

1 **TITLE:** Restoration ecologists might not get what they want: Global change shifts trade-offs among
2 ecosystem functions

3 **AUTHOR DETAILS**

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22 **ABSTRACT**

- 23 1. Ecological restoration increasingly aims at improving ecosystem multifunctionality and making
24 landscapes resilient to future threats, especially in biodiversity hotspots such as Mediterranean-
25 type ecosystems. Successful realisation of such a strategy requires a fundamental mechanistic
26 understanding of the link between ecosystem plant composition, plant traits and related
27 ecosystem functions and services, as well as how climate change affects these relationships. An
28 integrated approach of empirical research and simulation modelling with focus on plant traits can
29 allow this understanding.
- 30 2. Based on empirical data from a large-scale restoration project in a Mediterranean-type climate in
31 Western Australia, we developed and validated the spatially explicit simulation model ModEST,
32 which calculates coupled dynamics of nutrients, water and individual plants characterised by traits.
33 We then simulated all possible combinations of eight plant species with different levels of diversity
34 to assess the role of plant diversity and traits on multifunctionality, the provision of six ecosystem
35 functions (covering three ecosystem services), as well as trade-offs and synergies among the
36 functions under current and future climatic conditions.
- 37 3. Our results show that multifunctionality cannot fully be achieved because of trade-offs among
38 functions that are attributable to sets of traits that affect functions differently. Our measure of
39 multifunctionality was increased by higher levels of planted species richness under current, but
40 not future climatic conditions. In contrast, single functions were differently impacted by increased
41 plant diversity. In addition, we found that trade-offs and synergies among functions shifted with
42 climate change.
- 43 4. *Synthesis and application.* Our results imply that restoration ecologists will face a clear challenge
44 to achieve their targets with respect to multifunctionality not only under current conditions, but
45 also in the long-term. However, once ModEST is parameterized and validated for a specific
46 restoration site, managers can assess which target goals can be achieved given the set of available

47 plant species and site-specific conditions. It can also highlight which species combinations can best
48 achieve long-term improved multifunctionality due to their trait diversity.

49 **KEYWORDS**

50 Biodiversity, Functional Traits, Plant Traits, Climate Change, Ecosystem Services, Mediterranean-type
51 Ecosystem, Multifunctionality, Simulation Model

52

53 1 INTRODUCTION

54 Global change is contributing to a decline in biodiversity, and ecosystem functions and services people
55 rely on for well-being (IPBES, 2019). Degradation associated with past change, and concern for the
56 future supply of multiple ecosystem services is particularly apparent in Mediterranean-type
57 ecosystems where remarkably high diversity is threatened by multiple environmental changes
58 (Cowling et al., 1996; Sala, 2000). Ecological restoration is therefore required in such systems, with the
59 goal to maintain the long-term and simultaneous delivery of multiple ecosystem functions and services
60 in these socio-ecological systems (Shackelford et al., 2013; Gann et al., 2019).

61 Managing landscapes for multiple functions or services simultaneously requires a direct comparison of
62 their delivery (e.g. Byrnes et al., 2014; Manning et al., 2018). With increasing evidence that higher
63 levels of ecosystem functions and services are associated with greater species numbers (Cardinale et
64 al., 2012), the traditional focus of restoration on plant biodiversity appears justified (Perring et al.,
65 2015). Enhanced biodiversity, however, does not necessarily increase the simultaneous and resilient
66 provision of multiple ecosystem services as some services do not profit from greater species richness
67 and the effect of global change on species and service provisioning remains unclear (e.g. Cardinale et
68 al., 2012; Meyer et al., 2018).

69 In an attempt to further understanding of biodiversity's impact on ecosystems, restoration ecology has
70 more recently made use of the functional trait concept allowing selection of plant species based on
71 their response and effect traits (Lavorel & Garnier, 2002; Laughlin, 2014). A focus on effect traits, which
72 have been found to be linked to ecosystem functions (Lavorel & Garnier, 2002), allows for a better
73 comparison across individuals and plant species. We have a good understanding on how individual
74 environmental factors affect individual functions and services via plant traits (e.g. Lavorel & Garnier,
75 2002; Suding et al., 2008). However, nature is more complex and plant traits are not always linked to
76 single functions. Instead, multiple traits can affect one function, and multiple functions can be affected
77 by a single trait (de Bello et al., 2010), and multiple functions can influence a single ecosystem service
78 (Fu et al., 2013). This is particularly important if traits positively affect one function while at the same

79 time negatively impacting another one – so-called trade-offs (Bennett et al., 2009). Knowing the trade-
80 offs as well as synergies among plant traits and functions is therefore important for selecting plant
81 species based on their traits to simultaneously improve levels of multiple functions/services.

82 In addition, multiple environmental change factors that directly, or indirectly (via altering plant trait
83 distributions), affect ecosystem functions can have non-additive effects (e.g. Luo et al. 2008).
84 Restoration strategies based on individually studied effects could therefore be problematic when
85 trying to achieve a long-term supply of functions and services. Furthermore, traits within a plant
86 community may be affected differently by environmental factors, and therefore the provision of trait-
87 mediated ecosystem functions may be affected differently as well. Consequently, trade-offs among
88 ecosystem services observed under current environmental conditions might not be the same under
89 future conditions.

