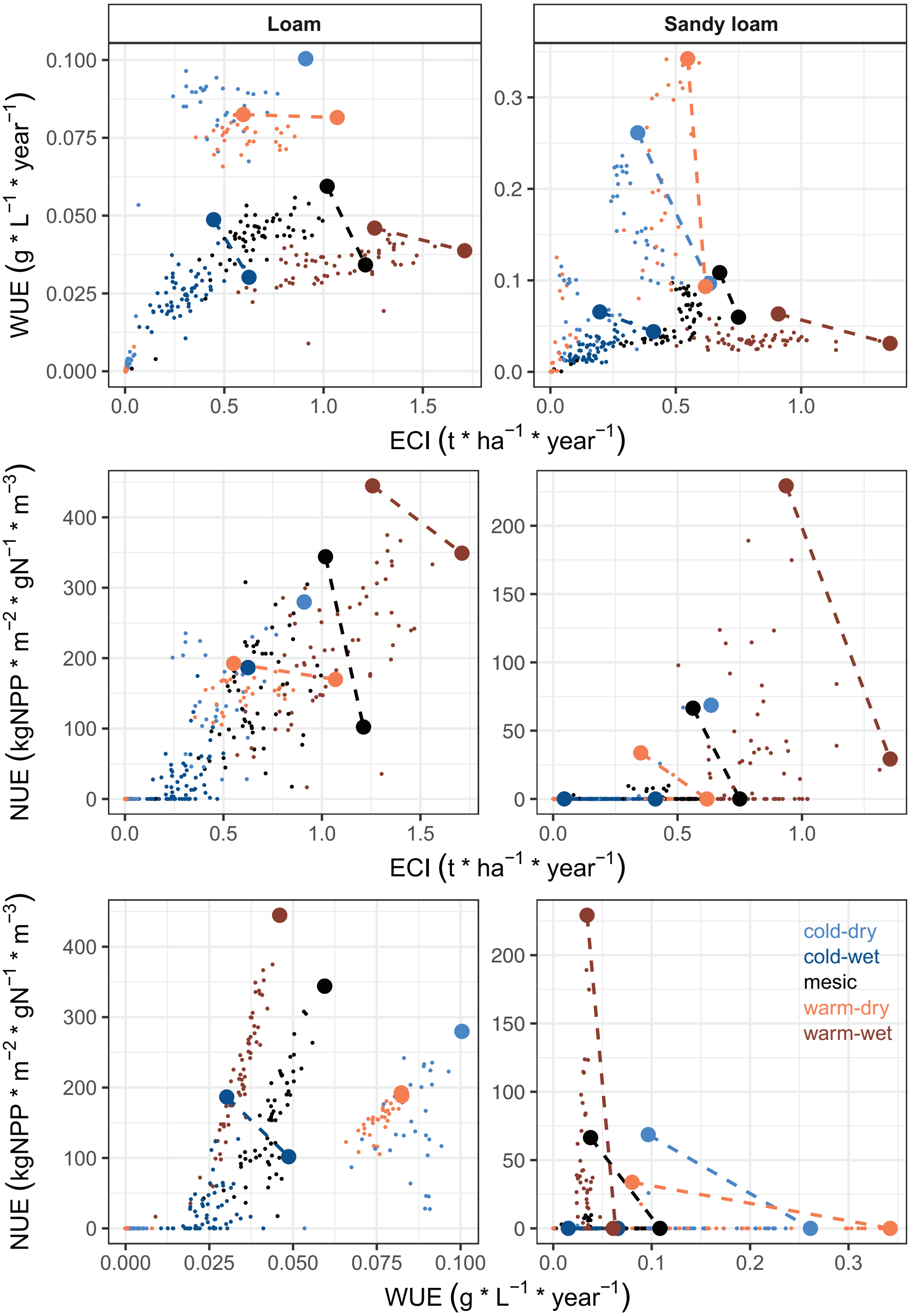

Figure 5. Relationships between ecosystem functions across all 63 restoration scenarios (dots) for five climatic conditions (colours) and for the two most common soil textures studied (columns). For each environmental setting, the best performing restoration scenario (i.e. plant assemblage) that provided the maximum value for each respective function (as shown in Fig. 4) is highlighted with larger dots. Differences in the maximised provision of ecosystem functions are indicated by two same-coloured large dots and dashed lines, with the direction and length of each line representing the magnitude of the trade-off. For instance, a long, near vertical line shows there is a large drop in the function on the y-axis for a marginal gain in the value of the function on the x-axis, and vice versa for a near horizontal line. If no dashed line is present, it means the same plant function type (PFT) assemblage maximised both functions simultaneously. Shown are relationships between ecosystem carbon increment (ECI), ecosystem water use efficiency (WUE), and ecosystem nitrogen use efficiency (NUE) for solar radiation at 40° latitude. Selected climatic conditions are (cf. with coloured bordered squares in Fig. 4) 'cold-wet' with MAP = 1100 mm and MAT = 9°C, 'cold-dry' with MAP = 300 mm and MAT = 9°C, 'mesic' with MAP = 700 mm and MAT = 13°C, 'warm-wet' with MAP = 1100 mm and MAT = 16°C, and 'warm-dry' with MAP = 300 mm and MAT = 16°C.

