Biodiversity–multifunctionality relationships depend on identity and number of measured functions

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Abstract: Biodiversity ensures ecosystem functioning and provisioning of ecosystem services, but it remains unclear how biodiversity–ecosystem multifunctionality relationships depend on the identity and number of functions considered. Here, we demonstrate that ecosystem multifunctionality, based on 82 indicator variables of ecosystem functions in a grassland biodiversity experiment, increases strongly with increasing biodiversity. Analysing subsets of functions showed that the effects of biodiversity on multifunctionality were stronger when more functions were included and that the strength of the biodiversity effects depended on the identity of the functions included. Limits to multifunctionality arose from negative correlations among functions and functions that were not correlated with biodiversity. Our findings underline that the management of ecosystems for the protection of biodiversity cannot be replaced by managing for particular ecosystem functions or services and emphasize the need for specific management to protect biodiversity. More plant species from the experimental pool of 60 species contributed to functioning when more functions were considered. An individual contribution to multifunctionality could be demonstrated for only a fraction of the species.

Biodiversity–multifunctionality relationships depend on identity and number of measured functions

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51 **Biodiversity ensures ecosystem functioning and provisioning of ecosystem services, but it**

52 **remains unclear how biodiversity–ecosystem multifunctionality relationships depend on**

53 **the identity and number of functions considered. Here we demonstrate that ecosystem**

54 **multifunctionality, based on 82 indicator variables of ecosystem functions in a grassland**

55 **biodiversity experiment, increased strongly with increasing biodiversity. Analysing**

56 **subsets of functions showed that effects of biodiversity on multifunctionality were**

57 **stronger when more functions were included and that the strength of the biodiversity**

58 **effects depended on the identity of the functions included. Limits to multifunctionality**

59 **arose from negative correlations among functions and functions which were not**

60 **correlated with biodiversity. Our findings underline that managing of ecosystems for the**

61 **protection of biodiversity cannot be replaced by managing for particular ecosystem**

62 **functions or services and emphasise the need for specific management to protect**

63 **biodiversity. More species from the experimental plant species pool of 60 species**

64 **contributed to functioning when more functions were considered. An individual**

65 **contribution to multifunctionality could be demonstrated for only a fraction of the**

66 **species.**

67

68 Ecosystem services, such as the supply of clean water, soil erosion control, or pollination,

69 depend on ecosystem functions that are controlled by the species living in an ecosystem[1].

70 Provisioning of these services is thought to be threatened by an ongoing loss of species

71 worldwide[2], driven largely by land-use change and overexploitation of natural populations[3].

72 Ecosystem functioning has been shown to decrease with decreasing biodiversity in

73 experiments that manipulate plant species richness[4]. However, when individual functions are

74 considered, species richness-ecosystem function relationships frequently saturate at low levels

75 of species richness, e.g. when three to six species are present in the system[5,6]. Such saturating

76 relationships have been taken as support for the redundancy hypothesis[7-9], which proposes

that high functioning can be achieved with only a few species. However, redundant species

may contribute to maintaining ecosystem functions when other species are lost, or under

changing environmental conditions[10], referred to as the insurance effect[10,11]. Also, a turnover

in the identity of species contributing to a particular function may increase the cumulative

number of species sustaining functioning over multiple years[12]. However, even with such

mechanisms accounted for, a large part of species still seem to be redundant[13]. This limit to

the number of species needed for ecosystem functioning has raised questions if provisioning

of ecosystem services can be a major argument for species conservation[14].

Humans rely on ecosystems for their ability to maintain multiple functions and services

simultaneously, as expressed in the concept of ecosystem multifunctionality[15,16]. The number

of species contributing to ecosystem multifunctionality is in general higher than the number of

species needed for single functions[17-22], and also rare species have been shown to contribute to

multifunctionality[23]. Thus, the importance of biodiversity for multifunctionality is higher than

for individual functions. When multiple years, places, and environmental change scenarios

(so-called contexts) were considered simultaneously by synthesising 12 functions across 17

biodiversity experiments, 84%, yet not all, of the 147 grassland plant species studied,

promoted ecosystem functioning in at least one context[20]. In addition to the question of

whether all species are needed to maintain ecosystem multifunctionality, an equally important

question is if and how the effect of biodiversity on ecosystem multifunctionality depends on

the identity and number of functions considered[24]. While a recent simulation study found no

relationship between the number functions included and the relationship between biodiversity

and ecosystem multifunctionality[24], this question remains untested with empirical data. This

question is important as different ecosystem functions not only differ in how strongly they

depend on biodiversity[25], but biodiversity and ecosystem functions may also be positively or

negatively correlated with each other. If ecosystem functions are positively correlated and

