

Effect sizes and standardization in neighbourhood models of forest stands: potential biases and misinterpretations

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Running head: effect sizes and standardization

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1 **Summary**

- 2 **1.** Effects of conspecific neighbours on survival and growth of trees have been found to be
3 related to species abundance. Both positive and negative relationships may explain
4 observed abundance patterns. Surprisingly, it is rarely tested whether such relationships
5 could be biased or even spurious due to transforming neighbourhood variables or
6 influences of spatial aggregation, distance decay of neighbour effects and standardization
7 of effect sizes.
- 8 **2.** To investigate potential biases, communities of 20 identical species were simulated with
9 log-series abundances but without species-specific interactions. No relationship of
10 conspecific neighbour effects on survival or growth with species abundance was expected.
11 Survival and growth of individuals was simulated in random and aggregated spatial
12 patterns using no, linear, or squared distance decay of neighbour effects.
- 13 **3.** Regression coefficients of statistical neighbourhood models were unbiased and unrelated
14 to species abundance. However, variation in the number of conspecific neighbours was
15 positively or negatively related to species abundance depending on transformations of
16 neighbourhood variables, spatial pattern and distance decay. Consequently, effect sizes
17 and standardized regression coefficients, often used in model fitting across large numbers
18 of species, were also positively or negatively related to species abundance depending on
19 transformation of neighbourhood variables, spatial pattern and distance decay.
- 20 **4.** Tests using randomized tree positions and identities provide the best bench marks by
21 which to critically evaluate relationships of effect sizes or standardized regression
22 coefficients with tree species abundance. This will better guard against potential
23 misinterpretations.

24

25 **Key-words:** community dynamics; multiple regression; neighbourhood model; population
26 dynamics; tropical forest.

27 **Introduction**

28 Whether or not conspecific negative density dependence (CNDD) at small
29 neighbourhood scales shapes species abundances in tropical tree communities at larger scales
30 is far from resolved and we probably should not even expect the answer to be simple. In
31 principle, there are several possibilities. First, the strength of CNDD is unrelated to
32 abundance. Second, the strength of CNDD is negatively related to abundance (strong CNDD
33 for abundant but weak CNDD for rare species). This would prevent abundant species
34 becoming even more abundant and thereby competitively excluding other species. Moreover,
35 it would confer a rare-species advantage and possibly lead to a community compensatory
36 trend (CCT, Connell *et al.* 1984). Third, the strength of CNDD is positively related to
37 abundance (strong CNDD for rare but weak for abundant species). This would explain the
38 rarity and low abundance of the species with strong CNDD and the high abundances of
39 species with weak CNDD (Comita *et al.* 2010). There remain though two further possibilities
40 which are that either a mix of positive and negative processes is operating, or the observed
41 relationships are simply spurious (*i.e.* the result of a statistical artefact).

42 In an empirical study, Newbery & Stoll (2013) showed negative effects of conspecific
43 neighbours on absolute growth rate of medium-sized trees. The argument was that reduced
44 growth of an individual tree will – other factors being equal – translate into survivorship and
45 fecundity reductions and hence affect species abundances. Nevertheless, direct effects of
46 conspecifics on survival could be more relevant for population dynamics of different species
47 within communities. Therefore, the tests reported here simulate both individual survival and
48 growth rate and use a framework of neighbourhood analysis similar to that of Newbery &
49 Stoll (2013) to show that all possible relationships of the strength of CNDD and abundance
50 may emerge without any species-specific or effects of abundances. Moreover, we show that
51 potential biases do not depend on the nature of the dependent variable.

52 Relationships between the strength of CNDD and abundance were investigated using a
53 simple, spatially explicit and individual-based, model which simulated identical species
54 without any species-specific interactions. Thus, any relationships between the strength of
55 CNDD and abundance in communities simulated under these assumptions would not be
56 expected. Nevertheless, relationships do emerge because of interfering effects of spatial
57 patterns and distance decay (i.e. the functional form relating neighbour effects to distance
58 from focal trees, Fig. 1) and, perhaps more importantly, due to transforming (e.g. log-
59 transformation) and/or scaling (e.g. standardization or z-transformation) of the input
60 variables. For example, if rare species have lower variability in the number of conspecifics in
61 their local neighbourhoods compared to common species, scaling is expected to decrease
62 effect sizes (or standardized partial correlation coefficients) of rare relative to common
63 species, possibly leading to spurious negative relationships between the strength of CNDD
64 and abundances. Scaling is recommended (e.g. Schielzeth 2010) and applied especially in
65 hierarchical Bayesian modelling to speed up or even ensure numerical convergence (e.g.
66 Gelman & Hill 2007).

