

1 **Title:** The function-dominance correlation drives the direction and strength of biodiversity-  
2 ecosystem functioning relationships

3

4 **Running title:** Function-dominance correlation drives BEF

5

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69 **ABSTRACT**

70

71           Community composition is a primary determinant of how biodiversity change influences  
72 ecosystem functioning and, therefore, the relationship between biodiversity and ecosystem  
73 functioning (BEF). We examine the consequences of community composition across six  
74 structurally realistic plant community models. We find that a positive correlation between  
75 species' functioning in monoculture vs. their dominance in mixture with regard to a specific  
76 function (the "function-dominance correlation") generates a positive relationship between  
77 realised diversity and ecosystem functioning across species richness treatments. However,  
78 because realised diversity declines when few species dominate, a positive function-dominance  
79 correlation generates a negative relationship between realised diversity and ecosystem  
80 functioning within species richness treatments. Removing seed inflow strengthens the link  
81 between the function-dominance correlation and BEF relationships across species richness  
82 treatments but weakens it within them. These results suggest that changes in species' identities in  
83 a local species pool may more strongly affect ecosystem functioning than changes in species  
84 richness.

## 85 INTRODUCTION

86

87 Anthropogenic environmental changes have led to drastic global biodiversity loss (*MEA*  
88 2005; Tittensor *et al.* 2014; Newbold *et al.* 2015; IPBES 2019). The rate of loss will likely  
89 accelerate in the coming decades (Pereira *et al.* 2010; Pimm *et al.* 2014; IPBES 2019).  
90 Biodiversity experiments demonstrate that the loss of randomly selected species from controlled  
91 communities generally decreases local ecosystem functioning (Tilman *et al.* 2014). However, in  
92 natural systems, effects of biodiversity change on ecosystem functioning and services are context  
93 dependent. Even within a single ecosystem type such as grasslands, there is significant  
94 divergence in the direction (negative vs. positive, Meyer *et al.* 2018), strength (Guerrero-  
95 Ramírez *et al.* 2017), and drivers (Barry *et al.* 2019a) of biodiversity-ecosystem functioning  
96 (BEF) relationships. This variation is even greater across ecosystem types (Duffy *et al.* 2017; van  
97 der Plas 2019). Understanding this variability is therefore of critical importance to anticipating  
98 the impacts of biodiversity change.

99 One likely cause of this variability is differences in local-scale processes such as species  
100 interactions, which influence community assembly and composition (Wright 2002; Holt 2013;  
101 Barry *et al.* 2019a). Depending on the nature and strength of local and regional community  
102 assembly mechanisms, variation in these processes may result in differences among BEF  
103 relationships across ecosystems and scales (Leibold *et al.* 2017). In particular, when comparing  
104 communities that differ greatly in *species richness*, those with high richness are more likely to  
105 include species that produce high levels of ecosystem functioning (e.g., biomass) through  
106 “sampling effects” (Huston 1997; Hooper *et al.* 2005), leading to positive BEF relationships.  
107 Conversely, when comparing communities with similar species richness, if a few dominant  
108 species contribute disproportionately to functioning and are able to suppress their competitors,  
109 then communities that include these dominant species will have low *realised diversity* but high  
110 functioning, leading to negative BEF relationships (Leibold *et al.* 2017, Fig. 1A). We refer to this  
111 characteristic pattern of contrasting BEF relationships across communities as a “counter-  
112 gradient” (Fig. 1). This type of counter-gradient is often associated with Simpson’s paradox,  
113 which arises when observed relationships vary across different subsets of data (Simpson 1951).

114 In addition to local processes related to species identity and dominance, regional  
115 processes such as seed dispersal can affect community composition by maintaining populations

116 that would otherwise go extinct (Thompson & Gonzalez 2016, Leibold & Chase 2018). These  
117 regional scale processes influence ecosystem functioning independently of local scale processes  
118 (Leibold & Chase 2018, Thompson et al. 2020). For example, if dispersal maintains populations  
119 of species that are poorly locally adapted, then dispersal can weaken, or lead to negative, BEF  
120 relationships (Thompson et al. 2020). Alternatively, if species that contribute strongly to  
121 ecosystem functioning are maintained by dispersal, then dispersal can lead to strong positive  
122 BEF relationships (Gonzalez et al. 2009, Shanafelt et al. 2015, Thompson & Gonzalez 2016,  
123 Thompson et al. 2020).

124 Here, we consider six independently derived and validated plant community models to  
125 explore the drivers of variation in BEF relationships across local and regional scales. We  
126 subjected these six models to a unified set of simulation experiments: first, testing local effects  
127 by varying initial diversity and composition, and second, testing regional effects by simulating  
128 communities that included, or were isolated from, seed dispersal. Although plant community  
129 models have been used in the past to explore BEF relationships (Morin *et al.* 2011, Holzwarth *et*  
130 *al.* 2015, Bohn & Huth 2017, Maréchaux & Chave 2017), here, we consider a much wider  
131 variety of models, systems (grasslands, forests, drylands) and community assembly processes.  
132 This diversity of modelling approaches leads to a much wider range of resulting BEF  
133 relationships, thereby better mirroring the context dependence observed in natural systems.

134 We use this modelling experiment to test two hypotheses. First, we hypothesise that  
135 context dependence in BEF relationships observed across simulations can be explained primarily  
136 by correlations between species' ability to dominate in mixture ('dominance') vs. their baseline  
137 capacity to contribute to ecosystem functioning in monoculture ('functioning'). We refer to this  
138 correlation as the "function-dominance correlation". When the function-dominance correlation is  
139 positive, we expect to observe positive BEF relationships across communities that differ in  
140 species richness (due to positive sampling effects), vs. negative BEF relationships across  
141 communities with similar richness (due to disproportionately strong contributions by dominant  
142 species) (Fig. 1A). Similarly, we expect to observe the opposite relationships when the function-  
143 dominance correlation is negative (due to negative sampling effects, and disproportionately weak  
144 contributions from dominant species) (Fig. 1B). We refer to these two different scales of  
145 expected BEF relationships as: across species richness treatments (black lines in Figs. 1A-B) or  
146 within species richness treatments (coloured lines in Figs. 1A-B).

147           Second, we hypothesise that reducing seed dispersal will increase the importance of the  
148 function-dominance correlation for BEF relationships, because seed dispersal decreases the  
149 relative abundance of the dominant species in our simulations. For example, if the function-  
150 dominance correlation is positive, lower relative abundance of the dominant species resulting  
151 from seed dispersal will lead to a lower community functioning (Leibold *et al.* 2017). Thus,  
152 when the community is isolated from seed dispersal, relative abundance of the dominant species  
153 will increase, leading to increased ecosystem functioning while reducing realised diversity.

