1 **Species interactions and random dispersal rather than habitat filtering**

2 **drive community assembly during early plant succession**

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31 **Abstract**

32 Theory on plant succession predicts a temporal increase in the complexity of spatial

33 community structure and of competitive interactions: initially random occurrences of early

34 colonising species shift towards spatially and competitively structured plant associations in

35 late successional stages. Here we use long-term data on early plant succession in a German

36 post mining area to disentangle the importance of random colonisation, habitat filtering, and

37 competition on the temporal and spatial development of plant community structure. We used

38 species co-occurrence analysis and a recently developed method for assessing competitive

39 strength and hierarchies (transitive versus intransitive competitive orders) in multispecies

40 communities. We found that species turnover decreased through time within interaction

41 neighbourhoods, but increased through time outside interaction neighbourhoods. Successional

42 change did not lead to modular community structure. After accounting for species richness

43 effects, the strength of competitive interactions and the proportion of transitive competitive

44 hierarchies increased through time. Although effects of habitat filtering were weak, random

45 colonization and subsequent competitive interactions had strong effects on community

46 structure. Because competitive strength and transitivity were poorly correlated with soil

47 characteristics, there was little evidence for context dependent competitive strength associated

48 with intransitive competitive hierarchies.

49

50 **Running title:** Plant community structure in early plant succession

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54

55 **Introduction**

56   Temporal change in community structure is driven by three major processes: 1) filtering

57 of species triggered by abiotic habitat and niche characteristics (Keddy 1992, Maire et al.

58 2012), 2) changes in the strength of positive and negative species interactions (Callaway and

59 Walker 1997), and 3) differential colonisation (Butaye et al. 2001, Bochet et al. 2007). These

60 processes comply with the familiar successional models of facilitation, tolerance, or inhibition

61 (Connell and Slatyer 1977) as well as many other sequences (Grime 2001, Meiners et al.

62 2015). Many studies postulate a temporal increase in the frequency of competitive

63 interactions and in the spatial complexity of community structure, from initially random

64 occurrences of early colonisers towards spatially segregated and competitively structured

65 associations in late successional stages (Baasch et al. 2009, del Moral 2009, Zaplata et al.

66 2013).

67   However, absence of species segregation does not necessarily imply a low impact of

68 competition. Most ecological studies assume a fully transitive order of species abundances in

69 which lower ranking species are always weaker competitors as compared to all higher ranking

70 ones (A>B>C). Consequently, communities of identical species composition should have

71 identical competitive, and consequently abundance hierarchies, among several sites of similar

72 ecological characteristics. However, this argument it too simplistic. Context dependent

73 competitive strength (Chamberlain et al. 2014), priority effects and founder control (Palmer et

74 al. 1997, Perry et al. 2003), and competitive loops (A>B>C>A) can be important in

75 multispecies communities and can substantially alter competition hierarchy, therefore weak

76 competitors to coexist with strong ones (Huisman et al. 2001, Kerr et al. 2002, Laird and

77 Schamp 2006, Reichenbach et al. 2007, Allesina and Levine 2011,Soliveres et al. 2015).

78   Most existing studies on either strongly hierarchical or intransitive competition networks

79 assume competitive interactions to be invariant across differing environmental conditions (but

80 see Bowker et al. 2010, Soliveres et al. 2011, Ulrich et al. 2014a). Using a Markov chain

81 model of invariant competitive strength, Ulrich et al. (2014b) showed that such invariant

82 hierarchies, whether transitive or intransitive, predict similar abundance hierarchies among

83 sites and do not generate species spatial segregation as predicted by competition-based

84 assembly rules models (Diamond 1975). On the other hand, at a variety of spatial scales,

85 replicated assemblages usually exhibit evidence for non-random species segregation, with

86 some pairs of species co-occurring less often than expected by chance, even if they do not

87 form perfect checkerboards (Ulrich and Gotelli 2010, 2013, Zaplata et al. 2013).

88   These conflicting results on species segregation can be reconciled if species competitive

89   hierarchies vary in space or time. Context-dependent competitive strength (reviewed in

90   Chamberlain et al. 2014), in which environmental conditions alter competitive hierarchies in

91   space or time, generates variation in the dominance ordering of species, which can lead to

92   spatial or temporal segregation of species pairs. Consequently, the degree of segregation

93   should be positively correlated with the variability of these environmental factors. The

94   strength of such correlations might therefore identify those factors that directly influence

95   competitive strength.

96   In heterogeneous environments –even within that spatial scale where species are able to

97   interact directly (interaction neighbourhoods according to Addicott 1987) – habitat filtering

98   may override competitive effects, resulting in a variety of patterns in spatial species co-

99   occurrences other than segregation. First, shared ecological requirements or mutualistic

100   interactions might promote small-scale positive species associations (Horner-Devine et al.

101   2007) resulting in a modular spatial distribution of species. Second, if dispersal overrides

102   competitive interactions, species richness is predicted to follow the gradient of local carrying

103   capacity (habitat quality; Elton 1958, Mata et al. 2013) leading to a nested pattern of species

104   occurrences in which the composition of species-poor patches is a proper subset of the

105   composition of species-rich patches (Patterson and Atmar 1986, Ulrich et al. 2009). In theory,

106   nestedness, modularity, and species segregation are therefore three different (although not

107   mutually exclusive) patterns of community organisation (Ulrich and Gotelli 2013). In

108   practice, distinguishing statistically among these patterns is difficult (Ulrich and Gotelli

109   2013). Natural communities will often be intermediate between these extremes, depending on

110   trade-offs among species competition, dispersal, and habitat filtering (Leibold and Mikkelson

111   2002, Presley et al. 2010, Ulrich and Gotelli 2013).

112   Here we use a unique data set on early plant succession (Zaplata et al. 2010, 2013) to

113   assess the change in plant community structure and patterns of species co-occurrences during

114   the first seven years of community assembly. The study system and the specific sampling

115   design allows for the first time a detailed analysis of the interplay between temporal

116   community assembly, spatial patterns of co-occurrences, and changes in competitive strength.

