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Roscher, Christiane ; Schumacher, Jens ; Petermann, Jana S ; Fergus, Alexander J F ; Gerighausen, Uta ; Michalski, Stefan G ; Schmid, Bernhard ; Schulze, Ernst-Detlef

Abstract: Initial plant diversity might control subsequent community assembly processes and plant productivity. To study these effects, we used a biodiversity experiment (Jena Experiment) with subplots of different sown diversity that were never weeded and spontaneously colonized control plots of different size (3.5×3.5 m, 20×20 m) with and without mowing in an 8-year study. On non-sown bare plots without mowing, colonizer accumulation depended on plot size resulting in a loss of diversity in large, undisturbed (unmown) control plots after initial colonization. On sown plots that were mown, species richness converged to high levels due to the accumulation of internal colonists (species belonging to the experimental pool of sown species), while initially high species richness of external colonists (species not belonging to the experimental pool) and residents (species sown on the plot) declined over time. The convergence of total species richness at higher levels was paralleled by increased taxonomic (Simpson index, QSimp), phylogenetic (QPhylo) and trait (FDQ) diversity, whereby FDQ was greatest on plots with low resident species richness after several years. Rates of change in terms of species colonization and extinction decelerated over time irrespective of resident species richness, mowing or plot size. While the contribution of residents declined and that of colonists increased, community biomass production did not change over time. The biomasses of residents and colonists were greatest at higher levels of species richness, partial QPhylo and FDQ of the respective species group, but community biomass was consistently weakly related to total species richness and diversity indices. Our study shows that in contrast to the period of succession, “mature” plant communities resulting from natural assembly processes, favouring the coexistence of multiple species and thus high biodiversity, do no longer show significant relationships between species richness and variables related to ecosystem functioning such as primary productivity.

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1 **Convergent** high diversity in naturally colonized experimental grasslands is not
2 related to increasing productivity

3

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Abstract

Initial plant diversity might control subsequent community assembly processes and plant productivity. To study these effects, we used a biodiversity experiment (Jena Experiment) with subplots of different sown diversity that were never weeded and spontaneously colonized control plots of different size (3.5×3.5 m, 20×20 m) with and without mowing in an 8-year study. On non-sown bare plots without mowing, colonizer accumulation depended on plot size resulting in a loss of diversity in large, undisturbed (unmown) control plots after initial colonization. On sown plots that were mown twice per year, species richness converged to high levels due to the accumulation of internal colonists (species belonging to the experimental pool of sown species), while initially high species richness of external colonists (species not belonging to the experimental pool) and residents (species sown on the plot) declined over time. The convergence of total species richness at higher levels was paralleled by increased taxonomic (Simpson Index, Q_{Simp}), phylogenetic (Q_{Phylo}) and trait (FD_Q) diversity, whereby FD_Q was greatest on plots with low resident species richness after several years. Rates of change in terms of species colonization, extinction and community composition decelerated over time irrespective of resident species richness, mowing or plot size. While the contribution of residents declined and the contribution of colonists increased, community biomass production did not change over time. The biomasses of residents and colonists were greatest at higher levels of species richness, partial Q_{Phylo} and FD_Q of the respective species group, but community biomass was consistently weakly related to total species richness and indices of diversity. Our study shows that in contrast to the period of succession, “mature” plant communities resulting from natural assembly processes, favouring the coexistence of multiple species and thus high biodiversity, do no longer show significant relationships between species richness and variables related to ecosystem functioning such as primary productivity.

51

52 **Keywords:** colonization, community assembly, phylogenetic diversity, productivity,

53 turnover, trait diversity

54 **Introduction**

55 The study of temporal dynamics of plant communities may help to identify the mechanisms
56 determining community structure and diversity and its consequences for ecosystem
57 functioning (Rees et al., 2001). Community assembly processes involve qualitative changes
58 (i.e. in species occurrences) as well as quantitative changes (i.e. in species abundances). Rates
59 of community change **during succession** often gradually decrease from rapid turnover during
60 early stages of community assembly to a more stable compositional structure during later
61 stages (Prach et al., 1993; Anderson, 2007). **Because assembly processes result from many**
62 **spatially dependent colonization and extinction events, the rate and patterns of succession**
63 **may also depend on spatial factors (Glenn-Lewin et al., 1992). In this context, the theory of**
64 **island biogeography (MacArthur and Wilson, 1967) may be considered a central framework**
65 **related to the temporal development of plant communities. Large isolated “islands” and those**
66 **with a nearby source pool of potential colonists should have a greater species richness than**
67 **smaller or distant “islands” (Holt et al., 1995; Cook et al., 2005). Furthermore, extinction rates**
68 **may be higher in small “islands” due demographic stochasticity and a greater risk of local**
69 **extinction for small populations (Joshi et al., 2006). The probability of successful colonization**
70 **is likely to decrease with increasing species richness because a greater fraction of the**
71 **available species pool has already arrived.**

72 Neutral theory (Hubbell, 2001) proposes that dispersal and demographic stochasticity are the
73 primary mechanisms controlling assembly processes. It further assumes that all species are
74 “functionally equivalent”, resulting in local communities with temporally randomly varying
75 species compositions if community equilibrium is achieved at equal immigration and
76 extinction rates. From the point of view of the niche-based theory of community assembly
77 (MacArthur and Levins, 1967), niche overlap among functionally similar species (limiting
78 similarity) may inhibit the colonization of new species with similar resource acquisition

79 strategies more strongly than the colonization of functionally more different species (Chesson,
80 2000). Under this scenario, local species richness is predicted to saturate and local
81 communities are assumed to have similar species compositions due to deterministic assembly
82 from the species pool (Chase, 2003). It has been suggested that a trade-off between colonizing
83 abilities and traits related to competition are core to processes of succession (Tilman, 1988;
84 Pickett and McDonnell, 1989). Species with high colonizing abilities will arrive faster, but
85 their persistence depends on how fast they are replaced by later-arriving species with a greater
86 competitive ability. Consequently, species diversity may also decline through time, when
87 competition results in the dominance of a limited number of species (Whittaker 1975;
88 Mouquet et al., 2003). Competitive exclusion is more likely in stable, uniform environments,
89 while periodic population reductions through moderate disturbance and environmental
90 fluctuations may promote consistently high levels of diversity (Huston, 1979).

91 Approaches restricted to analyses of temporal changes in taxonomic (species) composition
92 largely ignore ecological differences among the involved species. More recently, it has been
93 recognized that the comparison of phylogenetic and functional trait diversity with taxonomic
94 diversity might be more insightful for separating the various mechanisms involved in
95 community assembly processes (e.g. Gerhold et al., 2013; Purschke et al., 2013). For
96 example, increasing and convergent levels of trait diversity through time would support the
97 niche-based theory of community assembly, while decreasing levels of taxonomic and trait
98 diversity may indicate weaker competitor exclusion. Because the quantification of trait
99 diversity is based on a finite set of traits, it is assumed that phylogenetic diversity may cover a
100 larger set of biologically relevant information (Webb et al., 2002). An increasing role of biotic
101 interactions during community assembly may be reflected in decreasing phylogenetic
102 relatedness among species. This is true if important functional traits are shared by species that
103 have common ancestry or if phylogeny integrates information on biotic interactions, such as

104 shared co-evolved enemies or mutualists, which is not covered by measurable functional traits
105 (Cavender-Bares et al., 2009).

106 Guo (2003) suggested in a model based on data of natural plant succession that species
107 richness–productivity relationships would change from positive via neutral to negative during
108 succession because competition and competitive exclusion would decrease species richness
109 while increasing productivity as a community “matures”. In our study region, late-
110 successional vegetation is dominated by shrubs and trees, while early-successional pioneer
111 vegetation settling on open, frequently disturbed places mainly consists of annual herbaceous
112 species. Without disturbance the early-successional pioneer species are first replaced by
113 perennial herbaceous species representing a mid-successional stage before the establishment
114 of late-successional species (Whittaker, 1975). The long-term maintenance of mid-
115 successional vegetation dominated by perennial herbaceous plant species such as grasslands
116 depends on recurring moderate disturbances such as mowing or grazing (Ellenberg, 1988).

117 For natural grasslands, the validity of the positive species richness–productivity relationship
118 observed in many artificially maintained grassland biodiversity experiments has been
119 repeatedly questioned (Thompson et al., 2005). Jiang et al. (2007) argued that differences in
120 diversity–productivity relationships between immature experimental communities, where the
121 diversity gradient is artificially maintained by weeding, and more mature natural
122 communities, are attributable to differences in species abundance patterns. In natural “mature”
123 communities, it is more likely that rare species go extinct, while high productivity levels are
124 maintained through dominant, highly productive species. In an earlier sub-experiment of the
125 Jena Experiment we found that the removal of subdominant species from sown and weeded
126 communities increased total community biomass (chapter 4 in Schmidt, 2006). Thus, the
127 successional stage of the plant community may be a central factor for shifts in species
128 richness–productivity relationships. Grassland biodiversity experiments are often established

129 by sowing mid-successional temperate grassland species on vegetation-free spaces and the
130 experimental diversity gradient is maintained by regular weeding. Short-term studies in such
131 biodiversity experiments with temperate mesophilic grassland species have shown that
132 positive relationships between sown or total species richness and community biomass
133 production were rapidly lost after cessation of weeding within two years at the Swiss
134 Biodepth site (Pfisterer et al, 2004) or three years in the Jena Experiment (Petermann et al.,
135 2010). Similar results were obtained in biodiversity experiments in subalpine grasslands
136 (Rixen et al., 2008) and salt marshes (Doherty et al., 2011). The decay of positive species
137 richness–productivity relationships was even faster when the natural colonization of new
138 species was amended by seed addition (Petermann et al., 2010). The effects of sowing more
139 species on biomass production have also been investigated in applied studies of grassland
140 restoration on ex-arable land which did not weed unsown species after sowing. Studies
141 restricted to two levels of sown diversity (“low” and “high” diversity) have shown that
142 sowing more species enhances average productivity (Bullock et al., 2001; Lepš et al., 2007),
143 but that particular low-diversity mixtures may reach similar productivity levels as high-
144 diversity mixtures (Lepš et al., 2007).