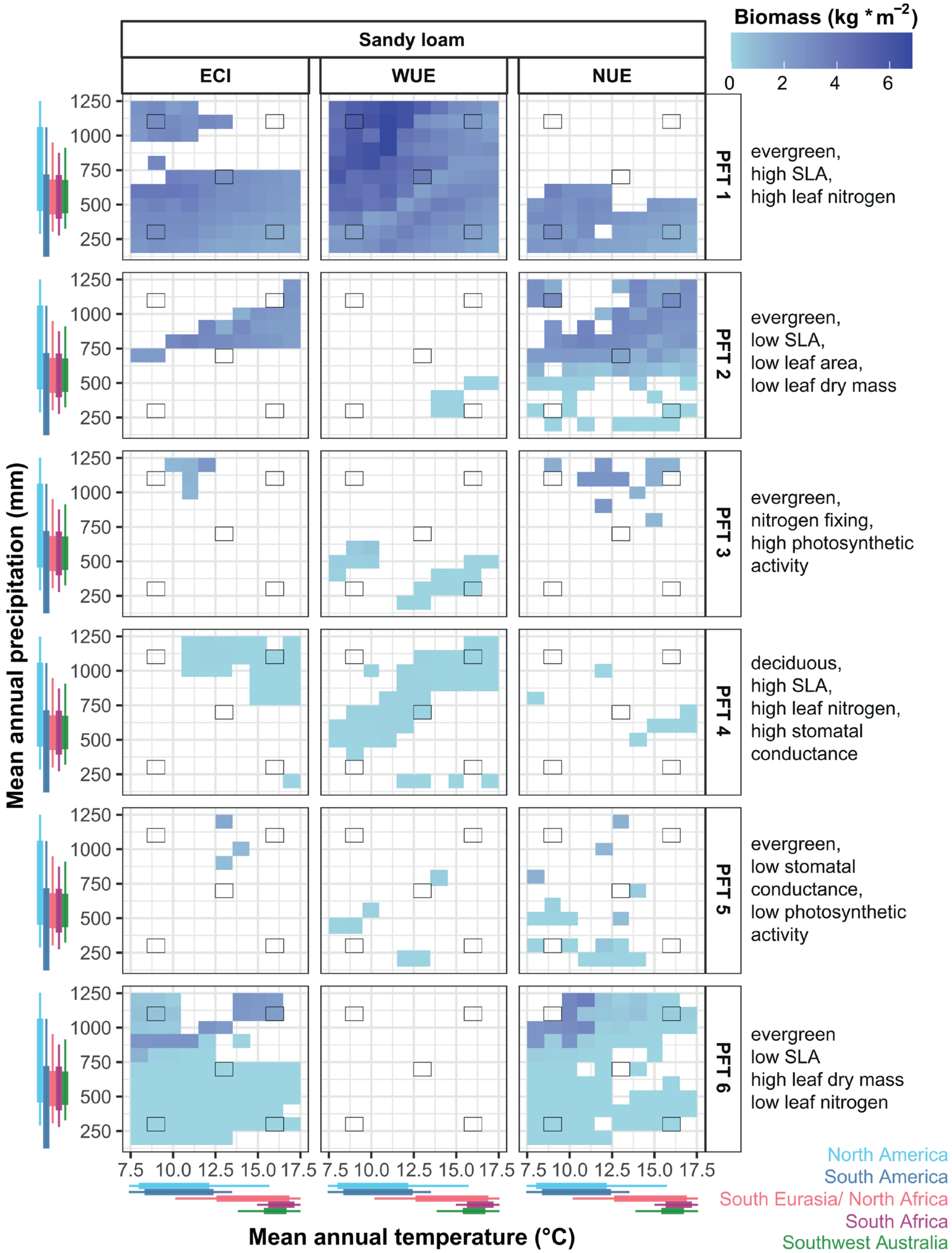

Figure 6. Biomass per plant function type (PFT) of the restoration scenarios that provided maximised ecosystem functioning for different abiotic conditions. A given PFT's mean biomass (between 90 and 100 years, 10 model replicates) is shown for each ecosystem function (columns) and for different mean annual precipitation (y-axis), mean annual temperature (x-axis) with soil texture 'sandy loam' (results for the two most common soil textures in the Supporting information) and solar radiation at 40° latitude. Coloured lines represent climatic ranges (25–75th percentile) of the Mediterranean-type climatic regions (c.f. Fig. 2). Black bordered squares highlight the focal climatic conditions shown in Fig. 5.

and PFT 4 was also present in warmer and wetter conditions. For maximising NUE, PFT 1 dominated in drier conditions, while PFT 2 dominated across warmer and wetter as well as cold-wet conditions. PFT 6 was, similarly to ECI, always present except under colder and wetter, warmer and mesic, or warmer and drier conditions. We found that when comparing loam (Supporting information) with the sandy loam results (Fig 6), PFT assemblages tended to show similar patterns. For instance, PFT 6 was always present except for some warm-wet and warm-dry conditions. However, on loam, PFT 1 was even more dominant and PFTs 2 and 4 were generally less present, as compared to sandy loam. A supplementary analysis, finding the assemblage that can provide the highest amounts of all ecosystem functions simultaneously, suggests PFT 1 and PFT 6 are generally dominant across all climate conditions in loam soils (Supporting information). In contrast, sandy loam soils exhibit assemblages that are similar to those maximising ECI alone, across all climatic conditions.

Discussion

Restoration of ecosystem functions in different environments