103   depend on biodiversity, then increasing biodiversity can increase many functions

104   simultaneously. In this case, maximising ecosystem multifunctionality will require high

105   biodiversity. Consequently, maximising multifunctionality would be equivalent to

106   maximising biodiversity. However, if functions are negatively correlated, then maximising

107   one function will result in decreasing the other function, and the relationship between

108   ecosystem multifunctionality and biodiversity will depend on the particular functions

109   considered and how they are correlated with biodiversity. The same holds true if functions are

110   uncorrelated, in which case they can be independently maximised. Thus, for the question

111   whether managing for ecosystem multifunctionality is equivalent to managing for a protection

112   of biodiversity, both the relationships among the different functions considered, and the

113   dependence on biodiversity are important.

114

115   Here, we analysed the correlation structure of a suite of ecosystem functions to test the

116   hypothesis that strong effects of biodiversity on ecosystem multifunctionality depend on a

117   large and diverse portfolio of functions to be included in the analysis that reflects the high

118   complexity of ecosystem functioning in nature. We base our analyses on a selection of 82

119   different ecosystem variables identified from a larger collection[25] that were measured along a

120   gradient of 1–60 plant species in a single biodiversity experiment (the Jena Experiment[26],

121   methods). Consistent with previous studies on ecosystem multifunctionality, we approximate

122   ecosystem functions by ecosystem variables[19,20,22,27]. These variables quantify ecosystem

123   functions either directly ("the changes in energy and matter over time and space through

124   biological activity" sensu Reiss, et al. [28]) or indirectly ("key ecosystem properties affected by

125   ecosystem functions" sensu Jax [29]). Restricting analyses of multifunctionality to only directly

126   measured functions would bias the portfolio of included functions considerably, because some

127   types of functions, especially species interactions and belowground functions, are notoriously

128   difficult to measure directly. The best way to include these functions into an analysis of

multifunctionality is quantifying state changes or differences in the size of ecosystem

compartments as indicators for the underlying changes in functions[30]. We chose a large

number of 82 ecosystem variables to cover a range of different ecosystem functions, including

above- and belowground plant productivity, nutrient and element cycling, antagonistic and

mutualistic multitrophic interactions, and invasion resistance (detailed in Table S1). Variables

include measurements of the abiotic environment, plants, and consumers. Information on

consumers was separated into different functional groups when possible. Otherwise, different

taxonomic groups were separated as these groups indicate not only secondary productivity,

but also mediate different ecosystem functions, e.g. herbivory, predation, parasitism,

decomposition, scavenging, pollination, and seed predation / dispersal. To ensure that each

ecosystem variable was included only once in the analysis, only the measurement in the last

available year was selected, thus excluding repeated measures. Correlated ecosystem

variables were not excluded *a priori,* as investigating how the relationships among functions

affect multifunctionality was an explicit goal of the present study. We also decided against

combining different ecosystem variables that appear to be related to the same ecosystem

function into a single "true" function, because what is considered an indicator of different

functions is arbitrary and depends critically on the research question. For example,

aboveground and belowground biomass production of plants are both indicators of overall

productivity, yet they are also individual indicators with particular impacts on the ecosystem;

aboveground biomass mainly represents carbon fixation, transpiration and potential for light

interception, while belowground biomass indicates potential nutrient and water uptake as well

as respiration. Similar arguments hold for the different groups of herbivores. While all

contribute to overall herbivory, they interact, depending on their feeding guild, with different

parts of the food web. In the following, we will refer to 'ecosystem variables that indicate

ecosystem functions' as 'functions' for simplicity as is commonly done in studies of

multifunctionality[19,20,22,27].

155

156 **Results**

157

158 To quantify the change in overall ecosystem functioning along the experimental gradient of

159 plant species richness, we calculated a multifunctionality index based on all 82 functions.