154           Consistent with our hypotheses, our results show that when the dominant species also  
155 contribute disproportionately to ecosystem functioning (i.e., positive function-dominance  
156 correlation), BEF relationships tend to be positive across communities with different species  
157 richness treatments and negative across communities within the same species richness treatment  
158 (i.e., a “positive counter-gradient”). Alternatively, BEF relationships tend to be weak, or lead to a  
159 “negative counter-gradient”, when the function-dominance correlation is weak or negative,  
160 respectively. Further, the importance of the function-dominance correlation for BEF  
161 relationships across communities is higher in the absence of external seed input. Thus, the  
162 function-dominance correlation provides an ecologically grounded and empirically tractable  
163 metric that appears to explain much of the context dependence observed across BEF  
164 relationships. This work therefore has major implications for how to apply BEF research to the  
165 problem of biodiversity change. In particular, if BEF relationships are determined by the  
166 function-dominance correlation, then changes in the identity of species in the local community,  
167 as is occurring in many communities worldwide (Dornelas *et al.* 2014, Blowes *et al.* 2019), may  
168 have larger impacts on ecosystem functioning than declines in species richness *per se*.

169

## 170 **MATERIALS AND METHODS**

171

### 172 *Model descriptions*

173           We included six published plant community models that cover a variety of ecosystems  
174 and model types, ranging from forests to succulent plants, and from systems of differential  
175 equations to spatially-explicit, individual-based models (Table 1). These capture key elements of  
176 their target systems and have been extensively analysed and documented in published literature  
177 (Clark *et al.* 2018, Turnbull *et al.* 2013, May *et al.* 2009, Weiss *et al.* 2014, R ger *et al.* 2020,

178 Maréchaux & Chave 2017, Reineking et al. 2006). They support realistic levels of biodiversity,  
179 and the mechanisms driving coexistence are well-understood.

180 *Grass1* (Clark *et al.* 2018) explores a trade-off between species' abilities to take up and  
181 retain resources, vs. to pre-empt other species from accessing resources. The model is designed  
182 to portray dynamics in a Minnesota tallgrass prairie, and was parameterised from observations of  
183 three plant traits measured in experimental monocultures. Model dynamics are deterministic, and  
184 allow for an arbitrarily large number of species to stably coexist, provided that their traits all fall  
185 within the correct regions of the trade-off space.

186 *Grass2* (Turnbull *et al.* 2013) is also designed to mimic dynamics in grassland plant  
187 communities and focuses on a classic trade-off between species relative growth rate and carrying  
188 capacity. The model explicitly considers effects of seasonal cycles. Fast-growing species can  
189 persist because they can rapidly exploit resources early in the growing season, before slower-  
190 growing species become dominant. Again, this model is deterministic and allows arbitrarily large  
191 numbers of species to stably coexist.

192 *Grass3* (May *et al.* 2009; Weiss *et al.* 2014) explores trade-offs between asymmetric  
193 competition for light and susceptibility to grazing within central European managed grasslands.  
194 Competition is individual-based and spatially-explicit. Given adequate belowground resources,  
195 larger, faster-growing species dominate competition for light, but are more vulnerable to grazing  
196 than their shorter, more stress-tolerant competitors. The resulting trade-off equalises fitness  
197 among competing species, and stable coexistence is realised through conspecific negative density  
198 dependence that reduces the fitness of individuals when surrounded by conspecific neighbours.

199 *Forest1* (Rüger *et al.* 2020) is designed to simulate dynamics of a diverse tropical  
200 rainforest at Barro Colorado Island, Panama, based on species demographic rates (growth,  
201 survival, and recruitment). It accounts for height-structured competition for light by  
202 distinguishing four canopy layers. Canopy gaps are filled by the tallest trees from lower canopy  
203 layers, regardless of their horizontal position (perfect plasticity approximation; Purves *et al.*  
204 2008). Tree species fall along two demographic trade-offs: a growth-survival trade-off and a  
205 stature-recruitment trade-off (Rüger *et al.* 2018). Here, as in Rüger *et al.* (2020), the model is  
206 deterministic, and stable coexistence within local communities relies on external seed inflow.

207 *Forest2* (Maréchaux & Chave 2017) is an individual-based and spatially-explicit model  
208 of tropical forest dynamics. It uses species-specific functional traits to parameterise tree

209 physiological function and demographic processes, according to relationships and trade-offs  
210 from the literature. Individual trees compete for light within a three-dimensional grid (1 m<sup>3</sup>  
211 voxels), in which tree death and gap formation create horizontal and vertical heterogeneity in  
212 light availability. Seed dispersal is spatially-explicit and includes both local sources and external  
213 seed inflow. Here, we used a model version without explicit conspecific negative density  
214 dependence, so that stable coexistence relies on external seed inflow.

215 *Dryland* (Reineking *et al.* 2006) is an individual-based, stochastic model based on  
216 allocation trade-offs and environmental heterogeneity. The model is parameterised for succulent  
217 communities in the Richtersveld, South Africa (see Appendix S1: Model preparation). Plants  
218 compete for water, and biomass allocation to leaves, roots, water storage and seeds affects plant  
219 growth, survival, and reproduction. At high water supply rates, species not investing in water  
220 storage outcompete species investing in storage, which in turn persist longer under drought.  
221 Coexistence is partially maintained by spatiotemporal heterogeneity in water supply. In the  
222 present study, higher levels of local diversity were maintained via seed inflow.

223

#### 224 *Experimental design*

225 For each model, a set of 64 species was selected by sampling a functionally diverse  
226 assemblage from its species pool. Depending on the model, this was achieved through either  
227 sampling species from the underlying trade-off surface (*Grass1*, *Grass2*, *Dryland*), or by running  
228 k-means clustering (k = 64) on the species pool (*Grass3*, *Forest1*, *Forest2*). For each model, we  
229 implemented an experimental design typical of BEF experiments (*sensu* Tilman *et al.* 1996;  
230 Roscher *et al.* 2004), including seven planted species richness treatments (1, 2, 4, 8, 16, 32 or 64  
231 species) with 64 replicates each (except for the 64-species treatment with only one replicate).  
232 The 1-species treatment consisted of monocultures of each of the 64 species, and the 2- to 32-  
233 species treatments were implemented by randomly sampling (without replacement) from the 64-  
234 species pool.