90 To improve understanding and allow more informed restoration, Fiedler et al. (2018) suggested an
91 integrated approach that focuses on plant traits and combines the strengths of empirical and
92 simulation modelling studies. Empirical approaches can support modelling approaches with essential
93 data, while simulation models can extend empirical approaches by allowing assessment of the multi-
94 layered relationship between multiple environmental factors, plant traits and ecosystem
95 functions/services on larger temporal and spatial scales. Current trait-based simulation models provide
96 a good basis for this approach (e.g. Esther et al., 2011; Fyllas & Troumbis, 2009; Schaphoff et al., 2017).
97 However, to be able to support restoration towards multifunctional and resilient ecosystems,
98 simulation models need to be combined and extended to meet the following criteria: (i) coupled
99 processes for soil water, nutrient and plants as well as the respective feedbacks allowing to
100 mechanistically study the impact of global change on vegetation, (ii) consideration of individual
101 interactions (e.g. facilitation and competition) as well as spatial heterogeneity relevant for applied
102 restoration projects implemented on smaller spatial scales, and (iii) a thorough validation of model
103 outcomes against field data to make simulation models applicable for restoration.

104 Based on existing model tools and a restoration experiment in a Mediterranean-type ecosystem in SW
105 Australia (Perring et al., 2012), we therefore developed and validated the individual- and trait-based
106 simulation model ModEST (Modelling Ecosystem Functions and Services based on Traits). ModEST links
107 water, nitrogen and plant processes dependent on climatic and other environmental conditions and
108 exhibits therefore enough generality to transfer findings beyond this specific study site. We used the
109 model to assess the following research questions:

- 110 1) What is the role of planted species richness under current and future conditions on
111 multifunctionality, and the provision of separate ecosystem functions and services?
- 112 2) How will environmental changes affect trade-offs and synergies among ecosystem functions and
113 services of simulated plant communities?
- 114 3) What sets of plant traits and correlations among them in the simulated plant communities provide
115 ecosystem functions under current and future conditions?

116 2 MATERIAL AND METHODS

117 2.1 Model description

118 We developed a spatially explicit model, ModEST (**M**odelling **E**cosystem Functions and **S**ervices based
119 on **T**raits) which simulates the coupled daily dynamics of nutrients, water, and individual woody plants
120 (Fig. 1), from which different ecosystem functions and services can be estimated (Fiedler et al., 2020).
121 The model landscape is subdivided into grid cells (5 x 5 m²), two soil layers, and individual plants
122 characterized by coordinates within the landscape. The model runs for different environmental
123 settings concerning soil texture, climatic conditions, topography, initial plant composition and their
124 traits, with full descriptions given in Supplementary S1 and S2. In the following, we briefly describe the
125 three coupled modules of ModEST.

126 The nutrient module is based on processes for simulating soil nitrogen and soil carbon described in the
127 model SWAT (Kemanian et al., 2011). Daily dynamics of soil organic matter (SOM), nitrate, and
128 ammonium in two soil layers are driven by *nitrogen deposition* from the atmosphere, *decomposition*

129 and *humification* of plants' residue to SOM, *immobilization*, *mineralization* to ammonium, *nitrification*
130 to nitrate as well as nutrient losses through *volatilization*, *denitrification* and *leaching*.

131 We based the hydrological module on the approach of Tietjen et al. (2009), who simulated surface
132 water and soil moisture in two soil layers. Daily water dynamics are driven by *precipitation*, *lateral*
133 *water redistribution of surface water*, *infiltration*, and *vertical fluxes*, and by water losses via
134 *evaporation* and *transpiration*. For ModEST, we adopted these processes with the exception of
135 transpiration which we implemented after the model LPJ (Sitch et. al., 2003) and LPJmL (Schapoff et
136 al., 2017), to better account for stomatal conductance (see description of the transpiration process in
137 Supplementary S1).

138 The plant module is mainly based on LPJ and LPJmL (Schaphoff et al., 2017; Sitch et al., 2003; Smith et
139 al., 2014) and local processes as described for an individual-based plant model by May et al. (2009).

140 The module simulates the life cycle of individual woody plants placed in the landscape, their dynamic
141 below- and aboveground carbon and nitrogen pools as well as structural components (e.g. plant
142 height, crown area) based on plant traits and abiotic conditions. We adopted – with some changes –
143 the plant processes *photosynthesis*, *transpiration*, *respiration*, *reproduction*, and *allocation* after Sitch
144 et. al. (2003) and Schapoff et al. (2017), *nitrogen uptake* after Smith et al. (2014), as well as *dispersal*
145 *and establishment* after May et al. (2009). We added a simple *plant mortality* process based on annual
146 plant growth and a species-specific growth threshold below which the individual plant dies. Given
147 these adaptations, we fully describe this module in the Supplementary S1.

148 2.2 Model parameterization and validation

149 We parameterised and validated ModEST based on the settings of the Ridgefield experiment, a large-
150 scale restoration experiment situated in the wheatbelt of SW Australia on former agricultural land
151 (Perring et al., 2012). The experiment is located in a Mediterranean-climate region (32°29'S 116°58'E,
152 elevation 350 m a.s.l.) with mean annual rainfall of 453 mm (2013 – 2019) and precipitation mainly
153 during winter. The average maximum daily temperature in January is 30.7 °C and the average minimum
154 daily temperature in August is 7.6 °C.

155 We parameterized eight evergreen woody plant species (Table S2.1) which were planted in different
156 plant assemblages representing increasing functional and species richness. We used the most
157 prevalent soil type (loamy sand, Table S2.2) in the experiment (see Supplementary S2 for full
158 description of model parameterisation).