145 In the present study, integrated into a large biodiversity experiment (Jena Experiment;
146 Roscher, et al. 2004), we established subplots which were never weeded after sowing, but
147 regularly mown twice per year. In a previous analysis, encompassing the first two years after
148 sowing (Roscher et al., 2009b), we showed that the species number of colonists and their
149 immigration rates decreased, while their extinction rates increased with sown species richness
150 and that total biomass production was initially positively related to sown species richness, but
151 varied independently from total species richness of residents (sown species) plus colonists.
152 The maturation of such unmanipulated communities could naturally lead to saturated
153 communities with high productivity. However, it is also possible that these “maturing”

154 communities do not achieve maximum productivity because productivity is primarily
155 determined by the efficiency of carbon fixation and stand structure, i.e. leaf area index
156 (Schulze et al., 2005), and community assembly processes starting from different initial
157 compositions are not necessarily concordant with maximizing productivity. However, this has
158 not been tested so far in a biodiversity experiment where the sown diversity gradient is not
159 maintained by weeding because experimental plant communities are rarely followed for many
160 years.

161 Here, we ask how persistently the initially sown plant diversity affects community assembly
162 processes and biomass production over a period of 8 years. In addition, we used control plots
163 at the same experimental site with free plant establishment (no sowing) on originally bare soil
164 with or without mowing twice per year and of different area (small vs. large plots) to test for
165 differences in assembly processes under these conditions. We tested the following
166 hypotheses: (1) According to the Theory of Island Biogeography, non-sown large control
167 plots show higher colonizer immigration rates and lower extinction rates and accumulate
168 more species than non-sown small control plots. (2) Unmown, non-sown control plots show
169 smaller colonizer immigration and larger extinction rates than regularly mown non-sown
170 control plots due to the accumulation of competitive mid- and late-successional species. (3)
171 Rates of community change in terms of colonizer occurrences are lower and decline faster in
172 communities initially sown with greater plant diversity because communities already
173 comprise a greater fraction of more competitive mid-successional species. (4) Species
174 richness, taxonomic, phylogenetic and trait diversity in mown communities increase and
175 converge over time because communities sown with lower plant diversity accumulate species
176 due to the occupation of free niches (local immigrations > extinctions) and communities sown
177 with the highest plant diversity lose species due to the exclusion of weaker competitors and
178 fewer open niches for the colonization of new species (extinctions > local immigrations). (5)

179 Even over a longer study period, strong diversity–productivity relationships do not develop
180 because assembly processes starting from different initial compositions lead to communities
181 with similarly high diversity and productivity.

182

183 **Material and methods**

184

185 **Experimental design**

186 The study was part of a large biodiversity experiment established on a former agricultural
187 field in 2002 (Jena Experiment; Roscher et al., 2004). The experimental site is located in the
188 floodplain of the river Saale near the city of Jena (Thuringia, Germany, 50°55'N, 11°35'E,
189 130 m a.s.l.) with a mean annual temperature of 9.3°C and annual precipitation of 587 mm
190 (Kluge and Müller-Westermeier, 2000). The soil is a Eutric Fluvisol. Soil texture is sandy
191 loam in the vicinity of the river which gradually changes to silty clay with increasing distance
192 from the river. The Jena Experiment is based on a pool of 60 species typically occurring in
193 Central European mesophilic grasslands used as hay meadow (Arrhenatherion community;
194 Ellenberg, 1988). These species were considered as potentially making up a complete
195 community or ecosystem from which species would go extinct to lead to reduced systems of
196 1, 2, 4, 8 or 16 species. We additionally assigned the species into four functional groups: 12
197 legumes, 16 grasses, 20 tall herbs and 12 small herbs. **The classification into functional**
198 **groups was based on a cluster analysis of a literature-derived trait matrix comprising**
199 **morphological traits (growth form, capacity for lateral spread by clonal growth, plant height,**
200 **leaf size, depth and type of the root system), phenological traits (life cycle, seasonality of**
201 **foliage, start and duration of the flowering period) and physiological characteristics (N₂**
202 **fixation) (for further details see Roscher et al., 2004).** The species richness gradient was thus
203 crossed with a gradient in the number of functional groups (from 1 to 4) with about four

204 replicates per possible species richness \times functional group number combination. Mixtures
205 were created by random selection of species with replacement. In addition, four replicates of
206 mixtures with all 60 experimental species were established resulting in a total of 82 plots of
207 20×20 m size. The experimental site was arranged in four blocks parallel to the riverside in
208 order to account for the gradient in soil characteristics; diversity treatments were equally
209 assigned to the blocks. Plots were sown with a total density of 1000 viable seeds per m^2 , *i.e.*
210 *seed numbers were adjusted according to germination tests under standardized conditions in*
211 *the laboratory. Mixtures were sown with equal numbers of viable seeds per species (for*
212 *details see Roscher et al., 2004).* A subplot of 2.00×2.25 m size in each large plot was
213 permanently marked and never weeded after sowing (Roscher et al., 2009b). Plots were
214 managed by mowing and removing the mown plant material twice per year (early June,
215 September) *as usual for extensively managed hay meadows in the region.* Plots did not
216 receive any fertilizer. Furthermore, we used four large (20×20 m size) and eight small ($3.5 \times$
217 3.5 m size) plots within the Jena Experiment which did not receive a seed mixture but were
218 open to spontaneous colonization (= control plots). Of these plots, two large and four small
219 plots (one in each experimental block) were never mown (= unmown control plots) and the
220 others were regularly mown at the same time as the plots of the biodiversity experiment (=
221 mown control plots). All plots were surrounded by a frequently mown lawn sown with grass
222 species not belonging to the experimental species pool (for details see Roscher et al. 2004).

223

224 **Sampling**

225 Species identities and cover were visually estimated with a decimal scale (Londo, 1976) on
226 the 2.00×2.25 m subplots twice per year shortly before biomass harvests. Two neighbouring
227 subplots of 2.00×2.25 m size were surveyed in large control plots to study the same area as
228 in the small control plots (central 3×3 m = 9 m^2). To get reliable data on short-lived spring or

229 annual plants, all plots were checked for additional non-experimental species in early April
230 (start of the growing season) and July (re-growth after first mowing). **Species initially sown**
231 **into a particular plot were considered resident species. All species not initially sown into a**
232 **particular plot were considered colonizing species.** Colonizing species were categorized as
233 internal colonists (belonging to the 60 experimental species) or external colonists (not
234 included in the experimental species pool). Species inventories were combined for each year
235 to derive **total** species richness and maximum cover abundances of each species per subplot.
236 Aboveground plant biomass was harvested twice a year except in 2008, at estimated peak
237 biomass immediately before mowing in all regularly mown large plots (late May and August).
238 Plant material was clipped 3 cm above soil surface in a randomly placed rectangle (20 × 50
239 cm) in the never-weeded subplot. Plant material was sorted into residents and colonists and
240 dried to constant weight (70°C, 48 h). Biomass data of both harvests were summed to get
241 annual biomass production.

242

243 **Trait and phylogenetic data**

244 Trait information was assembled for all plant species recorded in the plots (203 species in
245 total **including the sown species**) using published floras (Rothmaler, 2002), databases (LEDA:
246 Kleyer et al., 2008; BiolFlor: Klotz et al., 2003) and further literature (see Supplementary
247 Material, Appendix A.1). The set of traits comprised six traits related to growth and
248 competitive ability and six traits related to life history (Table 1). Specific leaf area for species
249 for which no data were available from published sources was determined from leaf samples
250 collected at the field site or in surrounding habitats in 2009.

251 The phylogeny was extracted from a dated, ultrametric supertree for 4685 Central European
252 vascular plant species (*Daphne I.0*, Durka and Michalski, 2012) using the library *ape* (Paradis
253 et al., 2004) in the statistical software R3.1.1 (R Development Core Team,

254 project.org). Blomberg's K statistic (Blomberg et al., 2003) was used to evaluate the extent to
 255 which phylogenetic relatedness between species is reflected in the chosen traits using the R
 256 library *phytools* (Revell, 2012). K values close to zero indicate less phylogenetic signal than
 257 expected from a Brownian motion model of trait evolution (Blomberg et al., 2003) and imply
 258 that closely related species are functionally distinct. The significance of the phylogenetic
 259 signal was tested by comparing the observed summed absolute node contrast values (K) to a
 260 null distribution of K values based on 1000 randomizations (Revell, 2012).