67 Motivation to investigate the relationships between the strength of CNDD and
68 abundance more carefully using simulations came from the opposite outcomes of two recent
69 publications. A consistent *negative* relationship between the strength of CNDD (i.e. effect
70 sizes derived from statistical neighbourhood models) and abundance (total basal area of
71 species) in randomization tests was shown by Newbery & Stoll (2013). By contrast, a strong
72 *positive* relationship between the strength of CNDD and abundance was found by Comita *et*
73 *al.* (2010). Whilst such different results are interesting, and might be explained by different
74 underlying biological mechanisms operating on different species at different locations, before
75 making such a conclusion possible differences arising from artefacts and biases of the
76 statistical methods should first be ruled out.

77 **Materials and Methods**

78 A completely neutral forest without any species-specific effects was simulated. Initial
 79 size distributions of individuals (basal area, ba) were log-normal with mean 2 and standard
 80 deviation 1, and simulations were initialized with no spatial dependency in individual size.
 81 Individuals of 20 identical species with log-series abundances (i.e. 2827, 1408, 935, 699, 557,
 82 462, 395, 344, 305, 273, 248, 226, 208, 192, 179, 167, 157, 147, 139, 132) were placed on
 83 plots (200 x 400 m) either randomly or with aggregated spatial patterns. The aggregated
 84 pattern was realized by dispersing individuals around ‘parent trees’ (assigned random
 85 locations according to a homogeneous Poisson process), using a Gaussian dispersal kernel
 86 with mean 0 and standard deviation 3 m. Thus the species distributions were modeled as a
 87 Thomas cluster process, which in turn is a special case of a Neyman-Scott cluster process
 88 (Neyman & Scott 1952), and this method means species are spatially independent of one
 89 another.

90 Individual survival was simulated in three steps. First, a linear predictor (y) for survival
 91 was simulated for individuals within a border of 20 m using the following multiple regression
 92 equation:

$$94 \quad y = \beta_0 + \beta_1 \log(ba) + \beta_2 \sum_r \textit{heterospecific neighbours} + \beta_3 \sum_r \textit{conspecific neighbours} \quad (1)$$

95
 96 with β_0 to β_3 the regression coefficients, ba the initial size (basal area) of individuals
 97 and the two neighbour terms simply summing the number of heterospecific or conspecific
 98 neighbours within a neighbourhood radius (r) of 20 m without taking size or relative size
 99 differences between focal individuals and neighbours into account. The regression
 100 coefficients were chosen to lead to roughly 50% mortality for each species. Specifically, $\beta_0 =$
 101 5, $\beta_1 = 2.5$, and $\beta_2 = \beta_3 = -0.05$. Second, the linear predictor was converted to individual

102 survival probabilities using the inverse logit transformation. Third, binomially distributed
 103 errors were used to convert the probabilities to the binary variable survival (0's and 1's) by
 104 drawing from binomially distributed random numbers. Survival was then used in logistic
 105 regressions as the dependent variable. Regressions were run for each species separately.
 106 Standardized regression coefficients (b) were obtained from regressions with independent
 107 variables standardized (or scaled) by subtracting their mean and dividing by their standard
 108 deviation. Unlike in the neighbourhood analysis for absolute growth rate (agr) as dependent
 109 variable (see below), fitted neighbourhood radii were fixed for the logistic regressions at 20
 110 m, because best fitting neighbourhood radii for rarer species were sometime smaller than the
 111 simulated 20 m radius. To investigate effects of transformations, the same multiple regression
 112 approach as described above, but now with log-transformed neighbour terms was used:

113

$$114 \quad y = \beta_0 + \beta_1 \log(ba) + \beta_2 \log(1 + \sum_r \textit{heterospecific neighbours}) + \beta_3 \log(1 + \sum_r \textit{conspecific neighbours}) \quad (2)$$

115

116 with β_0 and β_1 as above, and $\beta_2 = \beta_3 = -1.3$. The β 's of the neighbour terms needed to be
 117 adjusted in order to maintain 50% mortality. Again, unstandardized (β) and standardized (b)
 118 regression coefficients were estimated by logistic regressions (general linear models with
 119 binomially distributed error terms). Finally, β_3 and b_3 , as well as variability in numbers of
 120 conspecific neighbours within the neighbourhood radius r for each species, were correlated
 121 with species abundances (i.e. $\log(\text{number of individuals of each species at the plot level})$).

122 In the simulations of individual growth, different distance decays and relative size
 123 differences were also taken into account because competition is often size- and distance
 124 dependent. Size- and distance dependencies could also have been analysed for survival as
 125 dependent variable. However, since the parallel analyses yielded essentially similar
 126 conclusions, we present analyses with different distance decays for growth only. For each

127 individual, one single growth increment (absolute growth rate, *agr*) was simulated for
 128 individuals within a border of 20 m using the following multiple regression equation:

129

$$130 \quad \log(\text{agr}) = \beta_0 + \beta_1 \log(\text{ba}) + \beta_2 \log\left(1 + \sum_r \text{ba}_{\text{HET}} / w\right) + \beta_3 \log\left(1 + \sum_r \text{ba}_{\text{CON}} / w\right) + \text{error} \quad (3)$$

131

132 with $w = 1$ (no distance decay), $w = \text{distance}$ (linear distance decay) or $w = \text{distance}^2$

133 (squared distance decay, Fig. 1). The neighbourhood terms (ba_{HET} and ba_{CON}) summed the

134 basal areas of bigger heterospecific (HET) or bigger conspecific (CON) neighbours within a

135 neighbourhood radius (r) of 20 m. The random error term was $N(0, 0.3)$. Regression

136 coefficients were $\beta_0 = -0.1$, $\beta_1 = 0.3$ and $\beta_2 = \beta_3 = -0.2$. To verify the simulations, test runs

137 with random errors set to $N(0, 0)$ were performed. The simulations were realized using C++

138 (computer code is given in Appendix A of the supplementary material).

139 Neighbourhood models (as in Stoll & Newbery 2005) were then fitted to the simulated

140 data over all possible combinations of radii for HET and CON neighbours using R (R

141 Development Core Team 2012) and parameter estimates taken from those models yielding

142 the highest adjusted R^2 -values. Five runs with different seeds were performed and estimates

143 of regression coefficients from best fitting neighbourhood models, effect sizes (Cohen 1988;

144 Nakagawa & Cuthill 2007) or standardized regression coefficients (e.g. Warner 2012)

145 averaged across the five runs. Effect sizes (i.e. squared partial correlation coefficients, $t^2 / [t^2 +$

146 residual degrees of freedom], $t = t\text{-value}$) and standardized regression coefficients ($b = \beta$'s

147 obtained from regressions with standardized variables by subtracting their mean and dividing

148 by their standard deviation) were then correlated with species abundances (i.e. plot level

149 basal area, BA, log-transformed). Standardized regression coefficients can also be calculated

150 from unstandardized β 's as $b = \beta * SD_x$, if the dependent variable itself is not standardized

151 (e.g. survival). In the case of continuous dependent variables (e.g. *agr*), however, the

152 dependent variable itself is often also standardized as well. In these cases, variability in the
153 dependent variable is also involved in standardizing regression coefficients and $b = \beta * SD_X /$
154 SD_Y . In both cases, a positive correlation of b with abundance implies that less abundant, rare
155 species have stronger CON effects – β is more negative – (as in Comita *et al.* 2010), whereas
156 a negative relationship implies more abundant species have stronger CON effects (as in
157 Newbery & Stoll 2013). Note, however, that possible correlations of b with abundance may
158 be biased due to correlations of SD_X (or additionally SD_Y) with abundance. But if β 's are
159 negative, large SD_X lead to more negative b -values and the relationship with abundance may
160 switch direction not because of a difference in the strength of conspecific interactions
161 between rare and common species, but because of differences in the variability of number
162 and abundance of conspecific neighbours. Moreover, because the simulations and analyses
163 for both survival and *agr* as dependent variables are based on a multiple regression approach,
164 the basic consequences described above (i.e. possible biases in standardized regression
165 coefficients because of differences in SD_X between rare and common species) are essentially
166 the same independent of the nature of the dependent variable.