159 For model validation, we checked the outcome of the parameterized model against measurements
160 from Ridgefield plots (see Supplementary S2 for model settings). We quantitatively compared
161 simulated and observed dynamics using Spearman's rank correlation r and the root mean square error
162 $RMSE$. Simulated aboveground alive biomass, mean plant height, and surviving individual counts
163 agreed well with the measured data (i.e. significant [$p < 0.01$] correlations, low $RMSE$). Exceptions were
164 the biomass dynamic of *B. sessilis* and the population dynamics of *C. quadrifidus* and *C. phoeniceus*,
165 where correlations were insignificant (Fig. S2.2). However, $RMSE$ for these cases remained low ($RMSE$
166 < 1.0), indicating only small deviances between simulated and measured dynamics, and suggesting
167 reasonable model behavior.

168 2.3 Simulation experiments

169 We simulated a full-factorial design of plant species combinations using the eight species included in
170 the Ridgefield study (and thus simulating plant assemblages beyond those planted at Ridgefield) to
171 assess ecosystem functioning under current and future climatic conditions. The flat modelled
172 landscape ($50 \times 50 \text{ m}^2$) contained a homogenous soil texture of loamy sand, with initial soil moisture
173 ($= 0.15 \text{ m}^3 \cdot \text{m}^{-3}$), ammonium ($= 2.35 \text{ mg} \cdot \text{kg}^{-1}$) and nitrate ($= 9.92 \text{ mg} \cdot \text{kg}^{-1}$) set to the mean measured
174 values across all Ridgefield plots with soil texture loamy sand. Each scenario was repeated ten times
175 to account for stochasticity in the initialisation of plant individuals (see *Species richness scenarios*),
176 weather input (see *Climate change scenarios*), and the dispersal process (see model description in
177 Supplementary S1).

178 2.3.1 Species richness scenarios

179 All possible combinations of the eight woody plant species used in the Ridgefield experiment were
180 simulated leading to 255 different plant species compositions. Using this design, communities covered
181 a wide range of different plant trait combinations, and species richness varied from monocultures to

182 8-species mixtures. For each simulation, 500 one-year old individuals with the same or a similar initial
183 individual number of each present species were randomly positioned with 2 m distance to
184 neighbouring individuals. Initial plant heights were randomly drawn from a species-specific normal
185 distribution that was obtained from height distributions of the one-year planted individuals in the
186 Ridgefield experiment (Fig. S3.1).

187 2.3.2 Climate change scenarios

188 For current climatic conditions, we used corrected daily precipitation, minimum and maximum air
189 temperature and solar radiation data from 1990 to 2018 from the weather station in Pingelly (32°31'S
190 117°04'E, 297 m a.s.l.) about 12 km away from our study site (Bureau of Meteorology, 2019,
191 Supplementary S3.1). Atmospheric CO₂ was set to 400 ppm.

192 For assessing impacts of climate change, we obtained the anomalies for future conditions (2080 –
193 2099) compared to past conditions (1986 – 2005) separately for each season based on the four climate
194 projection Representative Concentration Pathways (RCPs) for SW Australia (Hope et al., 2015). We
195 added the median reported trend between past and future climate from different global climate model
196 simulations to the current weather data from Pingelly to generate realistic time series of future
197 weather data. Atmospheric CO₂ was set according to IPCC (2014).

198 For each model repetition, we randomly selected yearly weather data from the current or future
199 weather data set, given the climate scenario, to get 50 years of weather time-series input data.

200 As we found qualitatively similar patterns on ecosystem functioning across the different RCPs (Fig.
201 S4.1), we focused, for better clarity, on the most extreme climate projection RCP 8.5 with an increase
202 in mean annual air temperature by 3.4 °C and a decrease in mean annual precipitation by 16 % (Table
203 S3.1, Fig. S3.2).

204 2.3.3 Evaluation of simulation outcomes

205 To assess the provision of, and trade-offs and synergies among, ecosystem functions, we determined
206 the supply of six functions chosen to cover three major ecosystem services, namely *water supply*,
207 *nutrient supply*, and *carbon sequestration* (Table 1). *Water supply* involves two functions: groundwater

208 recharge – approximated by deep drainage of water below 2 meters soil depth – and ecosystem water
209 use efficiency – the net primary productivity of the ecosystem per unit precipitation. *Nutrient supply*
210 is represented by ecosystem nitrogen use efficiency – estimated by the net primary productivity of the
211 ecosystem per soil available nitrogen – and by litter quality – approximated by the nitrogen to carbon
212 ratio (N:C) of the plant’s residue in the ecosystem originating from plant senescence and mortality.
213 *Carbon sequestration* covers both plant and soil carbon increments.

214 Across these six functions we estimated the multifunctionality as suggested by van der Plas et al.
215 (2016). Accordingly, all ecosystem functions were standardized between 0 and 1 based on the
216 minimum and maximum value per function in a given climate scenario as well as across climate
217 scenarios. Multifunctionality was then defined as the number of functions above a threshold for each
218 species richness and climate change scenario. We chose a threshold level of 50 % which has been
219 shown to be comparable across different countries (van der Plas et al., 2016).

220 We evaluated plant trait distribution through calculating community weighted mean (CWM) for
221 selected traits (Table 2). These traits are measurable in the field and therefore applicable for ecosystem
222 restoration.