235 For each model, the 385 (6\*64+1) experimental communities were initialised with equal  
236 abundances of seeds or seedlings for each planted species (depending on each model's default  
237 settings) and run until stable abundance distributions were achieved (hereafter "equilibrium")  
238 (see Appendix S1: Experimental Design). Thus, due to their slower dynamics, forest models  
239 were run significantly longer than grassland and succulent models.

240 During this initial stage, seed inflow from the initial species pool took place (“*with seed*  
241 *inflow*”). Seed inflow for each species was constant and corresponded to average internal seed  
242 production across all equilibrium monocultures, divided by the number of species. This  
243 implementation generates equal numbers of saplings (forest models) or equal seed biomass  
244 (grassland/dryland models) per species per year, and therefore buoys abundances of poorly  
245 performing species. To explore the effect of isolating communities from their respective  
246 metacommunities, in a second stage of the same duration, seed inflow was stopped (“*without*  
247 *seed inflow*”). We measured diversity and ecosystem functioning on the last time steps of each  
248 stage.

249

### 250 *BEF relationships within models*

251 For the results presented here, we use Shannon diversity to quantify community diversity.  
252 We do so because Shannon diversity incorporates information about both richness and evenness,  
253 and in several models, species abundances decline to very low levels rather than to zero (i.e.  
254 “asymptotic” extinction). Thus, when species became functionally extinct, realised species  
255 richness remained unchanged. Note, however, that when analysed in terms of richness, our  
256 results are qualitatively similar (see Appendix S2). We also present results for two related  
257 ecosystem properties: 1. Aboveground biomass (main results) and 2. Net primary productivity  
258 (Appendix S3; results are identical to biomass for grassland models, but not for dryland and  
259 forest models.). To enable comparison between models with very different amounts of total  
260 biomass, we scaled the community biomass across all simulated communities to fall between 0  
261 and 100.

262 Our analysis consisted of two steps. In the first step, for each plant community model and  
263 seed inflow stage, we fit a Bayesian linear regression between realised Shannon diversity and  
264 biomass across planted species richness levels to estimate the “*across species richness*  
265 *treatment*” BEF slope (black line in Fig. 1, see Appendix S1: Statistical Methods). In the second  
266 step, we fit independent Bayesian linear regressions within each planted species richness level to  
267 quantify “*within species richness treatment*” BEF slopes (coloured lines in Fig. 1) for each plant  
268 community model and seed inflow stage (see Appendix S1: Statistical Methods).

269 Regressions were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter  
270 *et al.* 2017) through the ‘brms’ package (Bürkner 2017) in R (R Core Team 2019) using 4

271 chains, 2000 iterations (1000 as warm up) and Gaussian distributions for all models. We used  
272 weakly regularising default priors, and inspection of the HMC chains for each model showed  
273 excellent convergence, with R-hat values of 1.0 for all estimates. We used posterior predictive  
274 checks to visually inspect how well the statistical models reproduced the data (see Appendix S4).

275

### 276 *Comparison across models*

277 We quantified the function-dominance correlation for each seed inflow stage separately.  
278 To do this, we bootstrapped species' mixture biomasses (n=2500) using the 32-species mixtures.  
279 Each bootstrap contained 2048 species (32 species per mixture x 64 replicates) selected with  
280 replacement. We then calculated the Pearson's correlation between species' biomasses in  
281 monoculture ('function') and their respective mixture biomasses ('dominance'). Note that like  
282 the "selection effect" of Loreau & Hector 2001, our correlation coefficient effectively  
283 summarises overall effects of dominance on yield in mixture -- i.e., it tests whether highly  
284 functioning species in monoculture also tend to be highly functioning in mixture. We use this  
285 metric, rather than the classic Loreau & Hector metric, both for simplicity, and to avoid issues  
286 related to low or zero monoculture biomass that can complicate the classic Loreau & Hector  
287 metric (Clark *et al.* 2019).

288 We focused on the 32-species communities because they encompass the highest initial  
289 diversity of any treatment level beyond the single replicated 64-species treatment. We then drew  
290 2500 samples from the posterior distributions of the within-treatment and across-treatment BEF  
291 slopes of each model and regressed them against the function-dominance correlations. Since both  
292 metrics are estimated and thus incorporate error, we used Standard Major Axis regression  
293 (lmodel2, Legendre 2018).

294

## 295 **RESULTS**

296

### 297 *Communities with seed inflow*

298 In communities with seed inflow, community biomass was positively correlated with  
299 realised Shannon diversity across species richness treatments in five of the six models (all except  
300 *Forest2*). The most pronounced positive relationships emerged from *Grass1*, *Grass2*, and  
301 *Forest1* (Fig. 2). Within species richness treatments, the slope of the relationship between

302 realised diversity and biomass was negative in four out of the six models. This pattern was most  
303 pronounced in *Grass1* and *Forest2*. In *Grass2* and *Forest1*, the slope of the relationship between  
304 realised diversity and biomass was negative within communities with low species richness, and  
305 became positive with increasing species richness. In *Grass3* and *Dryland*, the slope of the  
306 relationship between realised diversity and biomass tended to be positive within species richness  
307 treatments.

308 Consistent with our hypothesis, the effect of realised diversity on community biomass  
309 was more positive across species richness treatments (Fig. 3) and more negative within species  
310 richness treatments (Fig. 4) in models where the function-dominance correlation was positive (cf.  
311 Fig. 1). This relationship also emerged when using realised species richness as a measure of  
312 diversity rather than Shannon diversity (Appendix S2), and productivity as a measure of  
313 ecosystem functioning (Appendix S3).

314

#### 315 *Communities without seed inflow*

316 After local communities were isolated from their metacommunity (by eliminating seed  
317 inflow), there was no consistent pattern in how the slope of the relationship between realised  
318 diversity and biomass changed across species richness treatments (Fig. 2). However, within  
319 communities of the same species richness treatment, the slope of the relationship between  
320 realised diversity and biomass often became more positive than in simulations with seed inflow,  
321 e.g. switching from negative to positive (*Grass2*, *Forest2*), becoming less negative (*Grass1*), or  
322 becoming more positive (*Dryland*).