117   Previously we used these data to detect a temporal progression towards large-scale negative

118   spatial species associations (Zaplata et al. 2013) and towards increased utilization of plant

119   trait space (Ulrich et al. 2014c). We further detected variability in phylogenetic community

120   composition at small spatial scales that could be traced back to important soil attributes

121   (Ulrich et al. 2014d).

122   Using co-occurrence and competitive strength analyses, we here link the strength of

123 competitive interactions to the trends in community assembly at three spatial scales. We

124 predict that

    1. Segregation due to competitive interactions will be apparent only at small spatial

126   scales. At large spatial scales, environmental variability should override the effect of

127   direct competitive interactions.

    2. As a consequence of (1), spatial and temporal species turnover should increase and the

129   degree of nestedness should decrease with increasing spatial scale.

    3. In the presence of small-scale habitat heterogeneity, the decrease in nestedness should

131   be accompanied by an increase in modularity.

    4. Along with the overall increase in species richness through the course of succession,

133   the importance of competitive interactions, and the frequency of intransitive

134   competitive loops should increase in time.

135

Material and Methods

137 *Study area and sampling*

138   From 2005 to 2011, we studied the early vegetation succession in a six ha constructed

139 catchment *Chicken Creek* (German: Hühnerwasser), located in an open-cast lignite mine in

140 NE Germany. Sand and loamy sand material originating from Pleistocene sediments was used

141 for the construction of the 1-3.5 m top layer of the catchment to cover a 1-1.5 m clay layer

142 (details in Gerwin et al. 2009).

143   Immediately after the top layer of the catchment was finished in October 2005, 119 25-m^2

144 cells (Fig. 1A), and, in their corners, a total of 474 plots of 1-m^2 (Zaplata et al. 2010) were

145 established (Fig. 1B). This arrangement caused that each plot had three neighbours in adjacent

146 cells at a distance of three meters forming a set of four plots (Fig. 1B). The distances between

147 the sets were 15 m. For the present study we used 107 of such sets. This number is not

148 identical to the number of 25-m² cells because we removed incomplete sets and a few water-

149 logged sets in the southern part of the catchment with a small area of surface water.

150   Vegetation was first recorded in 2005 in 360 1-m^2 plots, and since 2006 annually in all

151 plots and cells. For each species, we estimated the cover degree according to a modified

152 Londo scale (Londo 1976; 0.1: ≤0.1%; 0.5: >0.1–0.5%; 1: >0.5–1%; 2: >1–2%, in 1% steps

153 up to 10; 15: >10–15%, in 5% steps up to 30; 40: >30–40%, in 10% steps up to 100).

154 Bryophyta and Marchantiophyta were not identified to lower taxonomic levels. To study the

155 influence of initial substrate conditions on plant community assembly, we sampled the upper

156   30 cm of the substrate exactly at the grid immediately after completion of construction, before

157   the vegetation became established. Soil properties such as pH, texture, and carbonate content

158   have been previously shown to be important drivers of plant community assembly in this

159   study area (Zaplata et al. 2013, Ulrich et al. 2014c, d). Thus, we related these soil properties

160   to our metrics of community structure. To assess the variability in species richness among

161   plots and sets, we used the index of Lloyd ($J = \frac{s^2}{\bar{x}^2} - \frac{1}{\bar{x}} + 1$, where s denotes the standard

162   deviation and $\bar{x}$ the mean number of species; Lloyd 1967). Values of Lloyd's index less than

163   1.0 indicate species richness distributions more equal (overdispersed), and values greater than

164   1.0 more clumped (underdispersed), than expected from a Poisson random process. The raw

165   data used for all analyses is available as electronic supplement A.

166

167   *Metrics of community structure*

168   For all 25-m^2 cells, sets (4-m^2), and plots (1-m^2), we constructed species abundances

169   matrices (species in rows, samples in columns) for each study year. Thus, the single matrix

170   for the 25-m^2 cells contained 119 columns, the matrices for the sets (4-m^2) 107 columns, and

171   the matrices for the plots (1-m^2) between 360 and 426 columns. The set scale provided

172   therefore information on small scale spatial variability in plant community structure, whereas

173   the plots and cells captured different levels of resolution at the catchment scale. For each

174   matrix, we estimated the degree of species segregation (negative species associations) using

175   the abundance-**w**eighted **C**-**s**core (WCS; abbreviated CA_{st} in Ulrich and Gotelli 2010). The

176   WCS is a normalized count of the number of abundance checkerboard submatrices

177   ($\{\{a,b\},\{c,d\}\}$ in which a to d represent species relative abundances and either $a > c$ and $d > b$

178   or $a < c$ and $d < b$. A high WCS score is therefore an indication of negative species

179   association.

180   Nestedness refers to the ordered loss of species along a focal environmental or ecological

181   gradient (Patterson and Atmar 1986, Ulrich et al. 2009) and is therefore opposite (although

182   not mutually exclusive) to species turnover (Ulrich and Gotelli 2013). Below we quantified

183   the degree of nestedness using the standard NODF (**n**estedness from **o**verlap and **d**ecreasing

184   **f**ill) metric, which is a normalised count of the degree of species overlap among the sequence

185   of plots ordered according to decreasing species richness (Almeida-Neto et al. 2008). NODF

186   ranges from zero (perfect species turnover) to 1 (perfect nestedness).

187   'Seriation' sorts rows and columns of a matrix in a way that maximizes the number of

188   presences along the matrix diagonal (Leibold and Mikkelson 2002). This diagonal is

189 equivalent to the first axis of a correspondence analysis. Ulrich and Gotelli (2013) and Ulrich

190 et al. (2014a) showed that the rank correlation of row and column positions of all non-empty

191 cells in the 'seriated' matrix is then a measure of directional species segregation (species

192 turnover). Following Ulrich and Gotelli (2013), we used the respective coefficient of

193 determination R^2 as the test statistic for species turnover across our study plots.