223 We evaluated model outcomes between 40 and 50 years given attainment of dynamic equilibrium in
224 total plant species cover after 40 years (Fig. S3.3). All relationships were analysed by a Spearman’s rank
225 correlation.

226 3 RESULTS

227 3.1 Planted species richness effects on ecosystem functioning

228 With higher planted and realised richness, we found that our approximation of ecosystem
229 multifunctionality increased under current climatic conditions but decreased under future conditions
230 (Fig. 2A, left; see also Fig. S4.2). However, when considering current and future knowledge for the
231 standardisation of ecosystem functions, current and future multifunctionality decreased with greater
232 richness (Fig. 2A, right).

233 Some single ecosystem functions increased but others decreased with planted species richness under
234 current conditions (Fig. 2B). Climate change strengthened this pattern and increased variability for

235 most of the functions, except for groundwater recharge and litter quality. For communities with up to
236 three or four planted species, groundwater recharge decreased, whereas the water use efficiency of
237 the ecosystem increased. If more than three or four species were planted, both functions remained
238 stable. Nitrogen use was most efficient for monocultures. In contrast, litter quality increased with
239 higher planted richness under current conditions reaching maximum quality for the most speciose
240 community, while under future conditions litter quality decreased with higher planted richness. Soil
241 carbon, and to a lesser extent plant carbon, increments, were enhanced with higher planted richness,
242 reaching their maximum at an intermediate richness, and remaining stable for higher values. Except
243 for plant carbon increment, all ecosystem functions showed a decreasing variability with increasing
244 planted richness (Figs 2B and S4.3).

245 3.2 Trade-offs and synergies among ecosystem functions

246 With the eight plant species considered in this study, ecosystem multifunctionality could not fully be
247 achieved, in current or future conditions (MF much smaller than 6, Fig. 2A), since there are negative
248 correlations (trade-offs) among functions (Fig. 3). Multifunctionality benefited from a strong positive
249 correlation (synergy) between soil carbon increment and water use (Figs 2B and 3). However, stronger
250 trade-offs between ecosystem nitrogen use and litter quality as well as between groundwater recharge
251 and ecosystem water use or soil carbon increment mostly constrained the maximisation of the
252 multifunctionality.

253 Most relationships between nitrogen use efficiency and other functions reversed under future
254 conditions: in contrast to current conditions, an increase in nitrogen use efficiency was now
255 accompanied by a decline in groundwater recharge as well as a strong increase in water use and soil
256 carbon increment in the ecosystem. In addition, ecosystem litter quality and groundwater recharge
257 could be increased at the same time under future conditions, which was not possible under current
258 conditions. Some trade-offs and synergies observed under current conditions did not reverse but
259 rather strengthened under the future climate scenario: trade-offs between ecosystem litter quality
260 and ecosystem water usage, or soil carbon increment, became more apparent, whereas ecosystem
261 nitrogen use efficiency and plant carbon increment were more effectively maximised at the same time.

262 3.3 Plant traits in the community and ecosystem functioning

263 Community weighted mean plant traits could be linked to single ecosystem functions (Fig. 4A).

264 Particular trait combinations rather than single traits affected individual functions. Functions within
265 the ecosystem services of water and nutrient supply showed contrasting correlations to plant traits in
266 the community, explaining their strong trade-offs. For example, under current conditions groundwater
267 recharge (GWR) was enhanced by communities with a low specific leaf area (SLA), higher investment
268 into leaves than into roots (LM/RM), smaller crowns (maxCA), lower wood density (WD), and a higher
269 wilting point (WP). In contrast, to achieve a maximal ecosystem water use efficiency (EWU), wood
270 density and maximum crown area should be larger coupled with a deeper rooting system (low value
271 of rootL1). Almost the same features that maximised ecosystem water use efficiency also increased
272 plant carbon increment (PCI) and soil carbon increment (SCI) in the ecosystem, supporting the
273 synergies among the three functions.

274 Under future climatic conditions, traits gained or lost their importance especially for soil carbon
275 increment and functions related to water supply. Other functions, i.e. nitrogen use efficiency, traits
276 associated with ecosystem litter quality and plant carbon increment showed no or limited change in
277 importance. For example, under future conditions, wilting point, carbon to nitrogen ratio in leaves,
278 and leaf to root mass ratio gained importance for restoring water use efficiency. The same traits
279 remained important for restoring nitrogen use efficiency, which might explain the shift from a trade-
280 off to a synergy between these two functions. However, most trait-trait correlations remained the
281 same except for correlations involving wood density and wilting point (Fig. 4B) suggesting that changes
282 in the relationships among functions was not driven by underlying changes in trait-trait correlations.
283 Still, we found that trait compositions shifted with climate change in particular for more speciose
284 communities (Figs S4.4 and S4.5), i.e. shifts to plants with deeper roots, higher maximal crown area
285 and with lighter and far-dispersed seeds. These changes led to a stronger decrease in groundwater
286 recharge and ecosystem litter quality (Figs 2B and 4A), which explains the decreasing multifunctionality
287 with increasing planted richness under climate change (Fig. 2A).

288 4 DISCUSSION

289 4.1 Trade-offs prevent maximised multifunctionality

290 We found that trade-offs prevented the achievement of restoration goals with simultaneous
291 maximisation of multiple functions and services. Our integrated empirical-modelling approach allowed
292 us to reveal the mechanisms. Trade-offs emerged for two reasons: the same trait or group of traits can
293 have positive effects on one function, but negative effects on a second function (e.g. de Bello et al.,
294 2010; Teixeira et al., 2020), and the correlation of plant traits can mean that some traits reliably coexist,
295 while some never do (e.g. de la Riva et al., 2016).