261

262 Diversity indices

263 Rao's quadratic diversity (Rao's Q; Rao, 1982) expresses the average difference between two
 264 species as

$$265 \quad \text{Rao's Q} = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij} \quad (1),$$

266 where d_{ij} is the distance between the i -th and j -th species, p_i and p_j are their relative
 267 abundances, and S is the number of species in a community. Rao's Q can be applied to trait
 268 and phylogenetic data and is closely related to taxonomic diversity quantified as the Simpson

269 index D being $\sum_i p_i^2$, thus providing a statistical framework for comparing different aspects

270 of diversity based on trait or phylogenetic differences among species or species composition

271 (Pavoine and Bonsall, 2011). Trait diversity (FD_Q) was calculated from the literature-based

272 trait matrix (see Table 1). If necessary, trait data (specific leaf area, seed-bank longevity, seed

273 mass, growth height) were log-transformed to achieve normal distribution. In case of missing

274 data (Table 1), the mode, i.e. the most commonly occurring value across all species was used.

275 Calculations were based on standardized trait data (mean = 0, variance = 1) and a Gower

276 distance matrix to account for different data types (continuous, ordinal) (Pavoine et al., 2009).

277 A phylogenetic cophenetic distance matrix derived from the phylogenetic tree (using the R

278 library *ape*; Paradis et al., 2004) was used for calculating phylogenetic diversity (Q_{Phylo}). FD_Q
279 and Q_{Phylo} were weighted by annual maximum abundances for (1) all species present in a
280 community, i.e. residents and colonists, and partitioned into (2) residents, (3) colonists and (4)
281 dissimilarity between residents and colonists (= residents-colonists dissimilarity). In addition,
282 taxonomic diversity as Simpson index (Q_{Simp}) based on species abundances was computed.

283

284 **Data analysis**

285 Rates of community change in colonizer and resident species occurrences per year were
286 calculated as year-to-year species extinction rates $ER = 2E/(S1+S2)$, immigration rates $IR =$
287 $2I/(S1+S2)$ and species turnover $TR = (E+I)/(S1+S2)$, where E is the number of extinctions
288 from the previous year to the year under consideration, I is the number of immigrations from
289 the previous year to the year under consideration, and S1 and S2 are the numbers of observed
290 species in the respective years (Nilsson and Nilsson, 1982).

291 All response variables were analysed with linear mixed-effects models using the R library
292 *nlme* (Pinheiro et al., 2009). Starting from a constant null model with plot identity nested in
293 block as random effects, the sequence of the step-wise added fixed effects was chosen
294 following the a priori hypotheses of the Jena Experimental design: in all analyses along the
295 sown diversity gradient (including non-sown large mown control plots), a contrast for
296 spontaneously colonized vs. sown communities was fitted before entering sown species
297 richness (as a log-linear term) and functional group number (as a linear term). Afterwards,
298 year was entered as linear variable followed by interaction terms with the previously
299 mentioned experimental factors to test for directional changes over time. The maximum
300 likelihood method was applied and likelihood ratio tests (L ratios) were used to assess the
301 statistical significance of model improvement. In separate analyses of control plots, mowing
302 type (mown vs. unmown), plot size (large vs. small) and their interactions were entered as

303 fixed effects.

304 To evaluate whether assembly processes led to a convergence in community characteristics
305 over time, the coefficient of variation (CV) was calculated for each study year across plots
306 sown with different plant diversity. Linear regressions of standardized variables (corrected for
307 block-effects) were used to explore the effects of **total** species richness, taxonomic,
308 phylogenetic and trait diversity on community biomass production for each study year. **The**
309 **respective standardized variables were used to assess their relevance for the biomass**
310 **production of residents and colonists**. The R library *relaimpo* (Grömping, 2006) was used for
311 assessing the relative importance of different predictor variables defined as the R^2
312 contribution averaged over orderings among regressors (Grömping, 2007).

313

314 **Results**

315

316 **Spontaneous colonization in non-sown control plots**

317 On average, colonizer species richness on a standardized sampling area of 9 m² was higher in
318 small than in large control plots, but effects of plot size differed between mown and unmown
319 control plots (Fig. 1a; Table 2). After a strong increase in species richness during initial
320 settlement in the first two years, separate analyses (not shown) indicated that large mown
321 control plots gradually accumulated more species, while large unmown control plots lost
322 species from the third year onwards. Richness of colonizing species fluctuated at higher levels
323 in small control plots irrespective of mowing. Species richness of internal colonists was
324 higher, and species richness of external colonists was lower in mown than in unmown control
325 plots (Fig. 1b–c; Table 2). The temporal accumulation of internal colonists differed between
326 mown and unmown control plots and plot sizes: mown (large and small control plots) >
327 unmown (small control plots) > unmown (large control plots). After an initial increase from

328 the first to the second year, species richness of external colonists decreased continuously over
329 time (Fig. 1c). Year-to-year changes in colonizer occurrences did not depend on mowing type
330 and size of the spontaneously colonized control plots (Fig. 1d-f, Table 2). Year-to-year
331 changes in colonizer immigration and turnover rates declined over time, while colonizer
332 extinction rates did not show directional temporal changes, but fluctuated among years (Table
333 2). Temporal changes in colonizer extinction and turnover rates were greater in large than in
334 small control plots irrespective of mowing.

335 Taxonomic diversity (Q_{Simp}) and phylogenetic diversity (Q_{Phylo}) of colonists did not differ
336 between mown and unmown control plots, but were higher in small than in large control plots
337 (Fig. 1g, h; Table 2). Trait diversity (FD_Q) of colonists was higher in mown than in unmown
338 control plots (Fig. 1i; Table 2). Plot size effects on FD_Q depended on mowing type: FD_Q was
339 higher in small than in large unmown control plots, but did not differ between small and large
340 mown control plots. After an initial increase from the first to the second year of the
341 experiment, Q_{Simp} , Q_{Phylo} and FD_Q declined through time in large unmown control plots. FD_Q
342 also declined in small unmown control plots, while FD_Q in mown control plots fluctuated at
343 higher levels over time. Irrespective of mowing Q_{Simp} and Q_{Phylo} had constantly high levels in
344 small control plots, while similar high levels were reached after several years in large mown
345 control plots.

346

347 **Spontaneous colonization in plots of varying initially sown plant diversity**

348

349 *Effects of sown plant diversity on total species richness*

350 Overall, **total** species richness (total of residents and colonists) did not differ between unsown
351 mown control plots and sown (mown) plots, but increased with sown species richness as
352 expected by design (Fig. 2a; Table 3). **Total** species richness generally increased through

353 time. Species gain over time became smaller with increased sown plant diversity, and species
354 richness in communities initially sown with 60 species decreased over time. Resident species
355 richness decreased slightly through time, which was mainly due to a loss of species in
356 communities sown with higher plant diversity (Fig. 2b). Nevertheless, communities with
357 higher sown species richness retained greater resident species richness than communities with
358 low sown species richness. Species richness of colonists decreased with higher sown species
359 richness (Fig. 2c; Table 3). The overall gain of colonists through time was fastest on plots
360 with low sown species richness and functional group number. Opposing temporal trends
361 emerged for internal and external colonists. While species richness of external colonists
362 decreased, species richness of internal colonists increased through time (Table 3; Fig. 2d, e).
363 The enhanced colonization of internals in communities with lower sown plant diversity
364 increased through time, while effects of sown plant diversity on species richness of external
365 colonists did not change over time (Table 3). **Total** and colonizer species richness converged
366 among plots sown with different plant diversity over time (decreasing coefficient of
367 variation), while differences in resident species richness were maintained (Fig. A.1).

368

369 *Effects of sown plant diversity on rates of community change*

370 Immigration, extinction and turnover rates of resident species increased with sown species
371 richness. On average extinction rates of residents increased and immigration and turnover
372 rates of residents decreased through time (analyses not shown). Immigration, extinction and
373 turnover rates of colonists did not differ **between** non-sown plots and plots established
374 through sowing (Table 3). Colonizer extinction rates increased and colonizer immigration
375 rates decreased with sown species richness. Colonizer immigration, extinction and turnover
376 rates decreased through time (Fig. 3b-d; Table 3). Effects of sown species richness on

377 colonizer immigration and extinction rates declined through time (significant interaction $Y \times$
378 sown SR; Table 3).

379

380 *Effects of sown plant diversity on taxonomic, trait and phylogenetic diversity*

381 Blomberg's K values were below 1 in all considered traits with the exception of the species'
382 ability for symbiotic N₂ fixation and growth height (Table A.1). However, all traits apart from
383 life form, duration of flowering and type of reproduction had K values that were greater than
384 expected by chance indicating a low, but significant phylogenetic signal.

385 Taxonomic diversity (Q_{Simp}) and phylogenetic diversity (Q_{Phylo}) increased with sown species
386 richness, while trait diversity (FD_Q) did not depend on sown species richness (Table 4). On
387 average, Q_{Simp} , Q_{Phylo} and FD_Q increased through time (Table 4; Fig. 4a, c, e). This increase
388 over time was more pronounced in communities with a lower sown plant diversity resulting in
389 increased convergence of Q_{Simp} and Q_{Phylo} among communities (Fig. A.2a). In contrast, the
390 initially high levels of FD_Q in communities sown with high species richness were exceeded by
391 higher levels of FD_Q in communities sown with a low species richness in later years (Fig. 4e).
392 However, communities also became more similar in FD_Q through time (Fig. A.2a).