194   Metrics of species co-occurrences like R^2, NODF, and WCS are constrained by matrix

195 geometry (Gotelli and Ulrich 2012) and cannot be compared directly. Therefore, we used a

196 null model approach (Gotelli and Ulrich 2012) and used the effect sizes of these metrics as the

197 differences of observed and expected metric in the subsequent analyses. The expected values

198 were calculated by using a null model that randomises the focal matrix by placing individuals

199 into the plots proportionally to overall species abundances until the total number of

200 individuals of each species is reached. Ulrich and Gotelli (2010) advocated this null model

201 (termed IT) for abundance data as it best accounted for the effects of *a priori* unequal

202 occurrences probabilities (the mass effect).

203   We inferred possible competitive interactions of the species by the approach of Ulrich et

204 al. (2014b). Under the assumption that abundances are solely caused by competitive

205 interactions, these method allows to infer the underlying pairwise competition matrix from a

206 given abundance distribution. For doing this, the method uses a back engineering approach

207 using a large number of randomly constructed candidate matrices of competitive strengths,

208 from which the ones that best predicts the observed abundance distribution are selected.

209 Following Ulrich et al. (2014b) we calculated for each plot, set, and cell 100,000 random

210 species × species competitive strengths matrices, translated these into a column-stochastic

211 transition matrix, and used a Markov chain model to predict species abundances from this

212 transition matrix (see Ulrich et al. 2014b and Soliveres et al. 2015 for computational details).

213 For each plot, set, and cell we compared the predicted and observed species abundances by

214 rank order correlation (r_C) and chose the best-fitting competition matrix to assess the

215 maximum impact of competitive interactions on community assembly (Soliveres et al. 2015).

216 High values of r_C point therefore to a good match of the competitive strength matrix with the

217 observed matrix of species abundances and therefore to a higher importance of interspecific

218 competition as driver of species abundance distributions, whereas low r_C values imply a minor

219 importance of competition for community assembly (Ulrich et al. 2014b). Importantly, as the

220 predicted abundance distributions are derived from the observed ones, high r_C scores do not

221 exclude the possibility than factors other than competition influence observed abundances.

222 However, low r_C score unequivocally indicate that no competitive strength matrix is able to

223 predict observed abundances and that competition plays at most a minor role in community

224 assembly. Further, we calculated the metric

225 $$\tau_C = \frac{2N(c_{ij} < c_{ji})}{m(m-1)} \qquad (i < j) \qquad (3)$$

226 in which the entries c_{ij} are from the competition matrix ($c_{ij} = (1 - c_{ji})$) and denote the

227 probability that species i replaces species j in a competitive interaction. τ_C quantifies the

228 proportion of transitive pairwise interactions (number of species triads without a loop

229 [A<B<C] regarding the total number of possible species triads) in the pairwise competition

230 matrix (Ulrich et al. 2014b). The higher τ_C is, the more hierarchical (i.e., transitive) is the

231 competition network. Ulrich *et al.* (2014b) found values of $\tau_C > 0.95$ to indicate a fully

232 transitive competitive hierarchy. In contrast, a low τ_C indicates intransitive competitive

233 interactions.

234

235 *Linking metrics of turnover, dominance, and competitive strength*

236   We used general linear modelling (GLM, orthogonal sums of squares) at the set (4-m^2)

237 and cell (25-m^2) levels to explore the effects of small-scale habitat heterogeneity and

238 competitive strength on patterns of species co-occurrence. To account for the spatial non-

239 independence of the plots, we used spatial eigenvector mapping (Hawkins 2012) and included

240 the dominant eigenvector EV1 of the Euclidean distance matrix as an additional predictor

241 variable in the models. This eigenvector explained 83% of variance in spatial structure.

242 Multicollinearity among the variables was always low.

243   During subsequent study years, samples were taken on the same plots, as is required for

244 any real-time series. Consequently, temporal autocorrelation might influence our results by

245 artificially inflating the degrees of freedom. As soil conditions were also and inevitably

246 autocorrelated in time, we hesitated to use a simple nested GLM design. Nevertheless, to

247 account for this type of temporal pseudo-replication we followed a similar approach to Ulrich

248 et al. (2014c) and restricted the degrees of freedom in the parametric t-tests for all single

249 predictors to the total number of 1-m^2 plots (426 instead of >1280) to minimize the inflation

250 of the temporal degrees of freedom and the possible bias when estimating *p*-values.

251   Next, we related our metrics of competitive strength to patterns of species spatial co-

252 occurrences using the regression model

253     $Y = a_0 + a_1 Species + a_2 Carbonate + a_3 pH + a_4 Sand + a_5 EV1 + a_6(\tau_C)$

254 in which the dependent variable Y was the effect size of WCS, NODF, or R^2. We applied this

255 regression model to each study year to get information on how the relationship between τ_C

256 and Y changed during succession while accounting for species richness and substrate

257 characteristics. Finally, we used Mantel correlations applied to the set level to assess whether

258 spatial variability in competitive strength (r_C, τ_C) and co-occurrence (WCS, NODF, R^2)

259 metrics was dependent on the spatial distances and the variability in substrate variables

260 (carbonate, pH, sand). General and generalised linear models were calculated using Statistica

261 (Statsoft, Tulsa, USA), whereas co-occurrence analyses were performed with the Turnover

262 and NODF software applications, freely available at www.ulrichw.umk.pl.

263

264 **Results**

265 *Trends in community structure*

266   Total species richness increased from 16 species initially in 2005 to 141 species in 2011,

267 with an average richness per m^2 of 0.05±0.35 species in 2005 to 14.8±4.4 (mean ± standard

268 deviation) in 2011. Variability in species richness among the 1-m^2 plots, 4-m^2 sets, and 25-m^2

269 cells were in all years not significantly different from a Poisson random expectation (all

270 bootstrapped Lloyd index values were not significantly different from 1.0 at p < 0.05).