296 Even though we could not achieve full multifunctionality in our study, i.e. all functions at their
297 maximum, we found that in a restoration setting, bundles of functions with synergies among them
298 could be maximised instead. For instance, if managers want to improve ecosystem water use efficiency
299 and carbon sequestration (but not nitrogen supply), this can be achieved by planting communities with
300 deeper roots, greater crown area and wood density as well as small seeds with larger dispersal
301 distances. However, the two functions defining the service 'water supply' in our study, i.e. ecosystem
302 water use efficiency and groundwater recharge, could not be optimized at the same time. Thus, the
303 choice of the ecosystem services to be restored might be very crucial. Since only bundles of services
304 can be optimized at the same time, different bundles could be integrated across the landscape to
305 achieve landscape multifunctionality (e.g. Lovell & Johnston, 2009).

306 4.2 Trade-offs among functions shift with climate change

307 We found that trade-offs and synergies among ecosystem functions observed under current conditions
308 shifted under future conditions, posing a clear challenge for long-term restoration outcomes. These
309 shifts in the relationships among functions can be explained either by a direct change of ecosystem
310 functioning differently affected by changing environmental conditions or indirectly through uneven
311 shifts in underlying community plant traits and thus changes in the correlations among CWM traits
312 (e.g. Zirbel et al., 2017). In this context, we should note that the model did not incorporate trait
313 plasticity, which might attenuate or enhance shifts in relationships. In our study, simulated climate
314 change altered species and thus trait compositions as reviewed also by Maestre et al. (2012a) for

315 drylands as well as single trait-trait correlations as also shown by Ahrens et al. (2020). However, most
316 correlations among the traits within the community remained as observed under current conditions.
317 Therefore, shifts in the relationships among functions were mostly due to a direct climate change
318 impact, such as the simulated decrease in groundwater recharge via less available water for infiltration,
319 and higher evapotranspiration due to warmer temperatures (cp. Reinecke et al., 2020) and a
320 simultaneous increase in ecosystem nitrogen use efficiency via a carbon fertilisation effect (cp. Leakey
321 et al., 2009), leading to the observed trade-off among the two functions under future climate.

322 4.3 Multifunctionality might not always be the right choice

323 If restoration aims to only increase but not maximise ecosystem multifunctionality, we found that
324 promoting plant diversity achieved this goal, at least for our measure of multifunctionality and under
325 current climatic condition. This is in line with previous findings and different measures of
326 multifunctionality (Gross et al., 2017; Maestre et al., 2012b). However, a comparison of our chosen
327 measure of multifunctionality with two other measures showed that our findings are not always
328 apparent (Fig. S4.6, see also review by Maestre et al., 2012b and Manning et al., 2018). In addition, we
329 found that the environmental context can significantly affect multifunctionality outcomes. For
330 instance, in our study, minimum and maximum functioning, needed for the standardisation of each
331 function, differed within or across climate scenarios and thus resulted into different patterns
332 depending on the scope we looked at.

333 Furthermore, even though current multifunctionality in our study was improved by greater richness,
334 single functions such as ecosystem nitrogen use efficiency were not. This specific finding contrasts with
335 an empirical study that has shown complementary effects of diverse woody plant communities
336 (mixtures of up to 16 evergreen and deciduous plant species) on nitrogen use (Schwarz et al., 2014).
337 Here, we focused on eight evergreen woody species with similar C:N ratios (Table S2.1), thus
338 complementary nitrogen use was likely not prevalent.

339 Greater planted richness decreased variability in ecosystem functioning suggesting a more consistent
340 supply across the species combinations planted. This could be due to functional redundancy acting as

341 stabilizing effect for a resilient supply of ecosystem functions (Mori et al., 2013). Under future
342 conditions, however, higher plant diversity did not show greater resilience to environmental changes.
343 Instead, we observed that with climate change speciose communities experienced greater species
344 losses, potentially through higher interspecific competition (Ruiz-Benito et al., 2013), which in turn
345 significantly lowered functional redundancy and thus the potential higher resilience against
346 environmental changes. Also, even though multifunctionality decreased with higher planted richness
347 under future conditions, only single functions, i.e. ecosystem litter quality, were largely affected and
348 contributed to this decline, whereas most of the other functions increased with richness. Thus, the
349 choice of metrics for restoration success should be considered if the goal is to improve a set of equally
350 desired ecosystem functions and services at the same time.

351 **4.4 Broader applicability of this study for restoration world-wide**

352 We simulated the long-term effect of plant choice on multifunctionality and six separate ecosystem
353 functions, grouped to the ecosystem services water supply, nutrient supply, and carbon sequestration,
354 in a Mediterranean site in SW Australia. We found that the ultimate aim to improve restoration
355 outcomes with respect to maximizing multiple ecosystem functions and services at the same time
356 under current and future climatic conditions was limited by trade-offs among ecosystem functions
357 which shifted with climate change.