323 Eliminating seed inflow did not substantially alter the function-dominance correlation,  
324 except for *Forest2*, where this correlation changed from positive to negative (see Appendix S4).  
325 Consequently, the overall relationship between the function-dominance correlation and the slope  
326 of the relationship between realised diversity and biomass across species richness treatments  
327 became even more strongly positive (Fig. 3). In contrast, within species richness treatments, the  
328 relationship between the function-dominance correlation and the slope of the relationship  
329 between realised diversity and biomass tended to become weaker (Fig. 4). Similar results were  
330 obtained using productivity (rather than biomass) as the measure of ecosystem functioning  
331 (Appendix S3) or using realised species richness (rather than realised Shannon diversity) as the  
332 measure of community diversity (Appendix S2).

333

## 334 **DISCUSSION**

335

336 Biodiversity experiments have convincingly demonstrated the importance of biodiversity  
337 for ecosystem functioning. However, applying these findings to naturally assembled systems has  
338 proven challenging (van der Plas 2019). We show that the sign and magnitude of BEF  
339 relationships both across species richness treatments (as traditionally reported for BEF  
340 experiments) and within species richness treatments can be predicted by the correlation between  
341 species' contribution to functioning and species' dominance in mixture (the “function-dominance  
342 correlation”). When dominant species have a high capacity to provide ecosystem functioning,  
343 realised diversity and functioning are positively related across species richness treatments, but  
344 negatively related within species richness treatments. Further, removing seed inflow strengthens  
345 the explanatory power of the function-dominance correlation across species richness treatments,  
346 but weakens it within them. Importantly, our model intercomparison shows that these results are  
347 consistent for both biomass and net primary productivity, and across six different models that  
348 have been shown to accurately represent dynamics of grasslands, tropical forests, and a dryland  
349 succulent community.

350

### 351 *The function-dominance correlation mediates BEF relationships*

352 Relationships between realised Shannon diversity and biomass were positive across  
353 species richness treatments for five out of six models. This result is consistent with many  
354 biodiversity experiments (reviewed by Tilman *et al.* 2014). However, relationships between  
355 realised diversity and biomass were often negative within species richness treatments, especially  
356 in models that had the most positive relationships across species richness treatments (*i.e.* *Grass1*,  
357 *Grass2*, *Forest1*). This negative BEF relationship within species richness treatments is also  
358 consistent with results from the Jena Experiment (Ryčtecká *et al.* 2014; Leibold *et al.* 2017) but  
359 has not, to our knowledge, been tested elsewhere.

360 Our results show that this “counter-gradient” can be explained by the function-dominance  
361 correlation. Where this correlation is strong and positive (*Grass1*, *Grass2*, *Forest1*), BEF  
362 relationships across species richness treatments were most positive and BEF relationships within  
363 species richness treatments were most negative. A likely explanation is that communities with

364 more species are more likely to include dominant species that produce high levels of ecosystem  
365 functioning through a “sampling effect” (Huston 1997; Hooper *et al.* 2005). However, within  
366 species richness treatments, these same dominant and high-functioning species tend to displace  
367 poorly performing species, potentially driving the negative relationship between functioning and  
368 realised diversity. Conversely, where the function-dominance correlation is weak (*Grass3*,  
369 *Forest2*, *Dryland*), the relationship between realised diversity and biomass is weak or not  
370 significant, both across species richness treatments and within them.

371         This clear link between the function-dominance correlation and BEF relationships  
372 emerged despite the array of coexistence mechanisms and systems in our models. Interestingly,  
373 the strength of the function-dominance correlation was not related to mechanism type, i.e.  
374 resource partitioning (*Grass1*, *Grass2*, *Dryland*), seed inflow (*Forest1*, *Forest2*), or conspecific  
375 negative density dependence (*Grass3*). However, strong local coexistence mechanisms like  
376 resource partitioning (*Dryland*) and conspecific negative density dependence (*Grass3*) increased  
377 the slope of positive relationships between realised diversity and ecosystem functioning within  
378 species richness treatments. *Grass3*, for example, is spatially-explicit and incorporates  
379 conspecific negative density dependence. Individuals surrounded by conspecifics perform more  
380 poorly than individuals surrounded by heterospecifics (May *et al.* 2009). Because individuals are  
381 more likely to be surrounded by heterospecifics in communities with higher realised diversity,  
382 these more diverse communities are also higher functioning. In higher species richness  
383 treatments, effects of negative density dependence are weak regardless of realised diversity, and  
384 these effects disappear. Similarly, in *Forest1*, BEF relationships within species richness  
385 treatments are negative at low species richness but become positive at high species richness. In  
386 this model, more diverse communities are likely to include several species of similar competitive  
387 ability that are able to coexist. For example, communities of ‘tall’ vs. ‘slow’ species coexist  
388 because tall species maximise biomass in upper canopy layers while slow species maximise  
389 biomass in lower layers. Thus, at higher species richness levels, species with these strategies  
390 partition the vertical canopy gradient, leading to positive BEF relationships within species  
391 richness treatments. In contrast, only one of these strategies is likely to be represented in low  
392 species richness treatments, in which case the highest biomass occurs when one of these  
393 strategies dominates resulting in low realised diversity.

394 Unlike the function-dominance correlation, the specific slope and sign of the relationship  
395 between realised diversity and biomass varied with model structure both between species  
396 richness treatments and within species richness treatments. For example, the two tropical forest  
397 models show differing results. However, across model types, study systems, and community  
398 assembly mechanisms, we were able to identify a common pattern: the link between the  
399 function-dominance correlation and the strength and direction of BEF relationships. Thus, we  
400 expect that the function-dominance correlation is relevant for understanding variation in the sign  
401 and magnitude of BEF relationships across a wide variety of systems.

402

#### 403 *The effect of removing seed inflow*

404 One benefit of our modelling approach is our ability to eliminate external dispersal  
405 (inflow). In BEF experiments, although plots are weeded, it is usually not possible to distinguish  
406 whether new recruits of planted species result from seeding treatments, dispersal from within the  
407 plot, or external seed dispersal. Thus, it is impossible to fully isolate effects of local interactions  
408 from external metacommunity processes. Although external seed inflow is thought to influence  
409 BEF relationships (Roscher *et al.* 2004; Hooper *et al.* 2005), we found that completely removing  
410 seed inflow had little effect on BEF relationships observed across species richness treatments,  
411 which are the most commonly reported BEF relationships in the literature.