160 Different indices to quantify multifunctionality have been proposed[18]. Multifunctionality is a

161 multifaceted ecosystem property, much like biodiversity[31], and all of the proposed indices

162 quantify slightly different facets of multifunctionality[18]. We extended the averaging approach

163 proposed for individual functions[18,19,32] to a multivariate approach, based on a principal

164 component analysis (PCA) that analyses the correlation structure among the different

165 functions. The main advantage of this new multivariate index of multifunctionality over the

166 previous approaches[18] is the fact that it accounts for both positive and negative correlations

167 between ecosystem functions, which may otherwise bias results of multifunctionality

168 analyses[33]. We found that many of the functions analysed here were positively or negatively

169 correlated with each other (Fig. S2–4). The overall level of co-linearity was, however, limited,

170 as indicated by the fact that 24 PCA axes were needed to explain 80% of the total variance in

171 functional space (Fig S2–2). A visualisation of the first two principal components showed that

172 the most diverse 60-species plots form a distinct cluster at the right end of the first PCA-axis

173 (Fig. 1-A). Plant species richness was strongly positively correlated with the first principal

174 component axis ($r=0.80$, $t_{79}=12.0$, $p<0.001$). Consequently, plant species richness was the

175 most important single driver of ecosystem functioning in our experiment, because the first

176 principal component represents the maximum variance that can be summarised on one axis.

177 Individual functions that correlated with the first PCA-axis were also positively correlated

178 with plant species richness, e.g., biomass and height of the plant community, bare ground

179 cover (negatively correlated with plant species richness), microbial biomass, and the

180 abundance of earthworms and other animal groups. The PCA-approach was robust against the

7

181   inclusion of non-normally distributed data on ecosystem functions as demonstrated in a

182   sensitivity analysis using principle coordinates analysis based on Gower-distances (PCoA;

183   Supplementary material S3). Because principal components are uncorrelated, in contrast to

184   the original functions, multifunctionality of a plant community can be related to the scores of

185   the principal components, without adding correlated information. We quantified total

186   functioning of a particular plant community by adding the scores of all PCA-axes, weighted

187   by the eigenvector of the respective axis (see methods). An increase in this multifunctionality

188   index indicates increased functioning because the index was positively correlated with

189   variables characterizing primary (e.g. plant biomass, height, cover, and LAI) and secondary

190   productivity (e.g. number of many belowground fauna groups) as well as soil organic carbon

191   and biomass of microorganisms in the soil (Table S4). The multifunctionality index was

192   negatively correlated with disservices, such as the cover of bare ground and soil bulk density

193   (Table S4).

194

195   The multifunctionality index increased significantly with increasing plant species richness

196   ($F_{1,76}$=8.13, p=0.006; Fig. 1-B). Multifunctionality calculated using previously published,

197   complementary approaches, i.e. the averaging, the threshold and the multiple thresholds

198   approaches[18] confirmed this strong increase in multifunctionality with increasing plant species

199   richness (Fig. S5 A–D). Further, the effect of plant species richness on multifunctionality was

200   robust when restricting the analysis to the 54 ecosystem functions measured in the same year

201   (2004, Table S1; Supplementary material S6). Thus, biodiversity sustains multifunctionality

202   also when the previously demonstrated effects of temporal turnover[12,20] were excluded.

203

204   Next, we analysed how the number of functions used to calculate multifunctionality affected

205   the relationship between biodiversity and multifunctionality, by analysing random subsets of

206   two to 82 ecosystem functions. We observed consistent positive effects of biodiversity on

207   multifunctionality that, in contrast to simulated results[24], became stronger when a larger

208   number of functions was considered (Fig. 2). Increasingly strong effects of biodiversity on

209   ecosystem multifunctionality with higher numbers of considered functions indicate that in our

210   experiment there are properties of diverse plant communities that were not included in the

211   simulation study[24]. Thus, expected effects of biodiversity on multifunctionality are largest

212   when a high number of ecosystem functions are of interest. However, the strength of the

213   relationship between biodiversity and ecosystem multifunctionality showed large variation

214   around the mean slope for any given number of functions and critically depended on the

215   identity of the ecosystem functions used for calculating multifunctionality. These identity

216   effects imply that studies of multifunctionality based on different functions cannot be directly

217   compared. Identity effects occurred because of trade-offs among ecosystem functions (Fig.