271   The increase in species richness through time was accompanied by a constant change in

272 the pattern of species co-occurrences (Fig. 2). Across time, species spatial turnover decreased

273 (Fig. 2A) within the sets, but increased among them (Fig. 2B). Since 2008, turnover at the set

274 level was, on average, less than expected from the null assumption (bootstrapped t-tests: P <

275 0.001, Fig. 2A). Turnover was always lower than expected by the null model when calculated

276 among the sets (Fig. 2B). This comparably low turnover was accompanied by increasing

277 nestedness within and between the sets (positive effect sizes, Figs. 3C, D), although there was

278 no significant temporal trend in NODF. The WCS metric that quantifies spatial segregation

279 with respect to species abundances did not change significantly through time at the set level

280 (Fig. 2 E) but increased above this level (Fig. 2F). Within the sets, variability of all three

281 metrics decreased in time (Fig. 2A, C, E).

282   The GLM approach confirmed these spatial and temporal trends in the patterns of species

283 co-occurrences (Tab. 1): time accounted for 22.8% to 46.4% and spatial scale for 0.1 to

284 18.7% of variance in species co-occurrences. The significant year × scale interaction terms for

285 R^2 and NODF indicate that temporal patterns in species co-occurrences were spatial- and

286 temporal-scale specific. *Post-hoc* comparisons identified particularly strong differences in R^2

287 and NODF between the sets for the years 2007 and 2008 (Tukey tests: P < 0.001). The three

288 metrics were not significantly influenced by species richness and substrate attributes (Tab. 1).

289

290 *Scale matters when looking at competition and community structure during succession*

291   The r_C metric decreased with increasing species richness and was independent of

292 substrate attributes (Tab. 2). Age and spatial scale together explained as much as 64% of the

293 variance in r_C. At the set level, the importance of interspecific competition for the assembly of

294 the studied communities was $r_C = 0.56 \pm 0.16$ (mean ± standard deviation), meaning that 56%

295 of the variance in observed abundances could be explained by competition only, and did not

296 increase during succession (Fig. 2 G). At the 25-m^2 cell resolution, r_C significantly increased

297 during succession (mean $r_c = 0.83 \pm 0.17$; Fig. 2H).

298   The proportion of transitive competitive hierarchies increased during succession (Fig. 2I,

299 J) although this was statistically not significant at the 1-m^2 plot and 25-m^2 cell levels (Fig. 2I:

300 both $P > 0.05$). Full transitivity was most frequent at the set level (24.9% of communities, Fig.

301 2I) and decreased at the smaller spatial scale of the plot (10.0%) and the larger cell scale

302 (0.5%; Fig. 2J). Transitivity was weakly although significantly negatively correlated with

303 species richness at the plot level (Tab. 2). This negative correlation was visible in all study

304 years and was strongest in 2005 (Pearson $r = -0.80$, $P < 0.01$) and 2006 ($r = -0.51$, $P < 0.001$).

305 In later years, however, it became increasingly weak and statistically non-significant (all $r < |-$

306 $0.14|$, $P > 0.1$).

307   After statistically controlling for possible influences of species richness, spatial

308 autocorrelation, and substrate characteristics, NODF and WCS, and to a lesser degree R^2,

309 were strongly linked to τ_C (Tab. 2, Fig. 3). The degree of competitive transitivity τ_C was

310 negatively correlated with spatial abundance segregation and species turnover, but positively

311 correlated with NODF (Fig. 3).

312

313 *The spatial dimension of community structure during succession*

314   Effect sizes of NODF and R^2 with respect to the proportional null model were

315 significantly spatially autocorrelated (Tab. 1). Mantel tests (Fig. 4A) confirmed these results

316 and returned for the majority of study years positive – although weak (<2% of variance

317 explained) – spatial correlations. In contrast, abundance based patterns of co-occurrences

318 measured by WCS were not clearly spatially autocorrelated (Fig. 4A). There was also a

319 general trend towards positive correlations between differences in substrate characteristics

320 and the respective differences in species co-occurrences (R^2, NODF; Fig. 4B). These results

321 suggest that variability in substrate characteristics (Fig. 4B), rather than the average values

322 (Tab. 1), have most influence on patterns of species co-occurrences. These trends were

323 strongest for the first study year. The competitive strength metrics were not spatially

324 autocorrelated (Tab. 2, Fig. 4A) but were in all study years weakly positively correlated with

325 substrate conditions (Fig. 4B).

326

327 **Discussion**

328 *Temporal trends in community assembly*

329   Some theories of plant succession predict species richness to increase until a mid-

330 successional maximum is reached (e.g. Horn 1974). In our study system, such a maximum

331 was not visible after seven years of succession (Ulrich et al. 2014c, d). In line with major

332 hypotheses on primary succession, we also predicted (1) an initial random pattern of species

333 co-occurrences as a consequence of spatially random external colonisation and germination

334 from the soil seed bank (Hubbell 2001, Baasch et al. 2009, del Moral 2009). This was not the

335 case in our study system. The initial spatial distribution of species was significantly

336 segregated at the set level (Figs. 3A, D, t-test: $P < 0.01$) and aggregated at the cell level (Figs.

337 3B, E; bootstrapped t-test: $P < 0.01$). Within the Connell-Slatyer (1977) succession

338 framework, the inhibition model is consistent with a pattern of initial segregation by pioneer

339 species at a small spatial scale. In our study, one of the earliest dominant plant species,

340 *Conyza canadensis* (L.) Cronquist, is allelopathic (Djurdjević et al. 2011) and can suppress

341 the establishment of other early colonists. Allelopathy by pioneer species is also not in

342 accordance with neutral models that assume random dispersal of ecologically equivalent

343 species (Hubbell 2001, Alonso et al. 2006). Rather, our results suggest that preferential "safe

344 sites" (*sensu* Harper 1977) are shared by many colonizing species, but that species

345 interactions reduce the establishment success of some of these early colonists.