358 Even though we focused on a specific Mediterranean site, we believe that our general interpretations
359 pertain to terrestrial systems globally since underlying mechanisms driving trade-offs among functions
360 and shifts in the trade-offs have been fundamentally shown across different ecosystems: i.e.
361 ecosystem functions are affected by underlying plant traits (e.g. de Bello et al., 2010; Funk et al., 2017)
362 and environmental change either directly or indirectly, via changing plant trait compositions, affects
363 ecosystem functions (e.g. De Deyn et al., 2008; Garnier et al., 2007). Thus, restoration ecologists across
364 the world will face a clear challenge to achieve their targets under current conditions and in the long-
365 term.

366 However, ecosystem functioning as well as trade-offs among functions and how these will shift with
367 climate change is likely to be context-dependent (e.g. dependent on local species pool, soil texture,
368 weather, and regional projected climate change) and thus different across ecosystems (e.g. Ding et al.,
369 2020; Ratcliffe et al., 2017). In addition, various ecosystems are degraded differently, and thus
370 restoration managers might want to improve different desired functions.

371 With this study we applied the steps suggested by Fiedler et al. (2018) in order to improve ecological
372 restoration and showed that models like ModEST can serve as a planning tool to better understand
373 the suite of desired ecosystem functions and services that can be restored in any particular place based
374 on the plant species available and the local environmental conditions. If further developed and
375 combined with a graphical user interface and special training, this can help managers to set realistic
376 restoration goals and select from a list of potential species and traits to achieve these goals.

377 5 AUTHORS' CONTRIBUTION

378 SF, MP and BT conceived the project. SF implemented the hydrological and plant module,
379 parameterized ModEST, conducted the experiments, analyzed the simulation outcomes, prepared all
380 figures and tables, and wrote the first draft of the manuscript in close collaboration with BT and MP.
381 JM implemented the nutrient module. KH, MP and RS participated in the conception and
382 implementation of the Ridgefield experiment. All authors interpreted data, contributed critically to
383 drafts, and gave final approval for publication.

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394 Rebecca Campbell and Tim Morald for their support regarding the Ridgefield experiment.

395 7 DATA AVAILABILITY STATEMENT

396 The source code of ModEST available from GitHub <https://doi.org/10.5281/ZENODO.4034790> (Fiedler
397 et al., 2020). Simulated data available from the Dryad Digital Repository upon acceptance of this
398 manuscript.

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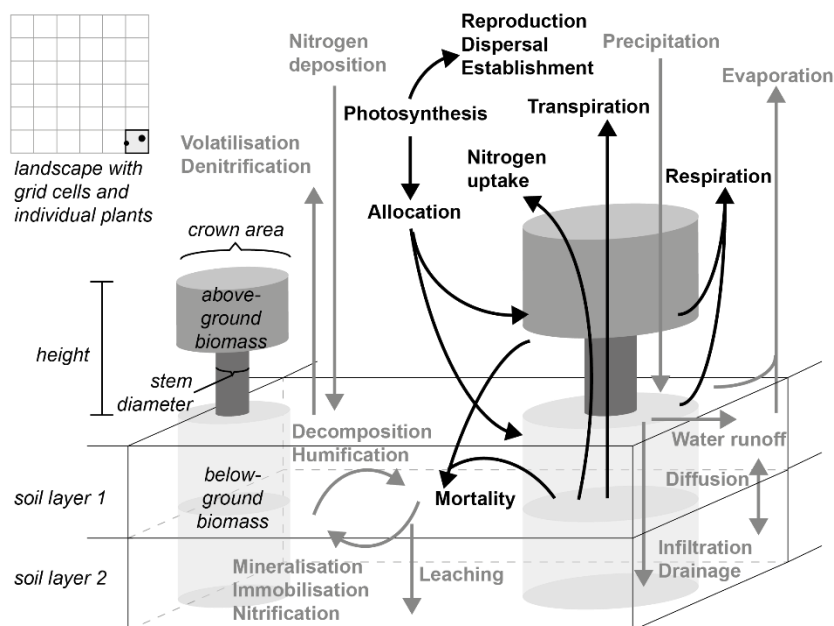
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540 9 FIGURES AND TABLES



541

542 **Figure 1: Structure (*italic*) and processes (**bold**) of ModEST.** The modelled landscape is sub-divided
543 into grid cells consisting of two soil layers as well as individual woody plants that are characterized by
544 above- and below-ground features and are continuously distributed over the landscape. Coupled

545 processes are calculated, i.e. hydrological and nutrient processes for each grid cell and soil layer (bold
 546 grey) as well as plant processes for each individual plant (bold black) depending on the resources of its
 547 covering grid cell.

548 **Table 1: Ecosystem functions.**

Related ecosystem service	Ecosystem function	Model output	Unit
Water supply	Groundwater recharge (GWR)	Annual deep (> 2 meters in soil depth) soil water drainage per m ²	mm · year ⁻¹
	Ecosystem water use efficiency (EWU)	Annual net primary productivity (NPP) per m ² / Annual precipitation per m ²	g · L ⁻¹ · year ⁻¹
Nutrient supply	Ecosystem nitrogen use efficiency (ENU)	Annual NPP per m ² / Annual mean soil avail. nitrogen per m ³	kgNPP · m ⁻² · kgN ⁻¹ · m ⁻³
	Ecosystem litter quality (ELQ)	Annual nitrogen per m ² / Annual carbon per m ²	gN · year ⁻¹ · kgC ⁻¹ · year ⁻¹
Carbon sequestration	Total plant carbon increment (PCI)	Annual plant carbon increment	kg · m ⁻² · year ⁻¹
	Total soil carbon increment (SCI)	Annual soil carbon increment	t · m ⁻² · year ⁻¹