218   S2-1, Table S2-2, Fig. S4-1A) and of functions that were only weakly or even negatively

219   related to multifunctionality (Fig. S4-1B, Table S4). Likely including such functions or

220   functions that are well sustained by low biodiversity in the random draw, explains the slight

221   decrease in average multifunctionality when very high numbers of ecosystem functions were

222   considered (Fig. 2). For particular subsets of functions, biodiversity had only minor effects on

223   ecosystem multifunctionality (Fig. 2). This can explain why studies may also find weak

224   effects of biodiversity on ecosystem multifunctionality[18].

225

226   Increasingly strong effects of biodiversity on multifunctionality when more functions are

227   considered were also confirmed when we calculated the proportion of plant species that

228   contributed to functioning using the 'turnover' approach[17]. For each ecosystem function,

229   informative species effects were extracted from a full model including the presence-absence

230   data of all 60 plant species as explanatory variables, using a stepwise AIC-approach. For each

231   number of ecosystem functions between 1 to 82, up to 2000 random subsets of functions were

232   drawn, and the proportion of species (out of the total of 60) that had informative, positive

233   effects on at least one of the functions in the subset was calculated. In the same way, negative

234   effects were analysed in a separate analysis. The proportion of species that contributed

235   positively to functioning increased strongly with the number of functions considered (Fig. 3).

236   Using a critical ΔAIC value of 2, as proposed by Hector and Bagchi [17] in the original

237   description of the turnover approach, the proportion of species contributing to functioning was

238   not statistically different from one, i.e., all species contributed to functioning when ten or

239   more functions were analysed (see also Fig. S7-1A). These results exceed the proportions of

240   species that were shown to contribute to functioning in earlier studies[17,20] also when only

241   ecosystem functions measured in the same year (2004, Table S1) were used in a sensitivity

242   analysis (Fig. S6-1A). In addition to positive effects of the presence of species on functioning,

243   every species also decreased at least one of the ecosystem functions investigated (Fig. S7-1B).

244   Yet, functioning increased with higher diversity because effect-sizes of positive contributions

245   were higher than of negative contributions (Fig. S7-2). We calculated a null model based on

246   data where the presence of species in plots had been permutated over the plots to disrupt the

247   association between the presence of species and ecosystem functioning (see methods).

248   Comparison to the null model showed that, when using a critical ΔAIC value of 2, a high

249   number of false positive species effects inflate the proportion of species with informative

250   effects. This inflation of the number of informative effects was confirmed in a simulation

251   study (Supplementary material S8). To compensate for the statistical effect of fitting a large

252   number of models estimating many parameters, we recalculated the analysis with a series of

253   increasingly strict critical ΔAIC values that needed to be surpassed for the effect of the

254   presence of a species to be considered informative (see methods). Using increasingly stricter

255   ΔAIC values, the proportion of species with informative effects continuously declined; as was

256   to be expected (Fig. 3A-F; supplementary material S8). The proportion of species showing

257   effects for the permutated data declined faster than for the measured data so that the

258   asymptote for the proportion of species with effects was about 20 percent points higher for the

259 measured data than for the permutated data (Fig. 3D-F). Thus, about 20% of the plants in the

260 species pool showed effects on ecosystem functioning that could be unambiguously separated

261 from potential statistical artefacts and are thus informative beyond doubt. It is important to

262 notice that this number is an extremely conservative estimate because a) the turnover

263 approach does not account for interactions between species (complementarity), and b) with

264 such strict criteria the chances of rejecting true effects increases. The proportion stated here

265 cannot be compared to previously published estimates of the proportion of species pool

266 affecting functioning[17,20] as these studies used much less strict criteria for the detection of

267 effects. Given that in the design of the experiment every species occurs only in a minor

268 fraction of the plots and given the proportion of species with effects increased with the

269 number of functions considered and that the number of functions in real-world ecosystems

270 likely exceeds even the 82 ecosystem functions considered in this study, we conclude that the

271 proportion of species individually contributing to ecosystem functioning is likely much higher

272 than can be shown here.