346   Surprisingly and again contrary to our first prediction, the initial species segregation at

347 the set level was followed by a trend towards random co-occurrences in comparison to the

348 null model (Fig. 2). Apparently, the arrival of new species mediated the initial spatial pattern,

349 resulting in a random distribution of species. Only at the largest, whole-catchment scale did

350 co-occurrences became increasingly segregated (Fig. 3 and Zaplata et al. 2013) through time,

351 and this segregation was associated with the underlying large-scale variation in substrate

352 conditions (Ulrich et al. 2014c). Consequently our results demonstrate a temporal divergence

353 in plant community structure at the catchment scale. Further, our study demonstrates that not

354 only spatial but also temporal patterns of species co-occurrences differ across spatial scales.

355   Our study design did not comprehensively allow us to disentangle dispersal and seed

356 bank effects on the initial community composition and competitive relationships. Given the

357 strong evidence for distance-dependent colonisation from neighbouring sites during primary

358   succession (e.g. Dzwonko 1993, Bochet et al. 2007, Latzel et al. 2011) we speculate that the

359   non-random occurrences of plant seeds in the catchment substrate had a major effect on the

360   earliest community composition. However, additional study is needed to assess seed bank

361   contributions, and potential trade-offs between dispersal and competition during early plant

362   succession.

363

364   *Spatial patterning of community assembly*

365   A first major aim of our study was to infer the spatial trends in patterns of species co-

366   occurrences during early plant succession. Previous work on small-scale variability focused

367   on environmental stress and found similar positive correlations of species aggregation and

368   nutrient availability and increases in species segregation with decreasing substrate pH

369   (Maestre et al. 2009). Kikvidze et al. (2005) and Dullinger et al. (2007) reported positive

370   relationships between species aggregation and plant cover and biomass, respectively. Our

371   findings only partly corroborate these results and do not match well with our first two

372   predictions on the scale dependence of species spatial segregation (Tab. 1, Figs. 3, 5).

373   Although NODF and R^2 - but not the abundance based WCS metric - were spatially

374   autocorrelated and related to substrate properties (Fig. 4), these effects explained in nearly all

375   cases less than 1% of variance. Of the substrate variables, only carbonate content was weakly

376   positively linked to the degree of spatial aggregation (Fig. 4B). Although this finding is in line

377   with filtering effects at the habitat patch scale (as reviewed by Götzenberger et al. 2011), we

378   notice that the observed effects in these previous studies and in our study system were usually

379   small (Tab. 1, Fig. 4). Moreover, substrate conditions were not clearly linked to differences in

380   species relative abundances (Tab. 1, Fig.1). These findings indicate, that small-scale

381   variability in substrate conditions (Zaplata et al. 2013) might not be the strongest driver of

382   community assembly, although soil may be very important at larger spatial scales (Tuomisto

383   et al. 2014, Zuquim et al. 2014). Our findings are thus in line with a hierarchical concept of

384   succession (Pickett et al. 1987), which emphasizes site availability, and differences in species

385   colonization and performance as being more important.

386   In a previous study (Ulrich et al. 2014c) we reported that small-scale variability in

387   phylogenetic community composition was correlated with substrate characteristics. Because

388   differences in phylogenetic community structure might be linked to species composition

389   (Webb et al. 2002), we expected to see a correlation between substrate characteristics and

390   species co-occurrences (Bennett et al. 2013). In this study, small-scale substrate variability

391   was not closely related to species composition. Habitat filtering implies small-scale

392   aggregation of species co-occurrences and a significant degree of species turnover at larger

393   spatial scales (Presley et al. 2010). This is equivalent to a modular meta-community

394   organisation (Presley et al. 2010, Borthagary et al. 2014). Species co-occurrences were indeed

395   scale dependent (Fig. 2). Significant nestedness was accompanied by a lack of species

396   segregation at the set scale (Fig. 2). However, this finding and the low degree of species

397   turnover at the 4-m^2 set and 25-m^2 cell scales do not match a pattern of modular meta-

398   community organisation, and suggests that the measured substrate variables do not act as

399   strong environmental filters.

400   We also did not find support for our third prediction of decreasing nestedness and

401   increasing modularity driven by substrate characteristics. Instead, the Poisson random

402   variability in species richness observed at all spatial-scales suggests that random species

403   colonisation was more important than habitat filtering. One possible explanation for this

404   pattern invokes the temporal increase in soil heterogeneity due to ecological engineering by

405   plants (Cuddington and Hastings 2004). This would reduce the impact of filtering on species

406   composition leading to medium scale randomisation of species composition in time and to an

407   increased importance of competition at the plot level.

408   Our first two predictions were partly based on the framework of nested, modular, and

409   turnover patterns advocated by Leibold and Mikkelson (2002) and Presley et al. (2010) who

410   linked these respective patterns to contrasting processes of community assembly. Our results

411   provide weak support for this classification. Effect sizes of R^2 (turnover) and NODF

412   (nestedness) were only moderately negatively correlated at the set levels (r = -0.53, Fig. 2)

413   and even correlated positively at the cell level (r = 0.18, Fig. 2). Consequently, many set and

414   cells could not be clearly separated along the nestedness – turnover continuum. Our results

415   contrast with a recent study by Meynard et al. (2013), who used snap-shot (i.e. non-dynamic)

416   data at several spatial scales and argued for clear indication of modularity.

417   However, our results also point to a shortcoming of the triangle model proposed by

418   Leibold and Mikkelson (2002). Although modularity is unequivocally defined as 'link-dense

419   regions in ecological networks' (Olesen et al. 2007) there is no rigorous way to measure

420   modularity (Newman 2006) and therefore this pattern may not be easy to discern with classic

421   frequentist (p < 0.05) yes/no tests for modularity (Gotelli and Ulrich 2012).