393 Partial Q_{Simp} of residents decreased with sown plant diversity in communities with 1 to 16
394 sown species, while communities with 60 sown species had the highest levels of residents'
395 Q_{Simp} (Fig. A.3a). In contrast, partial Q_{Phylo} and FD_Q of residents increased with sown plant
396 diversity (Fig. A.3c, e). Partial Q_{Simp} , Q_{Phylo} and FD_Q of residents decreased through time in
397 plant communities with 1 to 16 sown species, but remained large in communities with 60
398 sown species resulting in a divergence among communities through time (Fig. A.2b; Table 4).

399 Partial Q_{Simp} , Q_{Phylo} and FD_Q of colonists increased through time (Fig. A.3b, d, f). This
400 increase was more pronounced in communities with lower sown species richness leading to a
401 convergence among communities (Fig. A.2c). Taxonomic, phylogenetic and trait

402 dissimilarities between residents and colonists declined strongly from the first to the second
403 study year, in particular at higher sown species richness. In later years, taxonomic,
404 phylogenetic and trait dissimilarities between residents and colonists decreased in
405 communities with one, two or four initially sown species, while they increased in
406 communities with eight and 16 initially sown species and were close to zero in communities
407 initially sown with 60 species (Fig. 4b, d, f).

408

409 *Effects of sown plant diversity on biomass production*

410 Community biomass production did not differ between spontaneously colonized mown
411 control plots and sown (mown) plots. On average, community biomass increased with sown
412 species richness. Biomass production fluctuated among study years, but did not show directed
413 temporal trends (Fig. 5a; Table 3). Resident biomass production also increased with sown
414 species richness, but the biomass of residents declined through time. This decline was more
415 pronounced in communities sown with lower plant diversity (Fig. 5b; Table 3). In contrast,
416 biomass production of colonists decreased with increased sown species richness. Colonists
417 increased their biomass production and effects of initial sown species richness on biomass of
418 colonists became weaker over time (Fig. 5c; Table 3). After productivity levels across
419 communities diverged during the initial five years of the experiment, biomass production was
420 more similar among communities in later years (Fig. A.2a). In contrast, resident biomass
421 diverged and the biomass of colonists converged among communities over time (Fig. A.2b,
422 c).

423

424 *Disappearance of diversity–productivity relationships during community regeneration*

425 Diversity-related predictor variables explained a significant proportion of variation in
426 community biomass production (with the exception of 2004 (year 3), 2007 (year 6)), but the

427 proportion of explained variation was small in all study years (between 7–23%). While FD_Q
428 was the most important predictor positively related to community biomass production from
429 2004 to 2006 (year 3–5), the relationship between FD_Q and community biomass production
430 became weaker and even negative in the last study year (Fig. 6a). The relative importance of
431 SR_{real} , Q_{Phylo} and Q_{Simp} in explaining community biomass production varied over time (Table
432 A.3).

433 Partial diversity-related predictors explained a greater, but annually variable proportion of
434 variation in biomass production of colonists (41–63%), while the proportion of explained
435 variation in biomass production of residents (19–77%) increased over time. The relative
436 importance of partial resident SR_{real} , Q_{Simp} , Q_{Phylo} and FD_Q was similar in explaining resident
437 biomass production (Fig. 6b). In contrast, partial colonizer SR_{real} had a smaller relative
438 importance in explaining colonizer biomass production than partial colonizer Q_{Simp} , Q_{Phylo} and
439 FD_Q (Fig. 6c).

440

441 **Discussion**

442

443 **Rates of community change and species richness**

444 Rates of community change in terms of colonizer occurrences generally decelerated through
445 time. Decreasing species immigration and turnover rates are typical for succession and may
446 be ascribed to increasing competitive interactions and a decreasing pool of potential new
447 colonists (Anderson, 2007). Consistent with the concept of initial floristic composition (Egler,
448 1954) immigration rates were largest in the early phase of colonization and decreased sharply
449 from the second to the third year in non-sown control plots. Relative to immigration rates,
450 extinction rates have been shown to be low and to have less consistent temporal patterns
451 during succession (Anderson, 2007). Indeed, extinction rates in unsown control plots

452 fluctuated over time. Based on the framework of the Theory of Island Biogeography, we
453 hypothesized that large non-sown control plots show larger colonizer immigration rates and
454 lower extinction rates than non-sown small control plots (hypothesis 1). Contrary to our
455 expectation and to earlier studies such as Joshi et al. (2006), colonizer immigration and
456 extinction rates did not depend on plot size. Cook et al. (2005) reported from a succession
457 study in experimentally fragmented patches that "island" size did not show consistent effects
458 on species richness in the first 12 years, but greater richness on large "islands" developed
459 after this period. Furthermore, previous studies have pointed out that patch size effects might
460 be dependent on the isolation of the "islands" (Holt et al., 1995). In our study "islands" were
461 embedded in a matrix of neighbouring plots, which served as a source pool for internal
462 colonists. Thus, higher average numbers of colonizer species on small plots could indicate
463 greater edge effects. However, in later years more species were assembled on the same
464 sampling area in large mown than in small mown control plots suggesting negative effects of
465 small fragmented patches (Fahrig et al., 2003).

466 Contrary to our expectation, rates of community change on non-sown control plots did not
467 generally depend on disturbance by mowing (hypothesis 2), but depended on plot size. In line
468 with our expectation, species richness decreased in large unmown control plots after initial
469 colonization, while this process started in later years in small unmown control plots (Fig. 1a).
470 The accelerated loss of species in large unmown plots is most likely due to the accumulation
471 of biomass and thereby increasing light competition, which limits species diversity at small
472 spatial scale in highly productive habitats (Huston, 1979). In contrast, it is likely that larger
473 edge effects slowed down this process in small unmown control plots.

474 Immigration rates of colonists were lower and their extinction rates were higher at high sown
475 plant diversity, which is consistent with a previous study carried out shortly after the
476 establishment of our experiment (Roscher et al., 2009b). These results are in line with

477 hypothesis 3, although contrary to our expectation colonizer turnover rates did not depend on
478 sown diversity. In contrast to non-sown control plots, both colonizer immigration and
479 extinction rates decreased continuously and moderately through time (Fig. 3a-b). Both, mown
480 control plots and sown plots of the diversity experiment gradually accumulated a greater
481 number of internal colonists. External colonists generally declined over time, which is in line
482 with a study in weeded communities of the first three years of the Jena Experiment (Roscher
483 et al., 2009a). Consistent with the view that a colonization–competition trade-off is core to
484 succession processes (Tilman, 1988) and results from many studies of succession (Tilman,
485 1990), species with early-successional traits (i.e. annual life cycle, reproduction by seeds,
486 small seeds) dominated as colonists in species-poor, newly established experimental
487 communities, while mid-successional traits (perennial life cycle, taller growth, vegetative
488 reproduction) characterized later colonists and those in communities sown with greater
489 diversity (Roscher et al., 2015). Many colonists in the early years of our experiment were
490 species typical for ruderal and arable sites (Table A.1, Fig. A.3) and were present in the soil
491 seed bank of the experimental field. Later, internal colonists accounted for the largest
492 proportion of colonizing species, these were typically mid-successional grassland species
493 more tolerant to competition (Fig. 2d). The consistently negative relationship between
494 colonizer species richness and sown initial plant diversity, which was evident even after eight
495 years, was probably due to the greater stability of the resident communities when sown with a
496 larger number of mid-successional grassland species (Roscher et al., 2013). Nevertheless,
497 over time we found a gradual accumulation of species in communities sown with 1–16
498 species, which was weaker in plant communities initially sown with higher species richness,
499 suggesting that more open niches were available in these communities. Saturating levels of
500 species richness through species accumulation are often observed in secondary succession
501 (Tilman, 2004). Communities sown with all experimental species, however, gradually lost

502 species resulting in converging levels of species richness over time (Fig. A.2a).

503

504 **Taxonomic, phylogenetic and trait diversity**

505 Experiments with artificially assembled plant communities have shown that the colonization
506 of functionally similar species is more likely to be suppressed compared with the colonization
507 of functionally more different species, but so far these analyses have mostly been performed
508 on a functional-group level or have focussed on single species (e.g. Fargione et al., 2003;
509 Mwangi et al., 2007; Hooper and Dukes, 2010; Petermann et al., 2010). In the present study,
510 Rao's Q was applied as a continuous measure of trait diversity (FD_Q) and partitioned into the
511 contribution of residents, colonists and residents–colonists dissimilarity. Supporting our initial
512 hypothesis 4, FD_Q increased over time in all mown plots. In contrast, FD_Q declined after an
513 initial increase in unmown control plots. Thus, non-random assembly processes increased
514 functional dissimilarity and the chance for complementarity among species, which is in line
515 with previous analyses at the functional-group level. At the highest level of initially sown
516 species richness, however, FD_Q decreased after several years suggesting that declining species
517 richness **at the highest level of productivity** was due to the exclusion of weaker competitors
518 and that differences in competitive ability resulted in trait convergence (Grime, 2006; **Isbell et**
519 **al, 2009**). In spite of the remarkable stability of residents regarding their species richness,
520 partial FD_Q of residents declined in contrast to an increasing partial FD_Q of colonists. Thus,
521 colonists did not simply occupy “empty niche space”, but increasingly constrained the niche
522 space of residents. In line with the increased niche occupation by colonists, residents–
523 colonists trait dissimilarity decreased over time in communities initially sown as
524 monocultures or two-species mixtures. In contrast, trait dissimilarity between residents and
525 colonists increased over time with higher sown species richness, supporting the idea that
526 species are most likely to coexist if they are functionally different.