When restoring MTEs by planting woody plants, the resulting ecosystem functions can vary significantly depending on the plant assemblage used. This study examined the PFT assemblages that maximise three ecosystem functions: ECI, WUE, and NUE in different environments.

One key finding is that the maximised value of a given ecosystem function is highly dependent on the prevailing abiotic conditions at the restoration site. While the role of abiotic context in ecosystem functioning is well-documented (Cregger et al. 2014, Ratcliffe et al. 2017, Sun and Du 2017), our research extends this by showing how these functions vary when restored using the same pool of PFT assemblages, and across diverse abiotic conditions in Mediterranean-type regions. We found that mean annual temperature, precipitation, and soil texture (clayey versus sandy) most significantly affected maximised ECI, WUE, and NUE, either directly or indirectly through shaping plant assemblages after restoration. Solar radiation had a negligible effect, likely due to the narrow latitudinal range of MTEs. Below, we focus on the overall effects of environmental variation. For a more detailed discussion of direct and indirect effects, see ‘Plant assemblages maximising functions in different environments’.

In particular, we found that maximised ECI was highest under warm-wet conditions, highlighting the importance of water availability for plant and soil carbon storage in water-limited MTEs, as also shown by Pereira et al. (2007). Increasing soil sand content generally reduced ECI, likely due to the lower water-holding capacity of sandier soils, limiting plant growth. This negative effect of sand content on soil carbon stocks has also been observed in temperate North American regions (McLauchlan 2006, Augustin and Cihacek 2016). In contrast, maximised WUE was highest under drier conditions, consistent with findings across biomes with water limitations (Huxman et al. 2004). Maximised NUE was highest under warm-wet conditions and on clay-rich soils, likely due to reduced water limitation and higher primary productivity for the same quantity of nitrogen.