412 However, within species richness treatments, the relationship between realised diversity  
413 and biomass often became more positive when seed inflow stopped (*Grass1, Grass2, Forest1,*  
414 *Forest2, Dryland*). For example, in *Grass2*, the slope of the relationship between realised  
415 diversity and biomass changed from negative (with seed inflow) to positive (without seed  
416 inflow) within species richness treatments. In this model, species are dominant in mixture by  
417 having either a high carrying capacity or a high growth rate (Turnbull *et al.* 2013). With seed  
418 inflow, low-biomass species with high growth rates temporarily prevent their slower competitors  
419 from accessing soil resources. Consequently, higher functioning, slower-growing species are  
420 unable to reach maximum size. Without seed inflow, these high growth rate-low functioning  
421 species decrease in relative abundance, and the remaining species are better able to utilise  
422 available resources. These processes combined result in a positive relationship between realised  
423 diversity and biomass within species richness treatments.

424           Although eliminating seed inflow had noticeable effects on BEF relationships both across  
425 and within species richness treatments, function-dominance correlations remained largely  
426 unchanged with one exception. For *Forest2*, the slope of the function-dominance correlation  
427 changed from positive (with seed inflow) to negative (without seed inflow). In this model, small,  
428 low-biomass species disproportionately benefited from removing seed inflow because they reach  
429 their reproductive size more rapidly than tall, high-biomass species. Without seed inflow, these  
430 low-biomass species could colonise more empty sites and reach a higher biomass in mixture than  
431 tall species. This leads to a change in the function-dominance correlation from positive with seed  
432 inflow to slightly negative without seed inflow, which in turn caused a reversal of the counter-  
433 gradient (negative across species richness treatments and positive within species richness  
434 treatments without seed inflow). This reversal reinforced the relationship between the function-  
435 dominance correlation and the slope of the relationship between realised diversity and biomass  
436 across species richness treatments. This result, along with the *Dryland* model without seed  
437 inflow, is the only example that we know of a negative counter-gradient: a negative BEF  
438 relationship across species richness treatments, but positive BEF relationships within species  
439 richness treatments.

440           Seed inflow in our models is limited to the original species pool, and assumes constant,  
441 uniform seed input across species. While this approach is not realistic, our results are consistent  
442 with findings from a recent meta-analysis of seed addition experiments (Ladouceur *et al.* 2020)  
443 which found that when dispersal limitation was alleviated by seed addition, species richness  
444 increased (also reviewed by Myers & Harms 2009) while biomass was relatively unaffected.  
445 Similarly, in our models, communities generally had higher realised diversity with seed inflow  
446 than without it, with biomass remaining largely unaffected relative to changes in Shannon  
447 diversity (Appendix S5). Realised species richness was bolstered by seed inflow more than  
448 realised Shannon diversity, leading to a larger relative increase in the across-treatment slope once  
449 seed inflow was removed (Appendix S2). This strong response emerged because seed inflow was  
450 uniformly distributed, and thus kept realised richness artificially high, and reduced the  
451 importance of local competitive dynamics in driving communities' biomass and productivity.

452

453 *Applying our results to other functions and applications*

454 Here, we focus on relationships between realised diversity and aboveground  
455 biomass/productivity. Aboveground biomass and productivity are good indicators for many other  
456 functions and services, such as root biomass, carbon storage/sequestration, harvestable volume  
457 for forests, and ecosystem stability (Allan et al. 2013; Ratcliffe et al. 2017). We therefore expect  
458 that our results will hold for this set of functions. However, other functions such as above- and  
459 belowground decomposition, nutrient cycling, microbial biomass, or resistance to climate  
460 extremes are not easily predicted by biomass or productivity. Although we would not expect the  
461 biomass-based function-dominance correlation to be informative for these functions, it may be  
462 that function-dominance correlations that are based on these other functions or related functions  
463 could still prove to be useful predictors. For example, in microbial systems, if a species  
464 comprises a large amount of microbial biomass in monoculture and also plays a dominant role in  
465 contributing a large amount of microbial biomass in mixture (positive function-dominance  
466 correlation for microbial biomass), then we would predict that the relationship between realised  
467 diversity and microbial biomass across species richness treatments would be strongly positive.

468 Function-dominance correlations may be an effective ecosystem assessment tool that  
469 could be adopted by applied ecologists interested in maintaining or restoring ecosystem health.  
470 Assessing function-dominance relationships with respect to species losses and gains may allow  
471 better prioritization of management actions for conservation and more function-driven  
472 restoration (Ladouceur et al. 2021). Species loss and gain is commonly observed in many  
473 conservation areas, particularly those that lie within successional habitats such as old fields  
474 (Walker et al. 2007, Bourgeois et al. 2016). The function-dominance correlation, rather than  
475 species identity per se, may serve as an indicator of whether assisted community assembly (e.g.,  
476 through replanting or re-seeding) would be effective at restoring additional ecosystem  
477 functioning (Isbell et al. 2019, Ladouceur et al. 2020). The function-dominance correlation may  
478 serve as a community profile tool that allows assessment of ecosystem health and the success of  
479 management, conservation, or restoration (sensu Matthews & Whittaker 2014).

480

## 481 **CONCLUSIONS**

482

483 Global biodiversity loss and local and regional biodiversity change are among humanity's  
484 most pressing concerns. The current consensus is that this change is likely to have devastating

485 consequences on ecosystem functioning. However, our results suggest that diversity change will  
486 have the strongest impact on ecosystem functioning when dominant species provide the most  
487 function. If this is also found to be true in experiments and naturally assembled systems, it has  
488 important implications for biodiversity-ecosystem functioning research. Loss of – or change in –  
489 biodiversity may have smaller or larger effects on ecosystem functioning than currently  
490 predicted, depending on the species affected. If species that are lost are dominant and high  
491 functioning, we expect that their loss will cause declines in ecosystem functioning unless they  
492 are replaced by species that perform similarly well. Alternatively, if the species lost dominated  
493 the community while contributing little to functioning (e.g., by taking up space and pre-empting  
494 the establishment of higher-biomass species), the effect of biodiversity loss on ecosystem  
495 functioning may be positive even while other effects of losing these species could be negative.  
496 For example, recent research indicates that tall, high-biomass tree species may be more prone to  
497 extinction future climate conditions than smaller or low-biomass species (McDowell *et al.* 2020),  
498 with negative consequences for ecosystem functioning (Aubry-Kientz *et al.* 2019; Rüger *et al.*  
499 2020). Our results suggest that within these systems, ecosystem functioning may be likely to  
500 decline even if it is not reliant on species richness *per se*. Our results also suggest that isolation  
501 from seed sources may amplify the functional role of dominant species. This is particularly  
502 relevant in the context of land-use change, and the habitat fragmentation that follows it, which is  
503 currently regarded as the largest cause of biodiversity change globally (Intergovernmental  
504 Science-Policy Platform on Biodiversity and Ecosystem Services 2019). By comparing the  
505 outputs from six well-understood models that span different ecosystem types and community  
506 assembly mechanisms, we were able to identify an emergent community metric – the function-  
507 dominance correlation – that drives variation in BEF relationships. This synthesis provides key  
508 information about how changes in community composition rather than biodiversity loss *per se*  
509 are likely to influence ecosystem functioning under global change.