527 Phylogenetic diversity (Q_{Phylo}) also increased over time and converged at high levels, which is
528 in accordance with studies in biodiversity experiments in which weeding was stopped after
529 several years (Cadotte and Strauss, 2011; Allan et al., 2013). The initial decline in
530 communities with lower sown species richness was mainly due to a decrease in partial Q_{Phylo}
531 of colonists and suggested that the success of early colonists was controlled by interspecific
532 differences that were not covered by our trait matrix (Mayfield and Levine, 2010). Although
533 FD_Q and Q_{Phylo} showed parallel temporal trends, which can be expected given that most traits
534 showed phylogenetic conservatism (Table A.1), Q_{Phylo} did not decrease after several years at
535 high levels of sown species richness as observed in FD_Q . **These results support the notion that**
536 **traits and phylogeny may provide complementary information on species differences (Cadotte**
537 **et al., 2013),** i.e. species being similar in traits considered in FD_Q possess additional
538 phylogenetically conserved features that are important for their coexistence.

539

540 **Diversity–productivity relationships**

541 Strong diversity–productivity relationships are found if species are deliberately removed from
542 intact ecosystems. This is the basic idea of all biodiversity–ecosystem functioning
543 experiments, which simulate random species extinction by assembling communities with
544 reduced numbers of species (Schmid and Hector, 2004). In the present study we allowed the
545 experimentally reduced ecosystems to regenerate by admitting the experimentally
546 extinguished species to colonize. Our hypothesis was that the regenerated systems would not
547 show any strong diversity–productivity relationships **because assembly processes starting**
548 **from different initial compositions would lead to similarly high diversity and productivity**
549 (hypothesis 5). Varying diversity–productivity relationships may potentially be explained by
550 the reduced importance of positive selection and complementarity effects and a greater
551 importance of competitive exclusion in more “mature” natural communities (Jiang et al.,

2009). In our experiment, we found evidence for competitive exclusion in mixtures initially sown with 60 species, where **total** species richness as well as FD_Q declined after several years. Nevertheless, these communities maintained the highest productivity in all study years suggesting that at very high level a reduction of FD_Q does not result in reduced community productivity. **Interestingly, sown species richness as well as the realized number of resident species had consistently positive effects on the biomass production of resident species (Table 3, Fig. 6b).** This result is in line with the observed persistence of the positive relationship between sown species richness and their biomass production in a grassland biodiversity experiment, where weeding was stopped after several years. However, in this study colonists were predominantly non-native species (Huang et al., 2013), while the colonists in our study mainly consisted of native species or non-native species, which have a long history of introduction in the study area (Table. A.1). In our study, the biomass production of residents declined over time in communities sown with 1-16 species in parallel with a gradual decline in Q_{Simp} , FD_Q and Q_{Phylo} of residents (Fig. A.2 a, e, e), while these measures of diversity as well as productivity of residents remained more stable in the mixtures sown with 60 species. **Interestingly,** FD_Q reached the highest levels when colonization started in unsown plots yet these communities had low productivity throughout the study period. This is consistent with a previous experiment on ex-arable fields comparing non-sown plots with sown plots of low and high species richness (Lepš et al., 2007). Overall, however, partial diversity of residents and colonists, were reliable predictors of biomass production of residents and colonists of the respective species group, supporting the view that a greater diversity increases the chance for incorporating highly productive species. This is in line with common practice in agriculturally managed grasslands, where species with traits related to high biomass production are favoured **by sowing**, while promoting the extinction of other, unwanted species.

576 Although **total** species richness was the most important predictor of positive diversity effects
577 on productivity during the initial phase (Table A.3.), the diversity effects on community
578 biomass production disappeared over time as the systems with reduced sown diversity were
579 allowed to regenerate and accumulate similarly high levels of diversity as communities with
580 higher sown diversity (Fig. 6a). Interestingly, the trajectory from a strong to a weak diversity–
581 productivity relationship was not a smooth one. Instead, the proportion of explained variation
582 in community biomass production and the relative importance of different predictors
583 fluctuated between years. Most strikingly, positive effects of FD_Q on biomass production
584 peaked in the fourth year after sowing, but declined afterwards to even negative relationships
585 between FD_Q and biomass production. Thus, other aspects of community composition also
586 affect community productivity in the longer term and should be considered in future studies.

587

588 **Conclusions**

589 The aim of our study was to test the regeneration potential of plant communities after local
590 extinction events have reduced their diversity to different numbers and compositions of
591 species. We show that community assembly processes during recovery from the local species
592 pool are not random, but result in increased and convergent levels of phylogenetic diversity,
593 while trait diversity is limited through competitive exclusion at high levels of sown species
594 richness (Fig. 7). **Convergent high** levels of species richness, phylogenetic and trait diversity
595 among the communities are not associated with maximum community productivity suggesting
596 that “maturation” of the communities **starting regeneration from different initial compositions**
597 does not maximize productivity.

598

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604

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758 Table 1: List of functional traits used in analyses compiled from different sources (BiolFlor:
 759 Klotz et al., 2003; LEDA: Kleyer et al., 2008; Rothmaler, 2002; own measurements) and their
 760 completeness (i.e. proportion of species for which trait data were available)

Variable	Type of variable	Completeness
Traits related to growth		
Growth height	continuous (m)	100%
Specific leaf area	continuous ($\text{mm}^2_{\text{leaf}} \text{mg}^{-1}_{\text{leaf}}$)	97%
Root type	binary (0 = no taproot, 1 = taproot)	100%
N ₂ fixation	binary (0 = non, 1 = yes)	100%
Growth form	ordinal (1 = rosulate; 2 = semirosulate; 3 = without basal leaf rosette)	100%
Life form	ordinal (1 = annual; 2 = biennial or monocarpic perennial; 3 = perennial)	100%
Traits related to life-history		
Start of flowering period	ordinal (1 = before May; 2 = May; 3 = June; 4 = July)	99%
Duration of flowering period	ordinal (1 = two months or less; 2 = three months; 3 = four months; 4 = more than 4 months)	99%
Age of first flowering	ordinal (1 = less than 1 year; 2 = between 1-5 years, 3 = more than 5 years)	91%
Seed mass	continuous (mg)	94%
Seed bank longevity	continuous (between 0 and 1)	96%
Type of reproduction	ordinal (1 = by seed; 2 = mostly by seed, rarely vegetative; 3 = by seed and vegetative; 4 = mostly vegetative)	100%

761

762 Table 2: Mixed-effects model analyses of colonizer species richness (and partitioned into
 763 internal and external colonists), colonizer immigration, extinction and turnover rates between
 764 subsequent years, and taxonomic diversity (Q_{Simp}), phylogenetic diversity (Q_{Phylo}) and trait
 765 diversity (FD_Q) based on cover abundances (2002-2009) in spontaneously colonized control
 766 plots of different sizes either regularly mown or unmown.

Source of variation	Total colonizer species richness		Internal colonizer species richness		External colonizer species richness	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	2.49	0.115	13.47	<0.001 ↑	4.21	0.040 ↓
Plot size (S)	5.20	0.023 ↓	4.73	0.030 ↓	2.15	0.142
M x S	11.53	0.001	5.06	0.025	5.28	0.022
Year (linear)	6.29	0.012 ↑	74.57	<0.001 ↑	24.18	<0.001 ↓
Year x M	4.69	0.030	52.42	<0.001	4.61	0.032
Year x S	0.22	0.641	0.01	0.931	0.33	0.567
Year x M x S	6.29	0.012	17.29	<0.001	0.85	0.356
Source of variation	Colonizer immigration rate		Colonizer extinction rate		Colonizer turnover rate	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	1.74	0.188	0.46	0.498	<0.01	0.984
Plot size (S)	0.04	0.837	0.34	0.560	0.25	0.615
M x S	0.53	0.468	2.16	0.142	0.19	0.660
Year (linear)	46.75	<0.001 ↓	0.32	0.574	65.02	<0.001 ↓
Year x M	1.39	0.239	0.04	0.836	1.68	0.194
Year x S	0.92	0.337	4.64	0.031	6.47	0.011
Year x M x S	<0.01	0.965	0.84	0.360	0.03	0.864
Source of variation	Colonizer Q_{Simp}		Colonizer Q_{Phylo}		Colonizer FD_Q	
	L ratio	p	L ratio	p	L ratio	p
Unmown vs. mown (M)	0.61	0.435	0.29	0.588	8.15	0.004 ↑
Plot size (S)	26.68	<0.001 ↓	12.61	<0.001 ↓	2.47	0.116
M x S	8.61	0.003	6.54	0.011	13.18	<0.001
Year (linear)	9.19	0.002 ↑	8.97	0.003 ↑	2.31	0.129
Year x M	4.51	0.034	3.84	0.050	6.54	0.011
Year x S	1.34	0.247	0.87	0.351	<0.01	0.974
Year x M x S	7.54	0.006	8.04	0.005	4.55	0.033

767 Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood
 768 ratio tests (L ratio) that were applied to assess model improvement and the statistical
 769 significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the
 770 variables with management (unmown vs. mown), plot size (small vs. large) and year of the
 771 experiment.