In addition, we showed interactions among different abiotic factors affected maximised ecosystem functions. For instance, the positive effect of lower annual precipitation on WUE was stronger for warmer and sandier conditions. This suggests a more efficient use of water by plant assemblages under potentially drier soil conditions resulting from a combination of lower rainfall, lower water holding capacity of sandier soils, and higher evapotranspiration due to warmer conditions. Furthermore, our results showed that below 11°C in mean annual temperature, the maximised ECI tended to decrease under wetter conditions. This might be a result of ModEST implementing lower microorganism-mediated decomposition rates in highly moist soil conditions, thus restricting plant growth by limiting nitrogen release into the soil. For mean annual temperatures above 11°C, the positive effect of rainfall on ECI was enhanced by warmer temperatures. Such a positive interactive effect of rainfall and temperature has been found before on net primary production as an important driver of carbon sequestration (Luo et al. 2008).

Trade-offs and synergies among restored ecosystem functions in different environments

Our results revealed that restoration for maximising pairs of ecosystem functions (Fig. 5), and for all three functions simultaneously (Supporting information), can be constrained in a different manner, depending on the conditions found in MTEs. While evidence for trade-offs across functions has been mounting in the last decade for different ecosystems (Aryal et al. 2022), the mechanisms shaping these relationships are still not fully understood (Bennett et al. 2009). Usually, such trade-offs are attributed to specific functional plant traits that affect ecosystem functions differently (de Bello et al. 2010). Here, we show that trade-offs among restored functions are highly dependent on the prevailing abiotic conditions across Mediterranean-type regions. Such variation of trade-offs across abiotic contexts has also been found for soil functions across different European climatic zones and land uses by Zwetsloot et al. (2021).

In our study, we found the strongest trade-offs between maximised ecosystem functions occur on sandy loam soils, but the magnitude of the trade-offs varied with climatic conditions and the particular pair of ecosystem functions being considered. For restoration managers, this suggests there is a need for careful characterisation of sites prior to intervening to avoid unintended consequences. For instance, in loam soils and warm-dry environments, for a large gain in maximum ECI there is a small loss of optimal WUE. However, in the same warm-dry environment but in sandy loam, there would be a large loss of optimal WUE to gain a maximised ECI. As such, where maximising ECI is prioritised by practitioners in such an environment (i.e. dry and warm climate, sandy loam soil), there may be implications for the resilience of the system to drought. However, taking a small loss on ECI could improve the optimal WUE and secure the ECI in the longer term. Such warm-dry environments are characteristic of MTEs in South Africa while they would be rare in the Americas (Supporting information).

Plant assemblages maximising functions in different environments

We evaluated the PFT assemblages in various abiotic settings that maximised one of the three ecosystem functions. Our findings revealed that assemblages maximising these functions across most climatic conditions were mainly composed of a few key PFTs – specifically PFT 1, PFT 2, and PFT 6. PFT 1 has an acquisitive strategy, characterised by high SLA, which enables rapid growth and resource capture during favourable conditions. In contrast, PFTs 2 and 6 are more conservative, with a greater resistance to drought during dry summers. These contrasting strategies suggests that MTEs sustain functioning through partitioning resource consumption in their plant assemblages across environmental variation in time and space.

Furthermore, we observed that trait characteristics of the PFT assemblages maximising ecosystem functions differed across abiotic conditions with mean annual precipitation as the most important factor. Such a finding is in line with a study by de la Riva et al. (2018) who also found aridity to be a key abiotic factor in shaping the trait structure of Mediterranean woody assemblages. Despite the concordance between the broad conclusions from empirical results and modelling, we did observe some contrasts. For instance, in natural systems de la Riva et al. (2016) showed that SLA decreased in assemblages under drier conditions yet the modelling showed the assemblages that maximised functions exhibited greater SLA (Supporting information). One reason for this apparent contradiction may be that conservative strategies (i.e. lower SLA) are dominant in intact ecosystems found in drier conditions, but in an artificially manipulated ecosystem with the goal to maximise functions, acquisitive strategies (i.e. higher SLA) could be a more suitable choice for restoration. Future complementary empirical experiments validating our findings could offer deeper insights, particularly into the applicability of these strategies in restoration efforts across different stages of ecosystem development.

Although we did not always observe differences in PFT assemblages that maximised functions across simulated abiotic conditions, the maximised functions themselves still varied across these conditions. For instance, the SLAs of assemblages maximising WUE were similar across climatic ranges in sandy habitats but still the maximised WUE value varied significantly (c.f. Fig. 4 with the Supporting information). This suggests that the abiotic condition significantly drives variation in WUE, and the amount of associated growth, given the plant assemblage trait values were similar. Since these trait values were not identical, there may also be some indirect effects on functional values via changes in plant traits. Consequently, trade-offs between functions under different abiotic conditions result from combinations of direct and indirect effects as presented in Fiedler et al. (2021).