273

274 **Discussion**

275 Our findings have two major implications for the management of ecosystems. First, our

276 results demonstrate that not all ecosystem services can be maximised simultaneously when

277 these services rely on functions that show trade-offs[34,35]. Thus, management to maximise a

278 particular ecosystem service will probably decrease provisioning of other ecosystem

279 services[36] and may not maximise but may even decrease multifunctionality. A similar result

280 was found with respect to the effect of land use on the provisioning of 'ecosystem service

281 bundles', where the magnitude and even the direction of effects depended on the composition

282 and weighting of ecosystem services in a bundle[37]. However, our analysis also indicates a)

283 that adding species (if it is still possible to add a species) should be beneficial as adding a

284 species to an ecosystem would likely increase some ecosystem function (more than it would

285   decrease others), and b) that it is possible to maximise particular functions, such as biomass

286   production, and simultaneously favour other functions such as increased water- or nutrient-

287   use efficiency, resulting in reduced environmental impacts combined with potential economic

288   benefits. Second, our results increase misgivings about the assumption that managing

289   ecosystems to maximise ecosystem service provisioning guarantees the preservation of

290   biodiversity, as would be expected if high biodiversity always underlies high ecosystem

291   service provisioning[38]. While biodiversity was the strongest driver of ecosystem functioning

292   in our study underlining its importance, our results show that the particular combination of

293   ecosystem functions considered determines whether and to which extent multifunctionality is

294   related to biodiversity (Fig. 2). Consequently, managing an ecosystem to maximise

295   biodiversity will not necessarily maximise a particular subset of functions for which managers

296   are aiming, and management for services will not necessarily protect biodiversity. We thus

297   emphasise that ecosystem service provisioning cannot replace high biodiversity as the aim of

298   management interventions. The need for specific management to protect biodiversity is

299   further underlined by the result that only a minor fraction of the species pool showed a

300   significant functional importance of the individual species.

301

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396   **Figure 1:** Effects of biodiversity on multifunctionality. (A) The graph shows the position of

397   each plot (coloured dots) in a multifunctional space spanned by the first two axes derived

398   from a principal component analysis (PCA) based on 82 different ecosystem functions

399   measured in the Jena Experiment. The red dots (60-species mixtures) form a distinct cluster at

400   the right-hand side of the graph far from the centre of the plot. Each of the functions is shown

401   as a grey arrow (vector) pointing in which direction of the ordination space it increases in

402   value. The angles between function vectors represent the degree of correlation between them.

403   As angles between function vectors in the PC1/PC2 ordination plane can be distorted by

404   relationships with higher PCA axes, precise correlation coefficients among all functions are

405   given in Fig. S2-4 (supplementary material). Graphs with labelled arrows for the functions

406   can be found in Fig. S2-1. (B) Effect of plant species richness on ecosystem

407   multifunctionality as found in the Jena Experiment. The multifunctionality index was

408   calculated by summing up the PCA-axis scores for all experimental plots weighted by the

409   eigenvalue of the respective PCA-axis. The solid black line represents the effect of a linear

410   model fit, the dashed lines the 95% confidence intervals around the fit.

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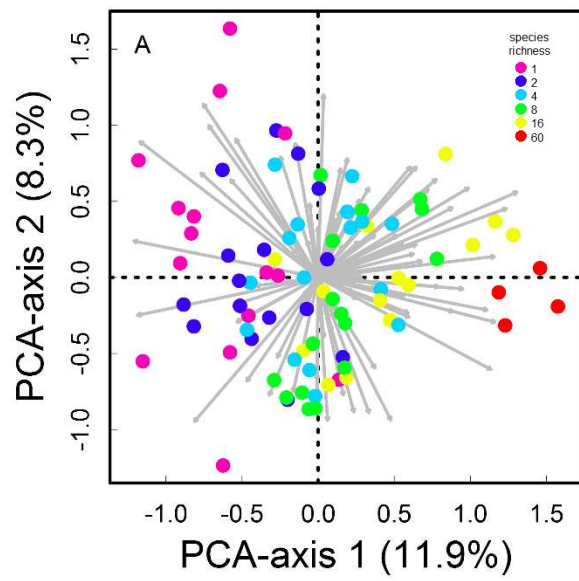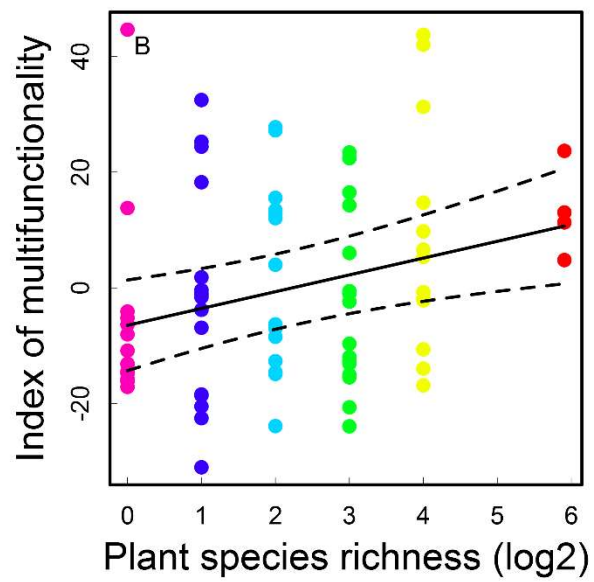
414   **Figure 2:** Effects of number and identity of ecosystem functions on the relationship between