772 Table 3: Mixed-effects model analyses of species richness (total, residents, colonists and
 773 colonists separated into internal and external species), colonizer immigration, extinction and
 774 turnover rates between subsequent years, and biomass production (community, residents,
 775 colonists) across experiment years (2002-2009) in large mown plots either spontaneously
 776 colonized or initially sown with different plant diversity.

Source of variation	Total species richness		Resident species richness		Total colonizer species richness		External colonizer species richness	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	0.05	0.816			3.50	0.061	1.78	0.183
Sown SR (log-linear)	22.98	<0.001 ↑	370.33	<0.001 ↑	86.37	<0.001 ↓	51.94	<0.001 ↓
Sown FG (linear)	3.14	0.077	0.57	0.452	3.71	0.054	1.90	0.168
Year (linear)	146.56	<0.001 ↑	20.36	<0.001 ↓	185.26	<0.001 ↑	384.07	<0.001 ↓
Y x non-sown vs. sown	1.97	0.160			1.72	0.190	0.55	0.460
Y x Sown SR (log-linear)	165.88	<0.001	4.55	0.033	130.31	<0.001	3.13	0.077
Y x Sown FG (linear)	4.45	0.035	7.13	0.008	6.09	0.014	0.24	0.624
Source of variation	Internal colonizer species richness		Colonizer immigration rate		Colonizer extinction rate		Colonizer turnover rate	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	2.44	0.118	0.02	0.892	0.82	0.365	1.32	0.251
Sown SR (log-linear)	66.01	<0.001 ↓	12.87	<0.001 ↓	4.91	0.027 ↑	2.72	0.099
Sown FG (linear)	0.25	0.617	1.21	0.271	0.02	0.902	0.92	0.337
Year (linear)	850.32	<0.001 ↑	54.45	<0.001 ↓	160.90	<0.001 ↓	257.95	<0.001 ↓
Y x non-sown vs. sown	0.10	0.756	2.65	0.104	3.38	0.066	0.06	0.809
Y x Sown SR (log-linear)	84.24	<0.001	7.72	0.006	14.67	<0.001	0.05	0.820
Y x Sown FG (linear)	9.97	0.002	1.37	0.241	3.22	0.073	0.45	0.503
Source of variation	Community biomass production		Resident biomass production		Colonizer biomass production			
	L ratio	p	L ratio	p	L ratio	p		
Non-sown vs. sown	2.62	0.105			3.72	0.054		
Sown SR (log-linear)	16.57	<0.001 ↑	55.66	<0.001 ↑	74.92	<0.001 ↓		
Sown FG (linear)	1.00	0.318	3.53	0.060	0.54	0.461		
Year (linear)	1.74	0.187	127.30	<0.001 ↓	194.65	<0.001 ↑		
Y x non-sown vs. sown	0.02	0.893			5.99	0.014		
Y x Sown SR (log-linear)	2.60	0.107	40.66	<0.001	3.10	0.078		
Y x Sown FG (linear)	0.21	0.646	4.65	0.031	0.16	0.688		

777 Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood
 778 ratio tests (L ratio) that were applied to assess model improvement and the statistical
 779 significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the
 780 variables between non-sown and sown plots, with sown species richness (= SR), functional
 781 group number (FG) and year of the experiment (Y).

782 Table 4: Mixed-effects model analyses of taxonomic diversity Q_{Simp} , phylogenetic diversity
 783 Q_{Phylo} and trait diversity FD_Q across all species, separately for residents and for colonists and
 784 as residents-colonists dissimilarity based on cover abundances across experiment years (2002-
 785 2009) in large mown plots either spontaneously colonized or initially sown with different
 786 plant diversity.

Source of variation	Total Q_{Simp}		Partial resident Q_{Simp}		Partial colonizer Q_{Simp}		Between resident-colonizer Q_{Simp}	
	L ratio	p	L ratio	p	L ratio	p		
Non-sown vs. sown	0.02	0.881			8.05	0.005 ↓		
Sown SR (log-linear)	71.43	<0.001 ↑	143.79	<0.001 ↓	126.99	<0.001 ↓	3.61	0.057
Sown FG (linear)	2.22	0.136	5.55	0.019 ↓	6.15	0.013 ↓	0.74	0.390
Year (linear)	148.74	<0.001 ↑	84.20	<0.001 ↓	201.78	<0.001 ↑	6.61	0.010
Y x non-sown vs. sown	1.88	0.170			2.97	0.085		
Y x Sown SR (log-linear)	75.41	<0.001	1.04	0.307	41.87	<0.001	33.65	<0.001
Y x Sown FG (linear)	0.03	0.853	0.04	0.840	1.07	0.300	0.30	0.584
Source of variation	Total Q_{Phylo}		Partial resident Q_{Phylo}		Partial colonizer Q_{Phylo}		Between resident-colonizer Q_{Phylo}	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	0.08	0.773			7.27	0.007 ↓		
Sown SR (log-linear)	53.00	<0.001 ↑	153.71	<0.001 ↑	128.66	<0.001 ↓	3.37	0.066
Sown FG (linear)	0.68	0.411	11.92	0.001 ↑	6.12	0.013 ↓	0.35	0.554
Year (linear)	139.66	<0.001 ↑	77.90	<0.001 ↓	181.70	<0.001 ↑	5.36	0.021 ↑
Y x non-sown vs. sown	1.72	0.189			2.74	0.098		
Y x Sown SR (log-linear)	53.95	<0.001	0.80	0.371	38.46	<0.001	31.95	<0.001
Y x Sown FG (linear)	4.94	0.026	0.09	0.765	1.33	0.249	0.05	0.820
Source of variation	Total FD_Q		Partial resident FD_Q		Partial colonizer FD_Q		Between resident-colonizer FD_Q	
	L ratio	p	L ratio	p	L ratio	p	L ratio	p
Non-sown vs. sown	1.21	0.271			6.77	0.009 ↓		
Sown SR (log-linear)	0.12	0.727	130.13	<0.001 ↑	127.83	<0.001 ↓	4.91	0.027 ↓
Sown FG (linear)	0.55	0.460	19.53	<0.001 ↑	7.74	0.005 ↓	0.03	0.855
Year (linear)	109.01	<0.001 ↑	64.89	<0.001 ↓	351.30	<0.001 ↑	31.20	<0.001 ↑
Y x non-sown vs. sown	5.11	0.024			1.90	0.168		
Y x Sown SR (log-linear)	82.57	<0.001	0.08	0.775	53.43	<0.001	14.01	<0.001
Y x Sown FG (linear)	13.05	<0.001	0.98	0.323	4.24	0.039	0.48	0.489

787 Models were fitted by stepwise inclusion of fixed effects. Listed are the results of likelihood
 788 ratio tests (L ratio) that were applied to assess model improvement and the statistical
 789 significance of the fixed effects (p values). Arrows indicate increase (↑) or decrease (↓) of the
 790 variables between non-sown and sown plots, with sown species richness (= SR), functional
 791 group number (FG) and year of the experiment (Y).

792 Figure captions

793

794 Figure 1: Colonizer species richness (a), partitioned into internal colonizer species (b), and
795 external colonizer species (c), colonizer immigration rates (d), colonizer extinction rates (e),
796 colonizer turnover rates (f), taxonomic diversity Q_{Simp} (Simpson index D) (g), phylogenetic
797 diversity Q_{Phylo} (h), and trait diversity FD_Q (i) across experiment years (2002-2009) in large
798 and small spontaneously colonized control plots (without seed addition), either mown or
799 unmown. Values are based on maximum annual species abundances from replicated
800 inventories (9 m^2) and represent arithmetic means ($\pm 1 \text{ SE}$) per treatment.

801

802 Figure 2: Total species richness (a), resident species richness (b), colonizer species richness
803 (c), partitioned into internal colonists (d), and external colonists (e) across experiment years
804 (2002-2009) in large mown plots either spontaneously colonized or initially sown with
805 different levels of plant diversity. Values are based on replicated species inventories on
806 subplots of $2.00 \times 2.25 \text{ m}$ size and represent arithmetic means ($\pm 1 \text{ SE}$) across all assemblages
807 per sown species-richness level.

808

809 Figure 3: Colonizer immigration rates (a), extinction rates (b), and turnover rates (c) between
810 subsequent years (from 2002-2009) in large mown plots either spontaneously colonized or
811 initially sown with different levels of species richness. Values are based on replicated species
812 inventories on subplots of $2.00 \times 2.25 \text{ m}$ size and represent arithmetic means ($\pm 1 \text{ SE}$) across
813 all assemblages per sown species-richness level.

814

815 Figure 4: Taxonomic diversity Q_{Simp} (Simpson index) (a), taxonomic dissimilarity between
816 residents and colonists (b), phylogenetic diversity Q_{Phylo} (c), phylogenetic dissimilarity

817 between residents and colonists (d), trait diversity FD_Q (e), and trait dissimilarities between
818 residents and colonists (f) across experiment years (2002-2009) in large mown plots either
819 spontaneously colonized or initially sown with different levels of plant diversity. Values are
820 based on maximum species abundances from replicated inventories on subplots of 2.00×2.25
821 m size and represent arithmetic means (± 1 SE) across all assemblages per sown species-
822 richness level.