422

423   *The interplay of competition and species co-occurrence*

424   Major models of community assembly focus on competitive exclusion (Diamond 1975,

425   Chesson 2000). Ideally, therefore, co-occurrence analysis should be combined with the

426   analysis of competitive hierarchies (Soliveres et al. 2015). A new framework developed by

427   Ulrich et al. (2014b) allows for the first time such a conjoint analysis. This framework

428   predicts an increasing frequency of negative interactions and transitive hierarchies through the

429   course of succession. Our results are in line with the predictions of this model (Prediction 4)

430   and point to a clear increase in the importance of competitive interactions during early

431   succession but a weaker effect of competition at larger spatial scales (Tab. 2). The latter

432   observation is most parsimoniously explained by the fact that competition acts at the scale of

433   individual interactions between plants and thus should be strongest at the smallest spatial

434   resolution (i.e., the interaction neighbourhood scale). This interpretation is also in line with

435   our finding that the variability in competitive strength and in metrics of co-occurrences were

436   strongest in the initial phases of succession and decreased through time (Fig. 2). Probably the

437   interplay of competition, facilitation and filtering causes communities at small scales to

438   become more similar in time and hence converge. These processes do not exclude divergence

439   in community composition among these small scale communities as indicated by the

440   pronounced increase in spatial segregation and competitive strength among the cells (Fig. 2).

441   Our approach allowed us to directly link competitive strength and patterns of co-

442   occurrences (Tab.2, Fig. 3). Community assembly theory (Diamond 1975, Weiher and Kedyy

443   1999) and competitive intransitivity models (Laird and Schamp 2006, Ulrich et al. 2014b)

444   predict contrasting patterns, and we were able to evaluate these predictions at different

445   temporal and spatial scales. The competitive intransitivity models of Allesina and Levine

446   (2011) and Ulrich et al. (2014b) assume constant pair-wise competitive interactions. Stable

447   abundance hierarchies (Ulrich et al. 2014b) and coexistence is then promoted by the internal

448   dynamics of the competitive looping that works according to rock-paper-scissors games

449   (Allesina and Levin 2011, Rojas-Echenique and Allesina 2011, Allesina and Tang 2012). This

450   interpretation is corroborated by our finding (Fig. 3) that high degrees of abundance

451   segregation and species turnover were in all study years linked to competitive loops (low

452   transitivity). If additionally interaction strength is context-dependent and changes with

453   environmental conditions (Grime 1973, Chamberlain et al. 2014, Gioria and Osborne 2014),

454   abundance hierarchies are predicted to differ from site to site leading to segregated patterns of

455   abundances and species co-occurrences. This effect is expected to increase with spatial scale

456   (Fig. 2) and thus the model predicts a positive correlation of the degree of species segregation

457   with spatial and/or environmental distance. Our finding of the spatial autocorrelation of R^2

458   (Fig. 4) corroborates this interpretation.

459

468

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612   Brazilian Amazonia. - J. Veg. Sci. 25: 1195-1207.

613

614

615 **Online resources**

616 **Electronic supplementary material A:** Raw data used for the present study.

617

618

619 **Table 1**. General linear modelling of effect sizes of species spatial co-occurrence in dependence on species richness and soil parameters as
620 quantitative, and age since catchment construction and spatial scale as qualitative predictors. Given are regression beta scores and variance
621 partitioned coefficients of determination r^2(variable). r^2(model) refers to the whole regression model. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.
622

| Variable		R^2		NODF		WCS	
	df	beta	r^2(variable)	beta	r^2(variable)	beta	r^2(variable)
EV1	1	-0.078	0.011*	0.032	0.007*	-0.022	0.001
Species	1	-0.047	<0.001	0.067	0.001	0.044	<0.001
Carbonate	1	-0.118	0.008*	0.05	0.006*	-0.073	0.004
Sand	1	-0.328	0.001	0.135	<0.001	-0.008	<0.001
pH	1	0.059	<0.001	-0.046	<0.001	-0.308	0.001
r_C	1	-0.067	<0.001	0.471	0.057***	-0.424	0.017**
Age	6		0.228***		0.241***		0.464***
Scale	1		0.001		0.187***		0.044***
Age×Scale	5		0.160***		0.066***		0.014
Error	426						
r^2(model)			0.566***		0.566***		0.545***

623

624 **Table 2**. General linear modelling of metrics of competitive strength (r_C) and transitivity (τ_C) in dependence on species richness and substrate

625 parameters as quantitative, and age since catchment construction and spatial scale as qualitative predictors. Given are regression beta scores and

626 variance partitioned coefficients of determination r^2(variable). r^2(model) refers to the whole regression model. In the case of the qualitative

627 predictors '<0' and '0>' signs indicate the respective covariance. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

628

| Variable		r_C		τ_C	
	df	beta	r^2(variable)	beta	r^2(variable)
EV1	1	0.005	0.001	-0.003	0.001
Species	1	-0.066	0.009*	-0.04	0.006*
Carbonate	1	-0.008	0.001	-0.002	<0.001
Sand	1	0.047	<0.001	-0.013	<0.001
pH	1	0.04	<0.001	-0.026	<0.001
r_C	1	-	-	0.404	0.141***
Age	6	>0	0.074***	>0	0.019**
Scale	2	<0	0.322***	<0	0.184***
Age×Scale	10		0.118***		0.006
Error	426				
r^2(model)			0.66***		0.489***

629

630 **Figure 1.** Chicken Creek catchment in August 2008 (aerial photograph provided by Vattenfall

631 Europe Mining AG) showing the positions of the 25-m^2 cells (A). In the cell corners four 1 m^2

632 plots form a set (B).