167

168 **Results**

169 There were no significant regressions for conspecific density-dependent effects
170 (regression coefficient β_3 in Eq. 1) on survival and species abundance (Fig. 2) regardless of
171 whether untransformed or log-transformed number of conspecific neighbours were used to
172 quantify the neighbourhood. However, variability in number of conspecific neighbours was
173 positively correlated with abundance if untransformed (Eq. 1) but negatively related if log-
174 transformed (Eq. 2). Consequently, standardized regression coefficients were negatively
175 correlated with abundance if number of conspecific neighbours was quantified on the
176 untransformed but positively correlated with abundance if number of conspecific neighbours

177 were log-transformed. Frequency distributions for the rarest ($n = 132$) and most common ($n =$
178 2827) simulated species on untransformed and log-transformed scales (Fig. 3) demonstrate
179 that log-transforming the number of conspecific neighbours for rare species (small values)
180 expands variability but compresses the variability in number of conspecific neighbours for
181 common species (large values). This variability in number of conspecific neighbours (SD_x)
182 increases from rare to common species on untransformed scales but decreases from rare to
183 common species on transformed scales.

184 There were no significant regressions for conspecific density-dependent effects on
185 growth (regression coefficient β_3 in Eq. 3) and species abundance (plot level basal area)
186 regardless of distance decay or spatial pattern (Fig. 4). Variation in parameter estimates was
187 largest for squared distance decay and random spatial pattern. Best fitting radii for bigger
188 conspecific neighbours were unbiased in neighbourhood models without distance decay and
189 random spatial pattern (Table 1). However, in the aggregated pattern and with linear distance
190 decay they were slightly underestimated. With estimates (mean \pm SD) of 15.9 ± 2.6 in the
191 random spatial pattern and 14.5 ± 3.2 , the underestimation was more pronounced with
192 squared distance decay.

193 Variability in local conspecific neighbour density (within 20 m) varied depending on
194 distance decay and spatial pattern (Fig. 5). A strong negative regression with abundance
195 emerged without distance decay in both spatial patterns. With linear distance decay, the
196 regression was not significant with random spatial pattern but still negative in the aggregated
197 pattern. With squared distance decay, the regression switched to positive in the random
198 pattern, but it was not significant in the aggregated pattern.

199 As a consequence of variation in local conspecific neighbour density, effect sizes (Fig.
200 6) and standardized regression coefficients (b_3 , Fig. 7) showed various relations with
201 abundance depending on distance decay and spatial pattern. Without distance decay both

202 effect sizes and standardized regression coefficients were positively related with abundance,
203 regardless of spatial pattern. This was also the case for effect sizes and linear distance decay,
204 whereas standardized regression coefficients were not significantly related with abundance in
205 random spatial pattern but still positively related with abundance in the aggregated pattern.
206 For squared distance decay, both effect sizes and standardized regression coefficients were
207 negatively related with abundance in random spatial patterns but unrelated in aggregated
208 patterns. Apparently, the squared distance decay cancelled the effect of aggregation.

209

210 **Discussion**

211 The simulations and neighbourhood analyses with individual survival or growth as
212 dependent variable showed that estimates of regression coefficients (β) were unrelated to
213 species abundances independent of transformations, spatial pattern and distance decay — as
214 expected based on the simulations of identical species without species-specific interactions.
215 However, variability in local density of conspecifics (SD_X) showed various relationships with
216 species abundances depending on transformations of neighbourhood variables, degree of
217 spatial pattern and form of distance decay. As a consequence (i.e. $b = \beta * SD_X$), relationships
218 between effect sizes, or standardized regression coefficients (b), and species abundances were
219 either non-significant, positive or negative.