823

824 Figure 5: Community biomass production (a), partitioned into biomass production of residents
825 (b), and biomass production of colonists across experiment years (2003-2009) in large mown
826 plots either spontaneously colonized or initially sown with different levels of plant diversity.
827 Values represent arithmetic means (± 1 SE) across all assemblages per sown species-richness
828 level. Note that no data were available for 2008 and for large mown control plots in 2003 and
829 2004.

830

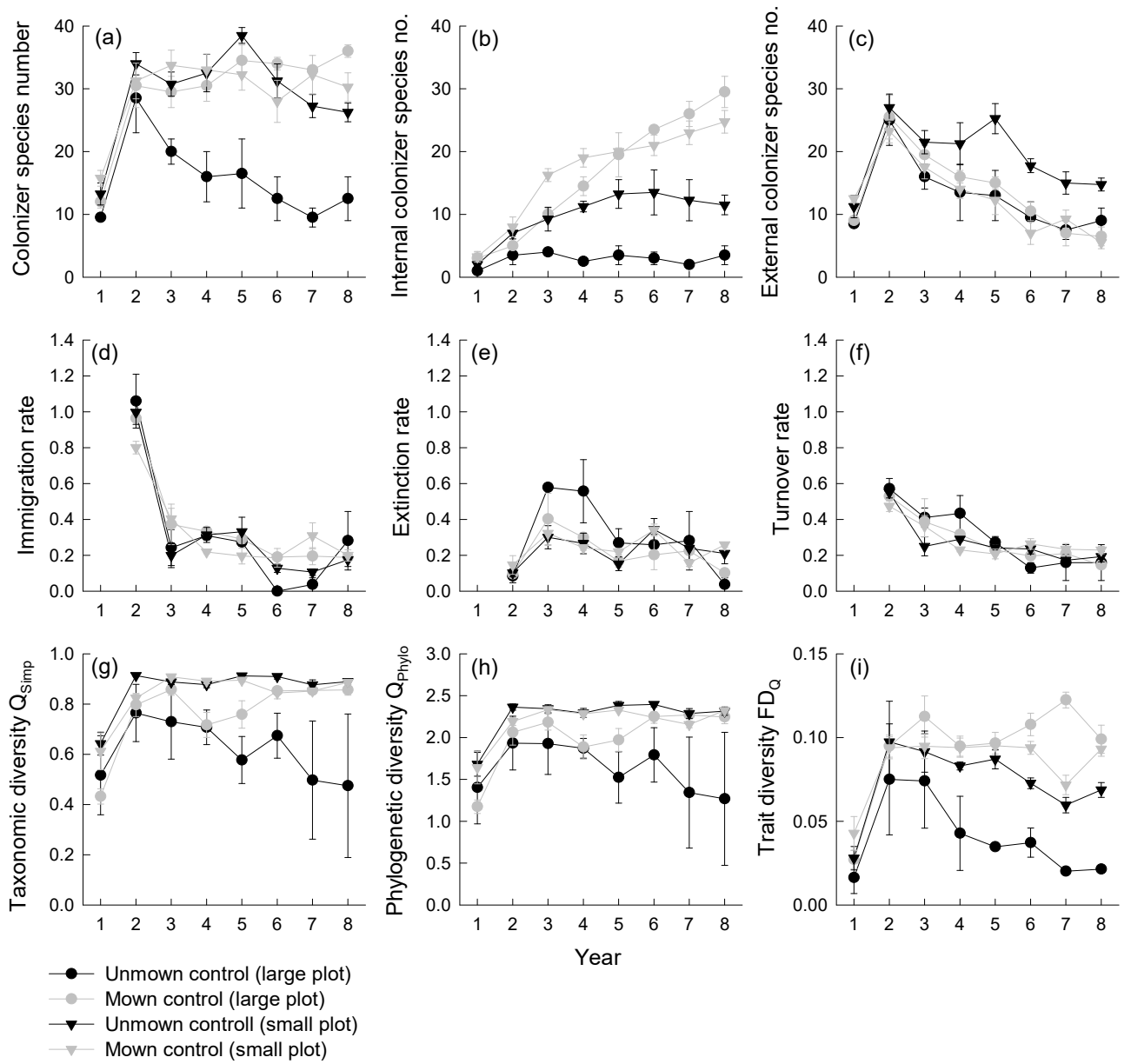
831 Figure 6: Standardized regression slopes (± 1 SE) using **total** species richness, taxonomic
832 diversity (Q_{Simp}), phylogenetic diversity (Q_{Phylo}) and trait diversity (FD_Q) as predictors for (a)
833 community biomass production, and **the respective partial variables as predictors for** (b)
834 biomass production of residents, and (c) biomass production of colonists in large mown plots
835 per experiment year.

836

837 Figure 7: Illustration of community assembly processes in naturally colonized experimental
838 grasslands sown with different diversity. The first three columns show average temporal
839 changes in species richness, trait diversity (FD_Q), phylogenetic diversity (Q_{Phylo}) and biomass
840 production differentiated into the contribution of residents and colonizers exemplarily for low
841 diversity (two sown species), medium diversity (eight sown species) and high diversity (60

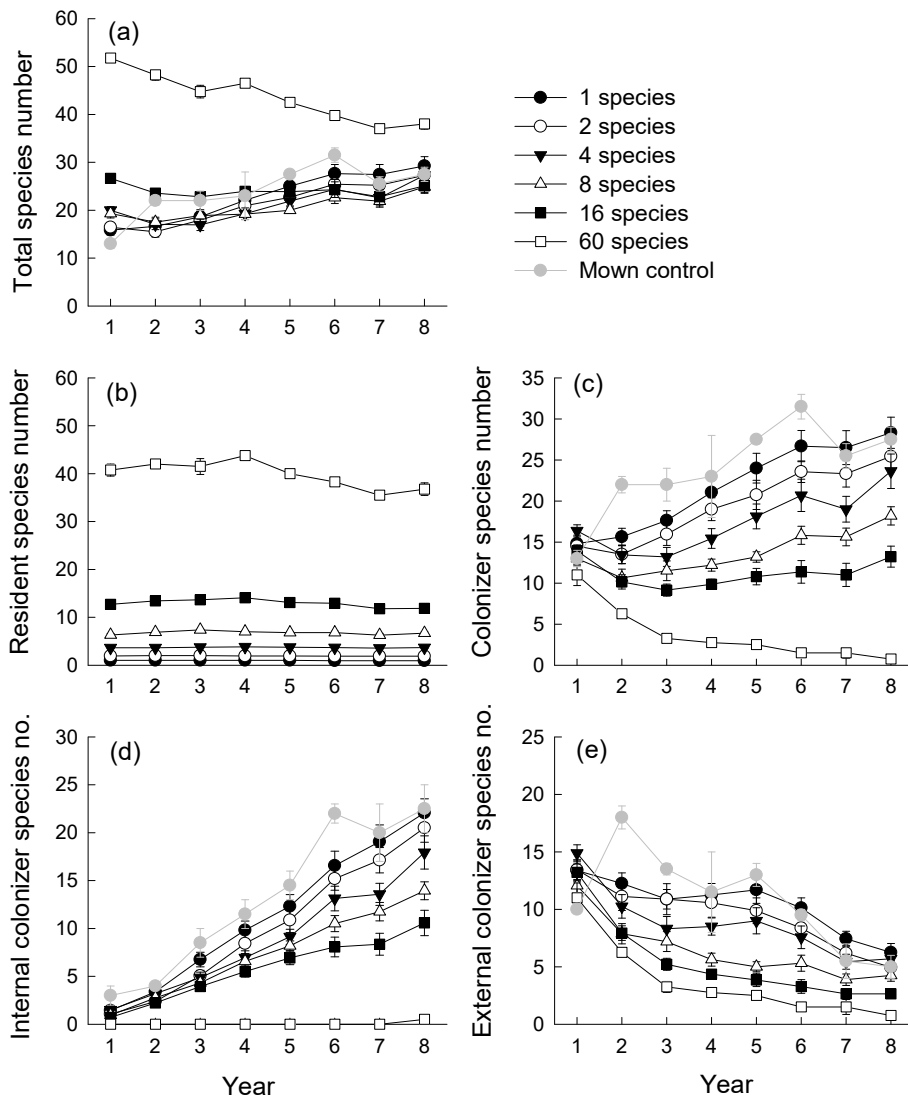
842 sown species). The right column schematically summarizes **convergence** in total species
843 richness, FD_Q and Q_{Phylo} across low, medium and high sown diversity and associated levels of
844 biomass production through time.