633
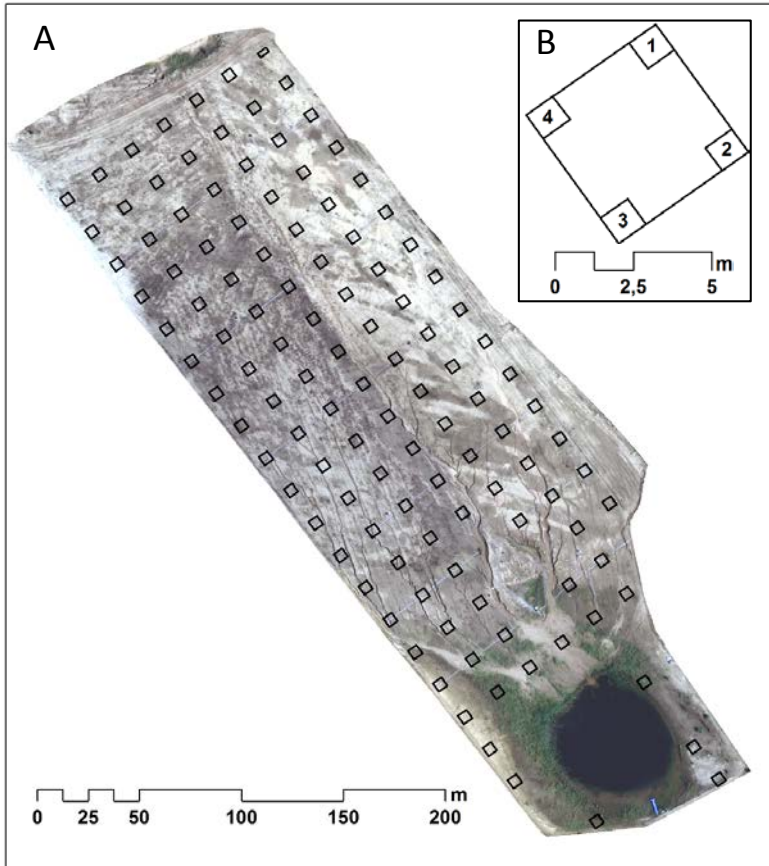
634

635 **Figure 2**. Temporal trends of effect sizes of species turnover (R^2) (A, B), NODF, (C, D), and

636 WCS (E, F) among the 4-m^2 set (A, C, E) and among the 25-m^2 cell (B, D, F) resolution

637 scale. Respective trends of competitive strength (r_C) (G, H) and degrees of transitivity (τ_C) (I,

638 J) at the 4-m^2 (G, I), and 25-m^2 (H, J) resolution. The trends for r_C and τ_C at the 1-m^2

639 resolution were very similar to those at the 4-m^2 scale and therefore not shown. Regression

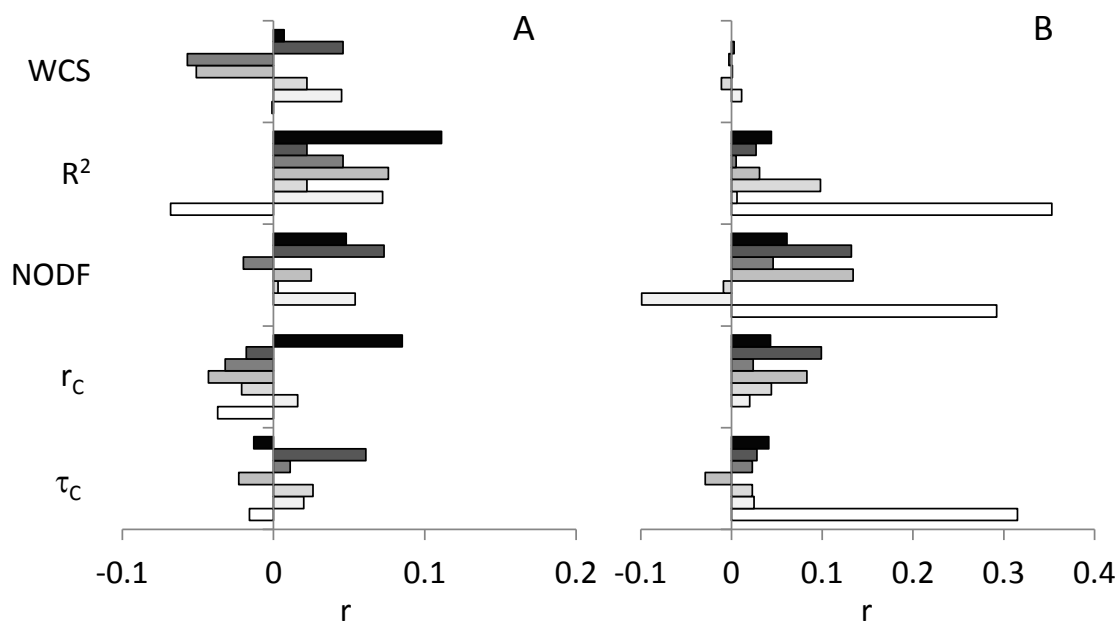640 lines are significant at $P < 0.001$ (A, H, J) and $P < 0.05$ (B, F).