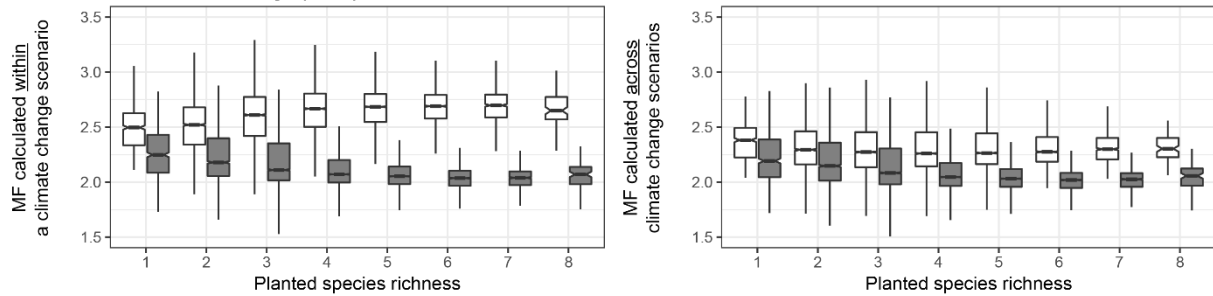
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550 **Table 2: Focal plant traits.**

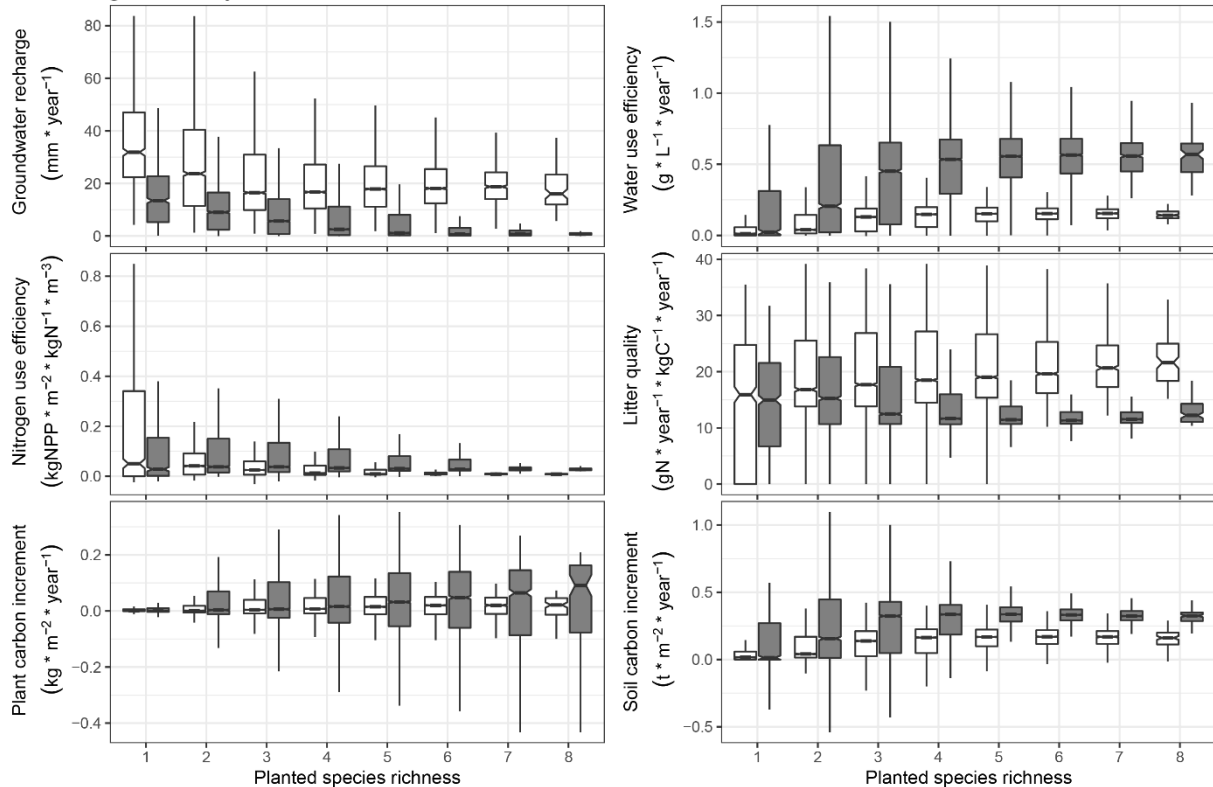
Abbreviation	Description of plant trait	Unit
SLA	Specific leaf area	m ² · kg ⁻¹
rootL1	Fraction of total root mass between 0 and 50 cm of the soil horizon	-
seedMass	Seed mass	mg
WP	Relative water content at wilting point for soil texture loamy sand	-
CNleaf	Carbon to nitrogen ratio in the leaves	-
LM/RM	Allometric constant describing optimal ratio of leaf to root mass	-
meanDisp	Mean dispersal distance of seeds	m
maxCA	Maximum crown area	m ²
WD	Wood density	kgC · m ⁻³

551

A – Multifunctionality (MF)