Overall, our results indicate the crucial role abiotic context plays in understanding ecosystem function interrelationships. In our results, this is exemplified by the fact that in drier sandy habitats, trade-offs between maximised WUE and ECI were due to direct effects of abiotic conditions, as plant assemblages that led to maximum values were alike. Yet, the influence of the biota can be important in other abiotic contexts, even though plant traits alone do not fully explain variation in ecosystem functioning (as shown for grassland in van der Plas et al. 2020). For instance, in our results and in the same sandy habitat but with warm-wet conditions, assemblages that maximised the different focal ecosystem functions showed variation in SLA. In such circumstances, plant traits can still serve as reliable predictors of ecosystem properties (Hagan et al. 2023). Our findings can provide valuable guidance for restoration efforts, helping to identify traits that should be tailored to specific climatic contexts and those that can be standardised across sites with differing abiotic conditions.

Conclusion

Our simulations showed that there can be large differences in the maximised delivery of ecosystem functions in different abiotic contexts that are representative of MTEs worldwide. These differences result from a combination of direct abiotic impacts on processes and mediation through indirect pathways, i.e. the plant assemblage at a site and its traits. Importantly, we have revealed that the PFT assemblage that may maximise a function in one abiotic condition may differ from the assemblage that maximises another function, resulting in trade-offs between maximal ecosystem function values. Such trade-offs between functions can differ between abiotic conditions, especially between soil types differing in the sand content. This demonstrates that selecting specific plant traits is crucial for optimising various ecosystem functions, while abiotic conditions continue to play a key role in ecosystem functioning, affecting both the maximum potential of these functions and, to some extent, the PFT assemblage that drives them.

While our study advances the general understanding of ecosystem function within the context of restoring MTEs, there are limitations to consider. Our simulations did not fully incorporate site-specific factors such as soil degradation, invasive species, and altered fire regimes – critical challenges in real-world restoration. Additionally, we did not account for the effects of management practices like weeding and fire control, which can be essential for successful restoration. For instance, invasive species management could significantly enhance the establishment and performance of target species. Realities of pre-existing conditions can lead to the failure of restoration efforts (as also explored by Maes et al. 2024). Future research should address these site-specific challenges and management strategies to refine restoration approaches under diverse ecological conditions. Despite these limitations, our research offers valuable strengths. The systematic assessment of plant community composition and ecosystem functioning across a broad range of abiotic conditions provides a strong theoretical foundation for restoration in MTEs. Our results can guide empirical testing, such as experimental planting of PFT combinations (Gellie et al. 2018) in areas with varied soil types and relatively consistent climates, to validate predicted maximised function values as well as trade-offs and synergies among them. These tests could contribute to a broader restoration strategy, providing actionable insights for improving restoration outcomes in MTEs and beyond.

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Author contributions

Sebastian Fiedler: Conceptualization (equal); Formal analysis (lead); Funding acquisition (equal); Methodology (lead); Project administration (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Michael P. Perring**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (lead); Validation (equal); Writing – original draft (lead); Writing – review and editing (equal). **José A. Monteiro**: Conceptualization (equal); Methodology (supporting); Software (lead); Writing – original draft (equal); Writing – review and editing (equal). **Cristina Branquinho**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Oksana Buzhdygan**: Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Lohengrin A. Cavieres**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Elsa E. Cleland**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jordi Cortina-Segarra**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **José M. Grünzweig**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jennifer A. Holm**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Katja Irob**: Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Trevor F. Keenan**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Melanie Köbel**: Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Fernando T. Maestre**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Jörn Pagel**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Natalia Rodríguez-Ramírez**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Paloma Ruiz-Benito**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Frank M. Schurr**: Methodology (supporting); Validation (equal); Writing – original draft

(equal); Writing – review and editing (equal). **Efrat Sheffer**: Conceptualization (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Enrique Valencia**: Conceptualization (equal); Methodology (supporting); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Britta Tietjen**: Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Software (supporting); Supervision (lead); Writing – original draft (lead); Writing – review and editing (equal).

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Data availability statement

Simulated data and R scripts for evaluation of the simulated data as well as full plant species list including imputed plant trait values and plant functional type classification are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mw6m90654 (Fiedler et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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