641
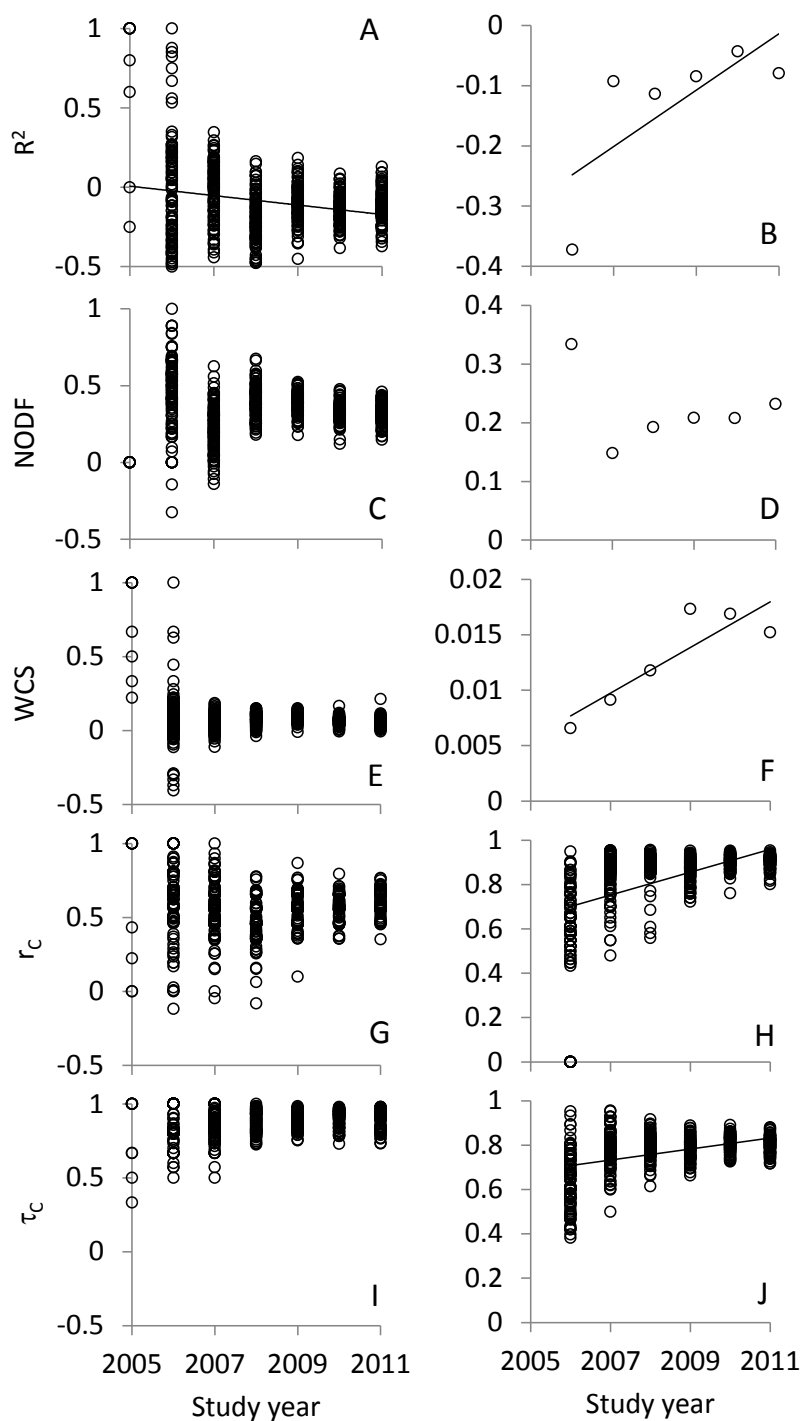
642

643 **Figure 3**. Annual GLM models applied to the set level τ_C as dependent variables. Given are

644 the beta values for X of the model

645 $Y = a_0 + a_1 Species + a_2 Carbonate + a_3 pH + a_4 Sand + a_5 EV1 + a_6(\tau_C)$, with Y being effects sizes of

646 WCS, NODF, and R^2. The vertical lines denote the approximate parametric 1% significance

647 levels. Bar shadows run from white (year 2005) to black (year 2011).

648
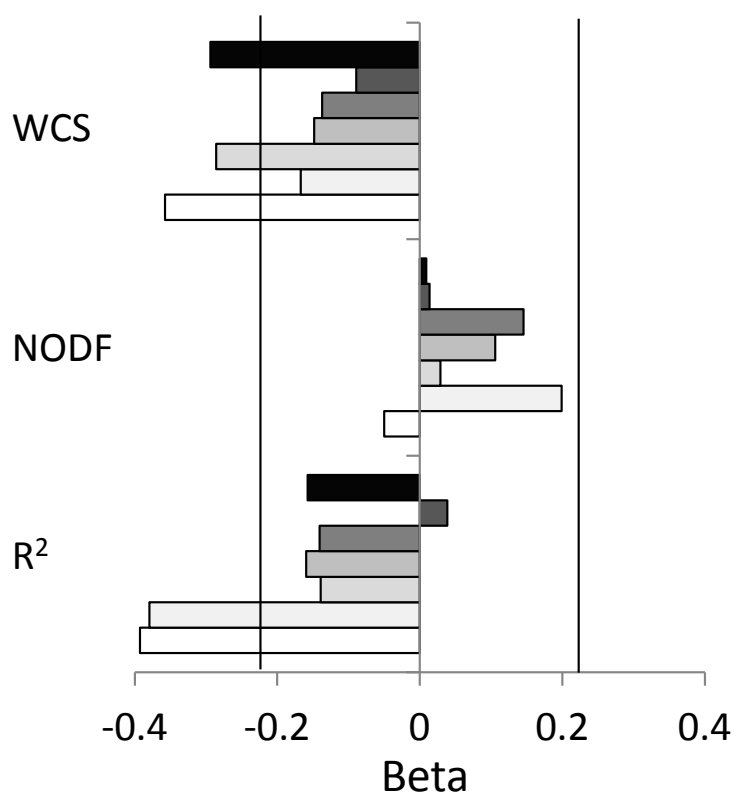
649
650
651

652 **Figure 4**. Mantel correlations r of metrics on community structure (effects sizes of WCS,

653 NODF and R^2) and competitive strength (r_C, τ_C), and Euclidean spatial (A) and soil

654 characteristics (B) distances. Data from the set level. Bar shadows run from white (year 2005)

655 to black (year 2011). Except for 2005 (N = 81) the large numbers of set pairs (N > 1000)

656 caused correlation coefficients r > |0.03| to be significant at P < 0.01. For 2005 correlations r

657 > |0.29| are significant at P < 0.01.

658