415   plant species richness and multifunctionality. Each open circle shows the slope between the

416   multifunctionality index and plant species richness, for a particular random subset of the 82

417   ecosystem functions included in the analysis. Red filled circles show the mean slope for a

418   particular number of functions, resulting from up to 500 random draws of this particular

419   number of ecosystem functions.
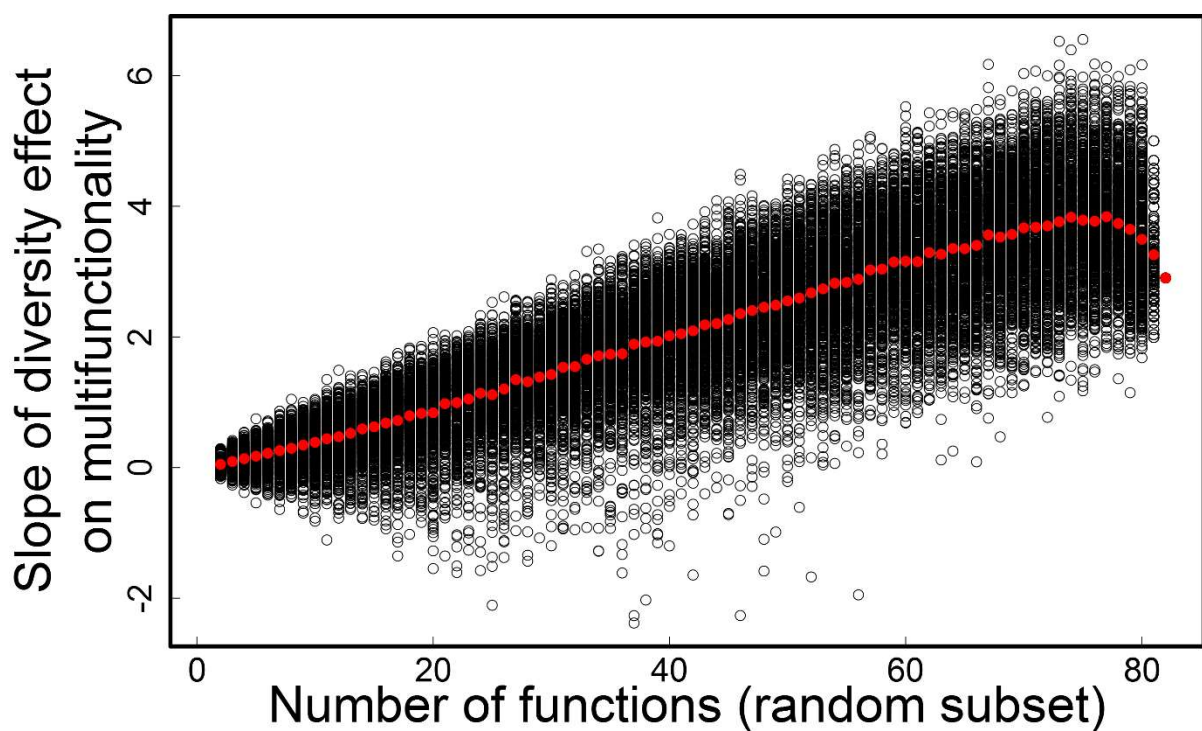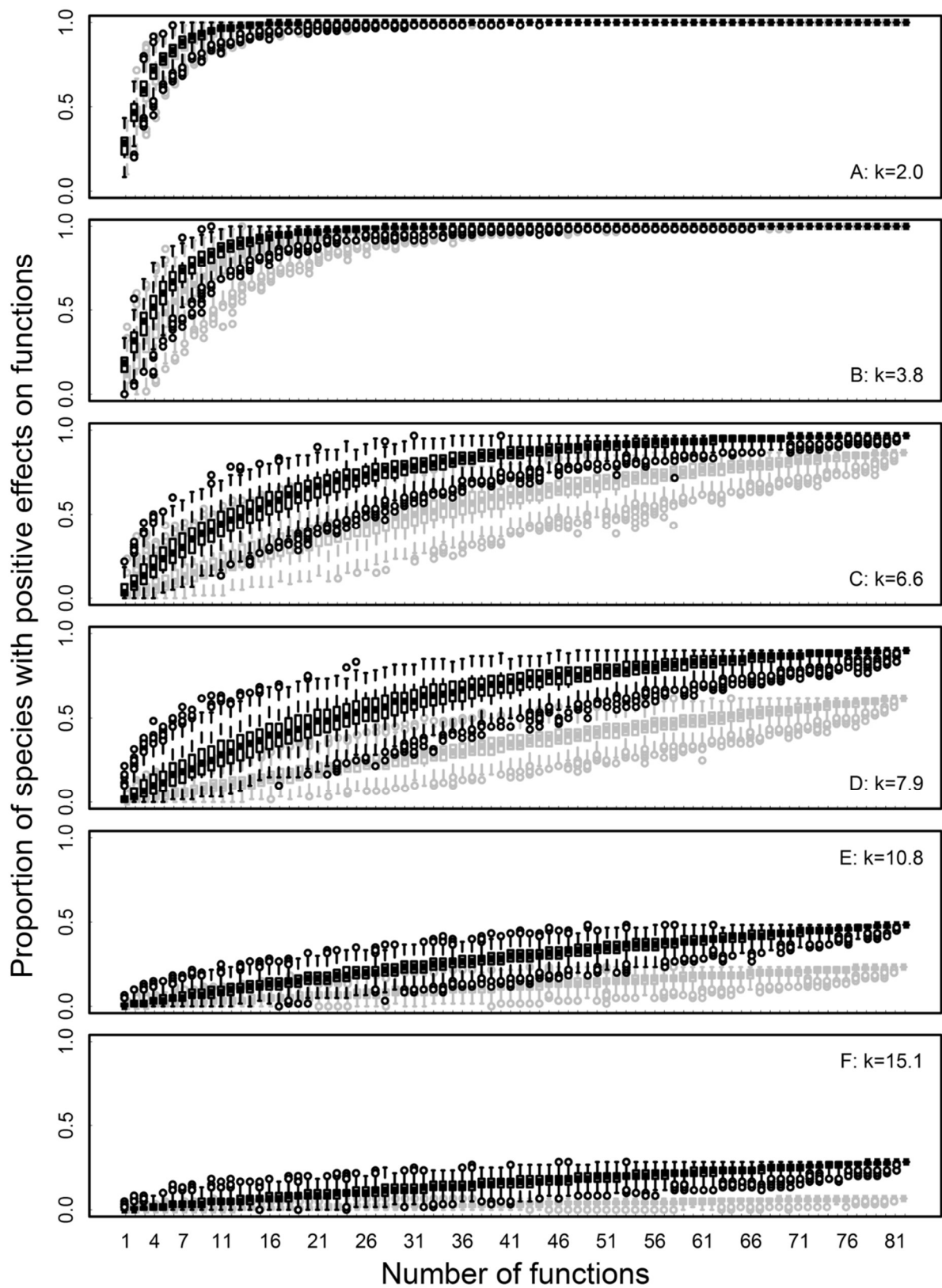
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423　**Figure 3:** Proportion of the plant species pool that contributes positively to functioning when

424　an increasing number of ecosystem functions is analysed simultaneously. The plant species

425　pool contains 60 species, and the total number of functions considered was 82. Shown are the

426　average proportion together with quartiles, the 1.5 times interquartile range as whiskers, and

427　outliers beyond this range as dots; all calculated for up to 2000 random draws of each number

428　of functions from the total of 82. Grey boxes show results of a null-model for which the

429　measurements of each function have been permutated over the plots of the experiment to

430　disrupt associations between the presence of species and the level of functioning in a plot (see

431　details in the methods). Each panel gives the results of an analysis with an increasingly strict

432　criterion for the effect of a species to be considered informative. The k-values stated are the

433　minimum ΔAIC-value needed for the comparison of a model containing the presence of a

434　species as explanatory variable compared to a simpler model without it to be considered

435　informative.