510

## 511 **AUTHOR CONTRIBUTIONS**

512

513 This study was devised as a product of a collaborative workshop attended by all authors.  
514 MC, NR, ATC, IM, FM, BR, and LAT designed the initial model intercomparison project with  
515 feedback from other authors. MC, ATC, IM, CF, and BR performed modelling experiments on

516 individual models and provided data and feedback to MC. MC conducted model intercomparison  
517 analyses with input from NR, KEB, and ATC. KEB, MC, NR, and ATC wrote and revised initial  
518 drafts of the manuscript. All authors contributed to the revision of the manuscript.

519

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521

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534

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- 680

681 **FIGURE LEGENDS**

682

683 *Figure 1.* We hypothesise that the strength and direction of the relationship between the diversity  
684 of a community and its total biomass will depend on the function-dominance correlation of its  
685 species (C). Communities with a positive function-dominance correlation (A) will tend to be  
686 dominated by species that also generate significant functioning. When included in a mixture,  
687 these species will decrease biodiversity as they increase total biomass. Across species richness  
688 treatments the likelihood of these species being incorporated into a community will increase,  
689 leading to a positive relationship between diversity and biomass. However, within species  
690 richness treatments, communities incorporating these dominant species will tend to have lower  
691 biodiversity – though more biomass – than communities in which they are absent. A negative  
692 function-dominance correlation (B) will lead to alternative diversity-biomass relationships, as  
693 they will tend to be dominated by species that provide little functioning. Across species richness  
694 treatments, this will lead to a negative relationship between diversity and biomass, as  
695 competitive – though low biomass – species are more likely to be incorporated into diverse  
696 mixtures. However, within species richness treatments, there will be a positive relationship  
697 between biomass and functioning as communities that lack these competitive species will  
698 subsequently contain higher diversity and biomass.

699

700 *Figure 2.* The relationship between realised Shannon diversity and total community biomass for  
701 six plant community models. Points represent individual plant communities. Coloured lines refer  
702 to the relationships within species richness treatments, while the black lines refer to the  
703 relationship across species richness treatments. Ribbons represent the 95% credibility intervals of  
704 the model fits. Significant relationships (95% CI does not include 0) are shown with solid lines.  
705 Insignificant relationships are shown with dashed lines.

706

707 *Figure 3.* The relationship between the function-dominance correlation and the slope of the BEF  
708 relationship across species richness treatments for six plant community models. Standard major  
709 axis regressions were run on each bootstrapped dataset ( $n = 2500$ ), which each contained one  
710 function-dominance correlation paired with one posterior sample of the BEF slope per model.

711 95% confidence interval for the mean where derived through nonparametric bootstrapping of the  
712 slope parameter (n = 1000).

713

714 *Figure 4.* The relationship between the function-dominance correlation and the slope of the BEF  
715 relationships within species richness treatments for six plant community models. Standard major  
716 axis regressions were run on each bootstrapped dataset (n = 2500), which each contained one  
717 function-dominance correlation paired with one posterior sample of the BEF slope per model and  
718 species richness treatment. Intervals indicate 95% confidence of the mean, derived through  
719 nonparametric bootstrapping of the slope parameter (n = 1000).