845 Figure 1



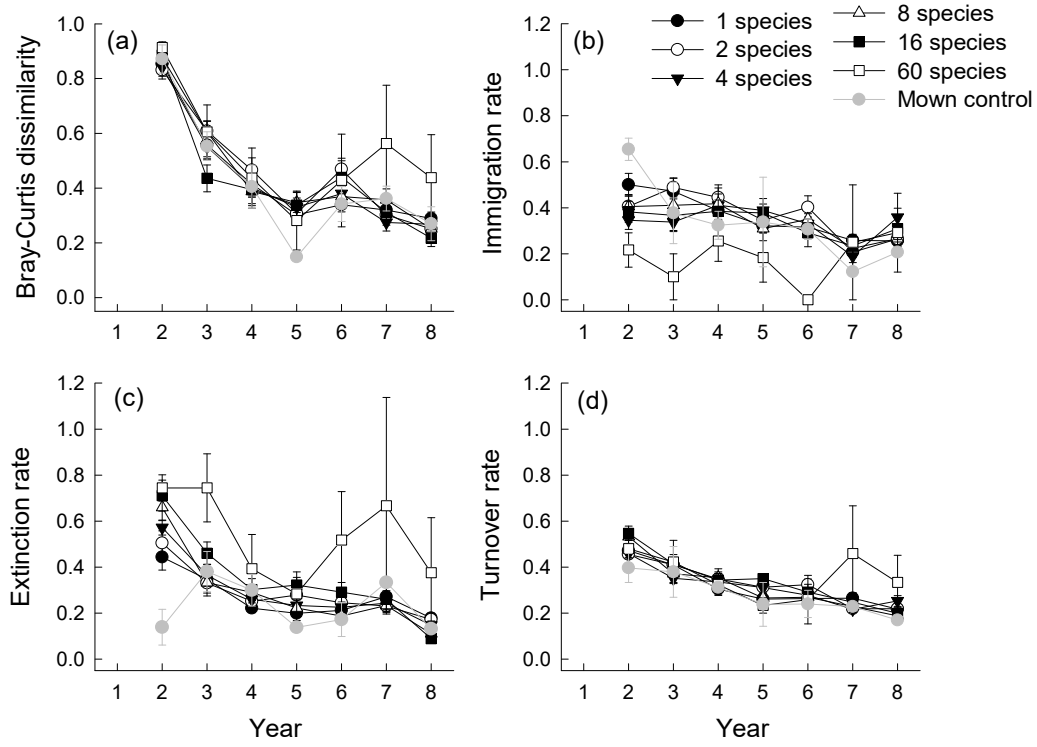
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848 Figure 2



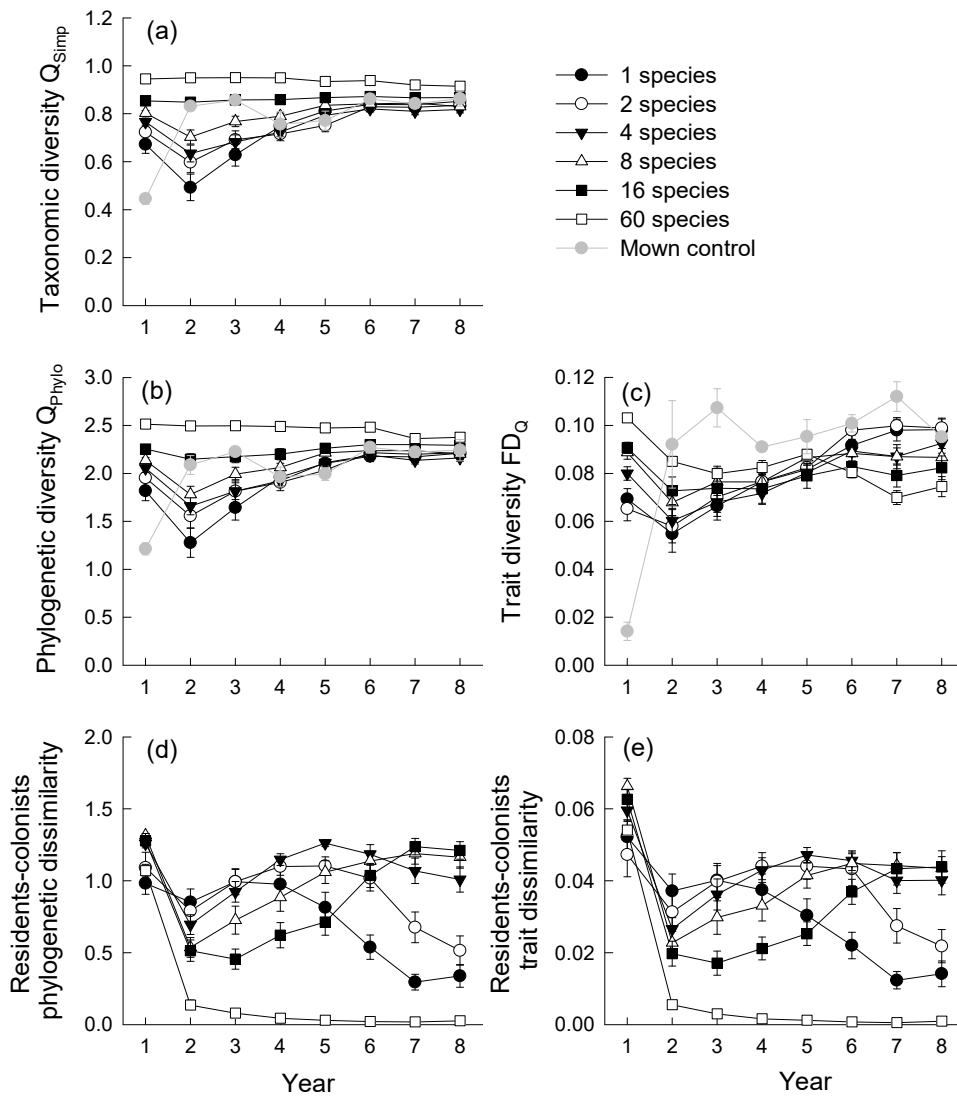
849

850 Figure 3



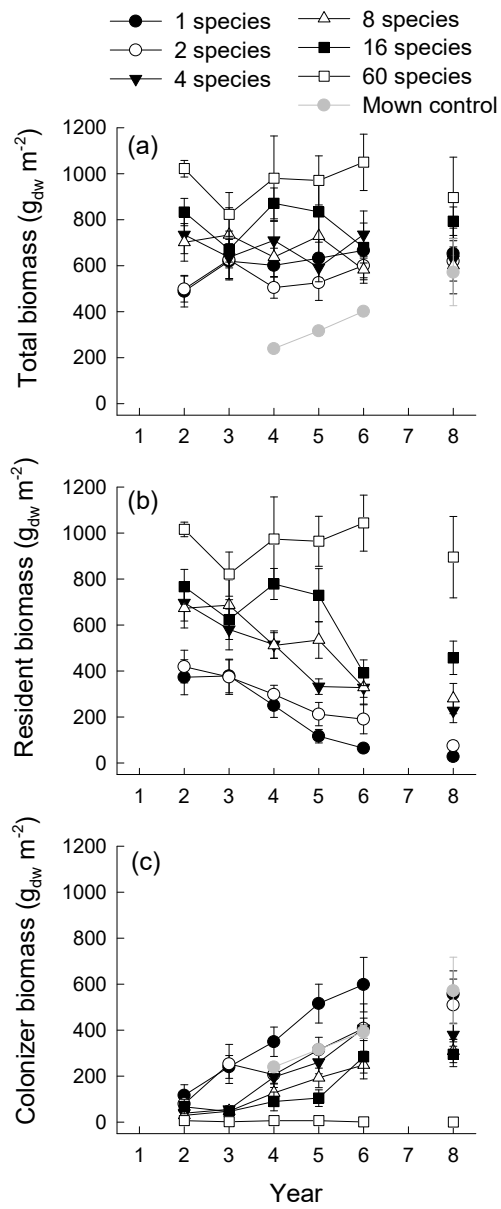
851

852 Figure 4



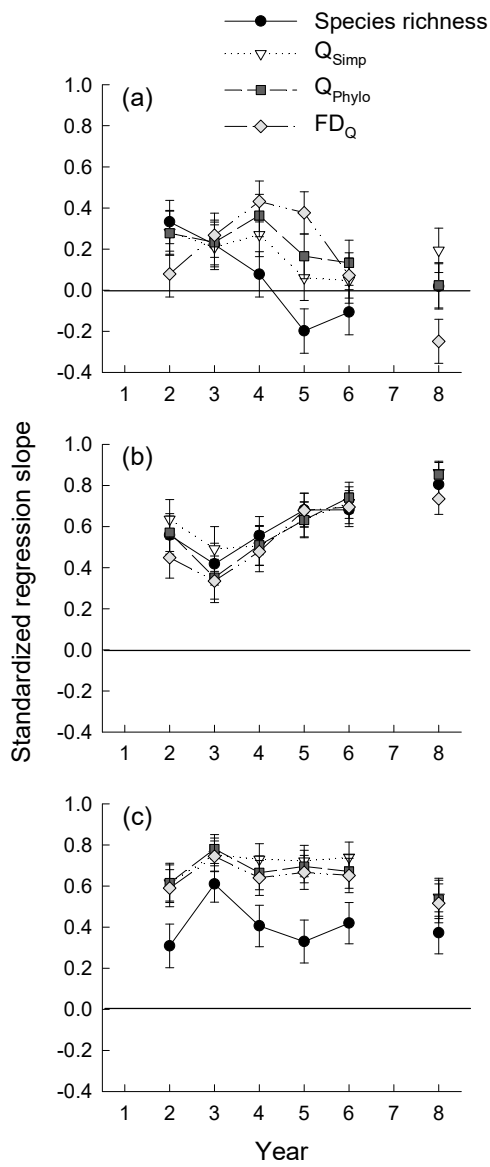
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854 Figure 5



855

856 Figure 6



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858