B – Single Ecosystem Functions



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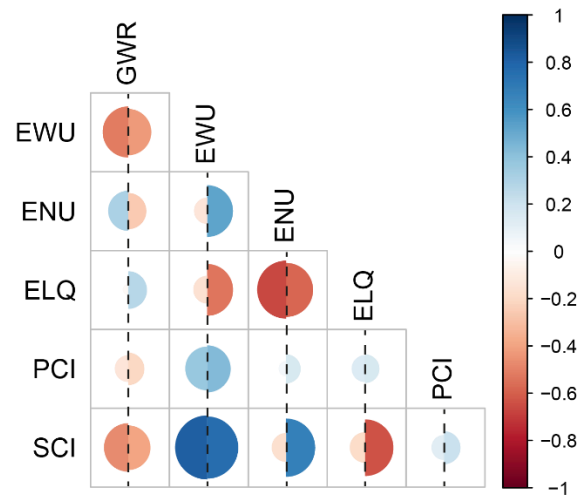
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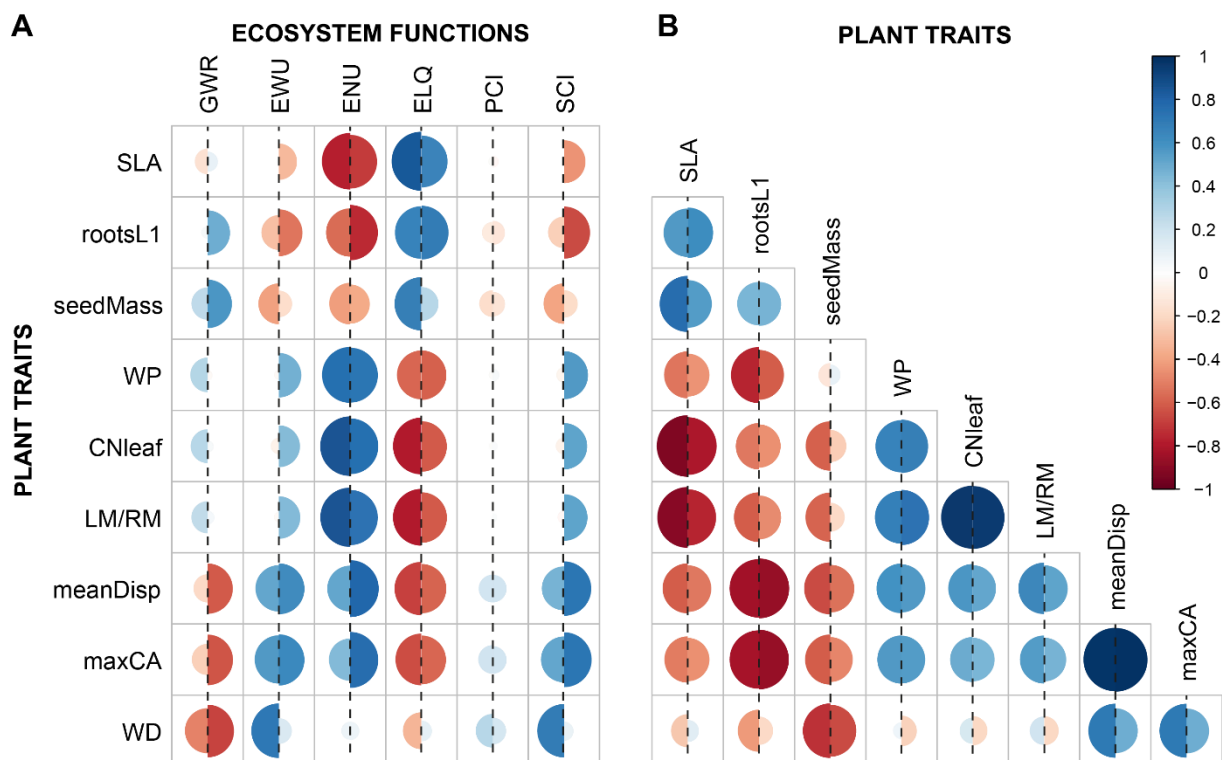
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Figure 2: Multifunctionality (A) and single ecosystem functioning (B) for each planted species richness under current (white boxplots) and future climatic conditions (grey boxplots). Multifunctionality is either calculated within each climate scenario (A, left) or across climate scenarios (A, right). Shown is functioning for the last 10 simulated years and for 10 model repetitions as well as for 255 different plant communities which are unevenly distributed across the different planted species richness scenarios according to maximal possible combinations out of the pool of eight focal plant species. For better comparability among boxplots, single outliers are not shown.



560

561 **Figure 3: Negative (trade-off, red) and positive (synergy, blue) relationships among ecosystem**
 562 **functions under current (left half circle) and future climatic conditions (right half circle).** Shown are
 563 significant Spearman's rank correlations ($\alpha = 0.05$) among ecosystem functions based on the last 10
 564 simulated years and for 10 model repetitions across all 255 simulated plant communities. Meaning of
 565 abbreviations can be found in Table 1.



566

567 **Figure 4: Plant trait – ecosystem function relationships and intrinsic community trait correlations**
 568 **under current (left half circle) and future climatic conditions (right half circle).** Spearman's rank

569 correlations (A) between CWM plant traits and ecosystem functions, and (B) among CWM plant traits.

570 Shown are significant correlations ($\alpha = 0.05$) based on the last 10 simulated years and for 10 model

571 repetitions across all 255 simulated plant communities. Meaning of abbreviations can be found in

572 Table 1 for ecosystem functions and Table 2 for CWM plant traits.

573