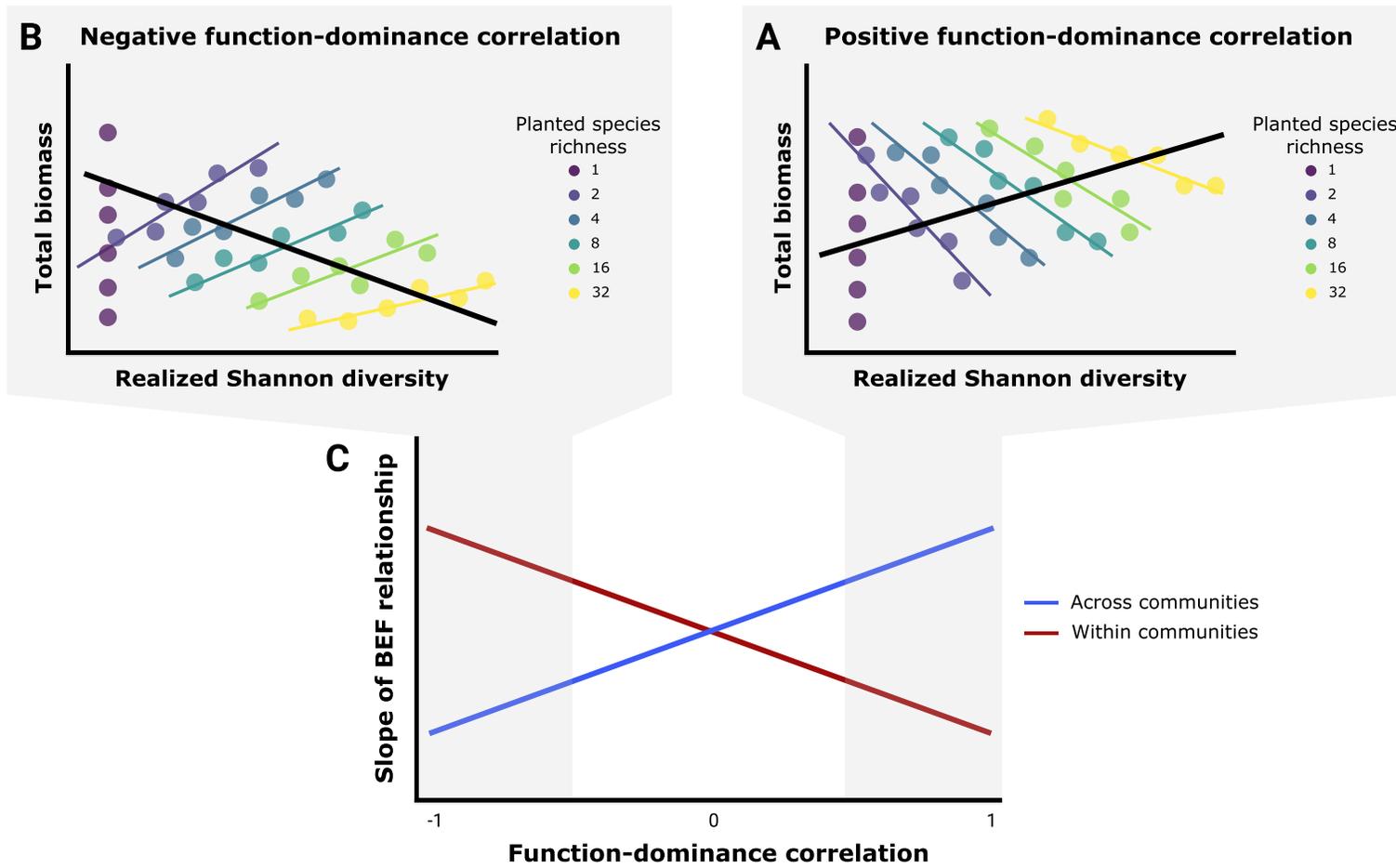
720 **TABLES**

721

722 Table 1. Model descriptions.

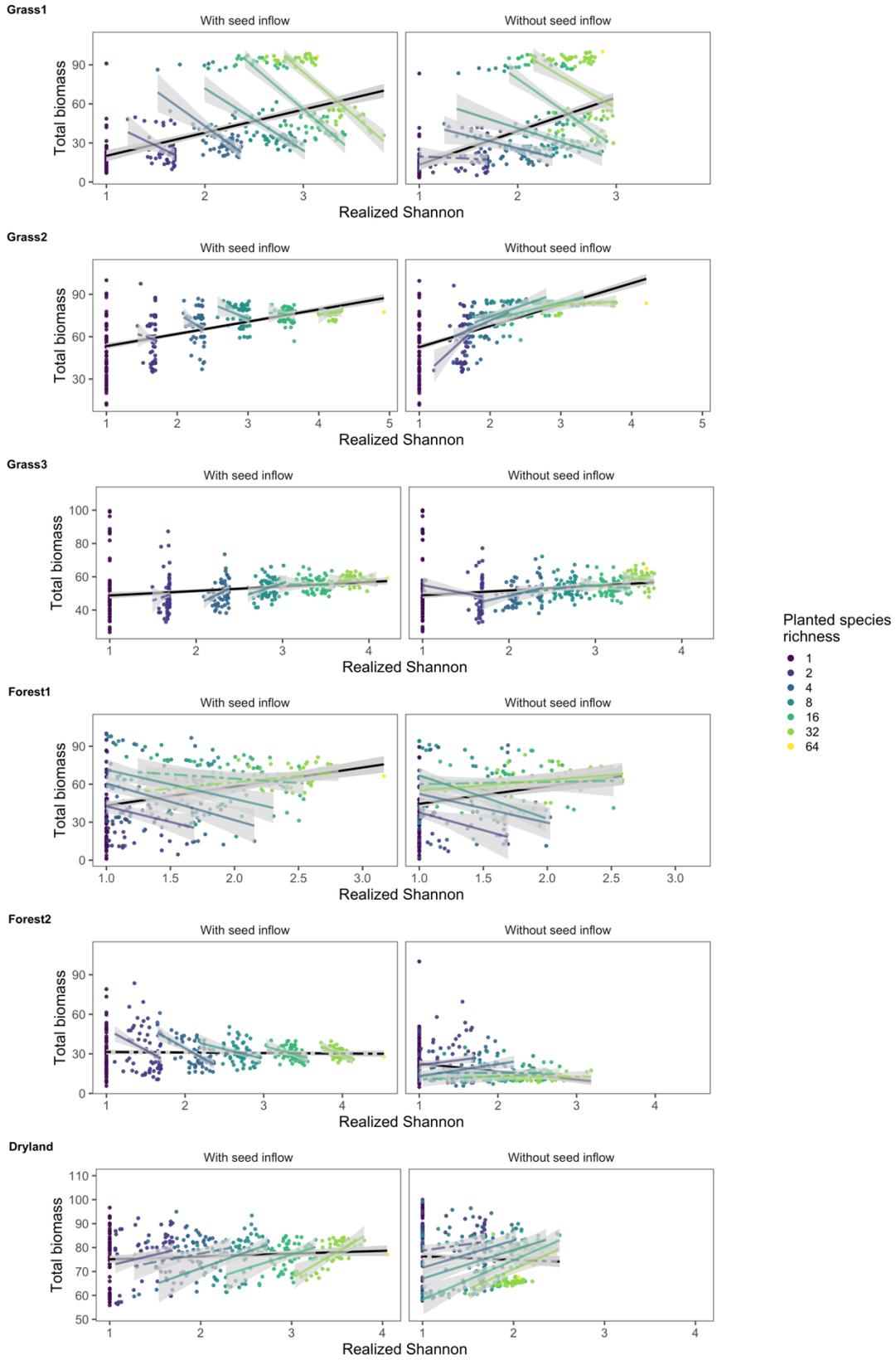
Model ID	Study Area	Model Type	Spatial Extent	Parameterization	Coexistence Mechanisms	Literature
Grass1	Cedar Creek, Minnesota, USA	Ordinary differential equations	1 m <sup>2</sup>	Field data	Trade-off between competitive ability for soil nitrate and nitrogen-use efficiency	Clark et al. 2018
Grass2	Temperate grasslands	Ordinary differential equations	1 m <sup>2</sup>	Theoretical	Trade-off between rooting depth and resource uptake rate	Turnbull et al. 2013
Grass3	Central European grasslands	Individual-based, spatially-explicit model	9 m <sup>2</sup>	Field data (see Weiss et al. 2014)	Trait-driven niche and fitness differences defining competition above- and belowground; CNDD	May et al. 2009, Weiss et al. 2014
Forest1	Barro Colorado Island, Panama	Spatially-implicit demographic cohort model	1 ha	Demographic trade-offs derived from forest inventory data	Demographic trade-offs; demography-driven niche differences within a vertical canopy gradient; external seed input	Rüger et al. 2020
Forest2	French Guiana	Individual-based, spatially-explicit model	1 ha	Field data (functional traits)	Trait-driven among-species niche differences within a heterogeneous environment, both vertically (canopy gradient) and horizontally (gap dynamics); external seed input	Maréchaux & Chave 2017
Dryland	Richtersveld, South Africa	Individual-based, spatially-explicit model	25 m <sup>2</sup>	Literature	Trade-offs between competition and storage ability for water, mediated through stochastic variation in water supply rate	Reineking et al. 2006

723



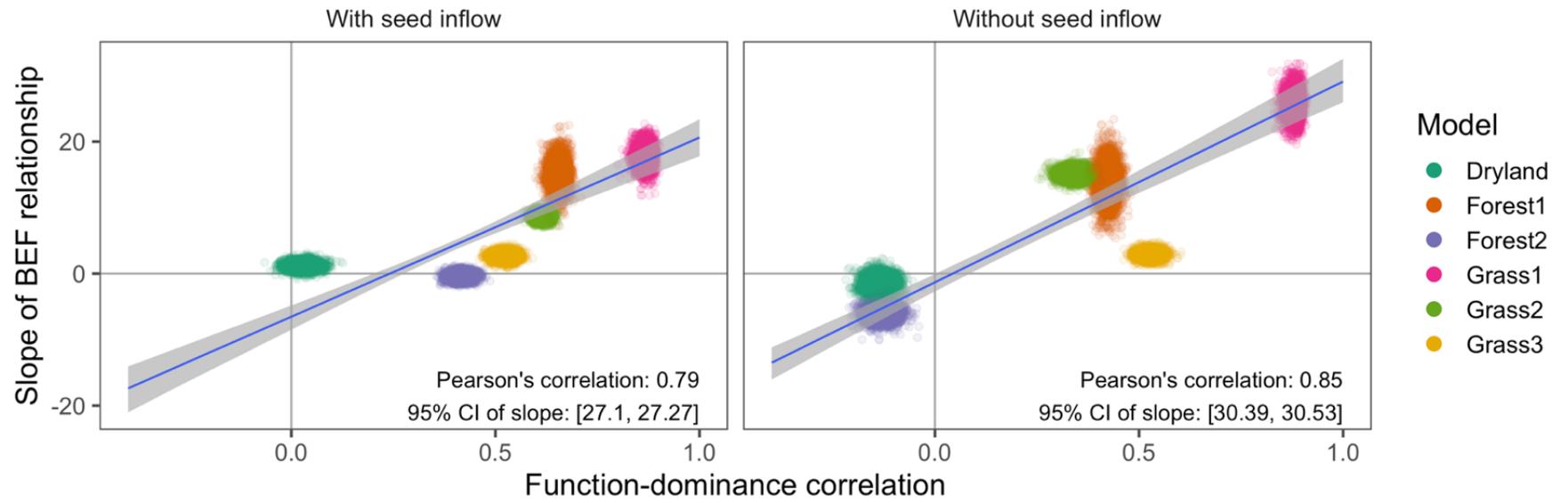
725

726 Figure 1.



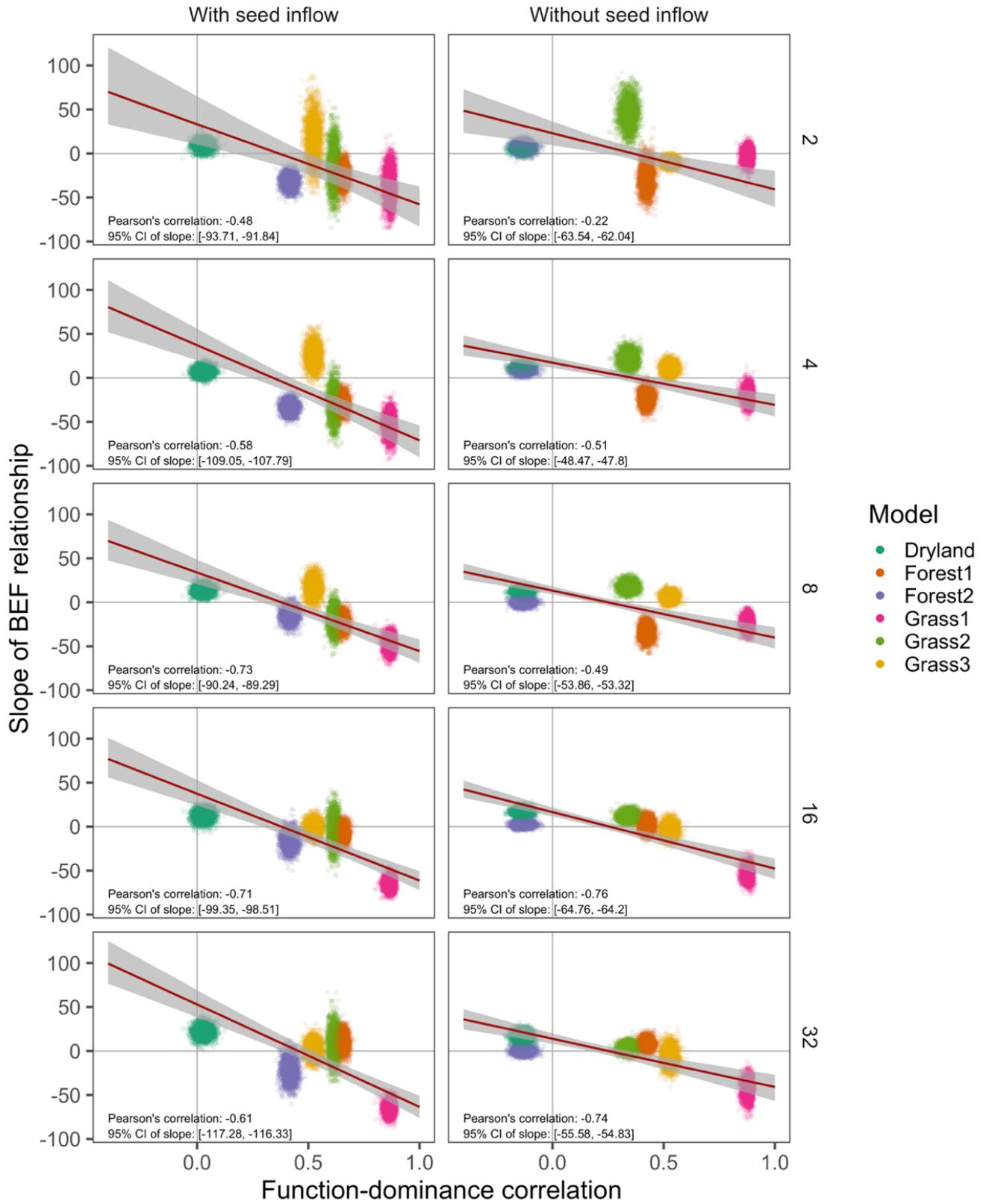
727

728 Figure 2.



729

730 Figure 3.



731  
732 Figure 4.