220 If untransformed scales are used to quantify conspecific neighbourhoods, relationships
221 with variability and abundance are expected to be generally positive (Fig. B2 in Appendix B)
222 at least in the cases and range of abundances investigated here. In these cases, relationships
223 between standardized effect sizes with abundance will be negative. If, however, log-
224 transformed scales are used to quantify conspecific neighbourhoods, relationships with
225 variability and abundance (Fig. B2) can be modified in all possible ways, i.e. be absent,
226 positive or negative, depending on spatial pattern, exact form of distance decay, but also on

227 whether or not relative size differences are taken into account. There are many and
228 sometimes rather non-transparent possibilities making it very difficult to systematically
229 evaluate the published literature on neighbourhood models and possible relationships
230 between the strength of CNDD and species abundance, especially where details of how
231 variables were handled are incompletely reported, and data have not been archived to allow
232 independent checks.

233 By using neighbourhood models without distance decay and unstandardized input
234 variables, in single-species analyses, a negative relationship between CNDD and forest-level
235 abundance was found, at least for the first of the two 10-year periods analyzed (Newbery &
236 Stoll 2013). Using no distance decay, yet standardizing before fitting their models, Lin *et al.*
237 (2012) found positive relationships over their dry-season interval. Using an exponential
238 distance decay, Comita *et al.* (2010) centered (subtracted the mean) but did not standardize
239 (divide by standard deviation) their input variables (L. Comita, pers. comm.) and found a
240 strong positive relationship too. Whereas Lin *et al.* (2012) fitted mixed models using
241 maximum likelihood estimation, i.e. without any prior information being involved, Comita *et*
242 *al.* (2010) used a hierarchical Bayesian analysis with non-informative priors distributed
243 according to the scaled inverse-Wishart function. This conjugate distribution models the
244 covariance matrix of the species-level regression. Nevertheless, both studies did find positive
245 relationships, thereby apparently supporting one another's conclusions.

246 The specific scale and distribution of the priors used by Comita *et al.* (2010) might
247 have introduced additional critical information that determined in part the estimation of their
248 coefficients, in a similar way as standardization did in our simulations, and may also have
249 done for Lin *et al.* (2012). Gelman & Hill (2007) discuss the use of the inverse Wishart
250 distribution in some detail, and highlight in particular the need to confirm that Bayesian
251 priors are indeed non-informative across the same ranges of independent variables that result

252 in the posterior probabilities. Dennis (1996) has discussed fundamental issues concerning the
253 use of non-informative priors and Bayesian analysis for ecology in general.

254 The results of Newbery & Stoll (2013) dealt with effects of conspecific neighbours (as
255 large tree abundance) on growth of small trees, whereas those of Comita *et al.* (2010)
256 concerned conspecific neighbour effects (as either local tree seedling density or tree
257 abundance) on survival of those seedlings. Their result could be more generally important if
258 confirmed to be fully robust to statistical treatment. It might then support the notion that
259 fundamentally different density dependent processes are likely operating at the seedling as
260 opposed to the small-tree stage in tropical forest dynamics (Uriarte *et al.* 2004 a, b; Newbery
261 & Stoll 2013).

262 Because of conceptual similarities of neighbourhood analyses of Comita *et al.* (2010)
263 and those of others (e.g. Uriarte *et al.* 2004a, b; Lin *et al.* 2012), the analysis presented here
264 could be more widely relevant. Since standardization can lead to spurious relationships
265 between CNDD and species abundances, its potential influence needs to be carefully
266 considered when interpreting relationships of small-scale effects of conspecific neighbours
267 on larger scale abundance patterns within diverse tree communities. Similarly, care should be
268 taken when specifying and justifying prior information in hierarchical Bayesian analyses. Our
269 recommendation, following from Newbery & Stoll (2013), is that tests that randomize tree
270 positions and identities indeed provide the best benchmark by which to critically evaluate and
271 judge relationships between effect sizes, or standardized regression coefficients, and tree
272 species abundances.

273

274 **Acknowledgements**

275 We thank the Editors and M. Uriarte for comments on earlier drafts of this forum article.

276 **Supplementary Materials**

277 **Appendix A**

278 Documented computer code used for the simulations. A detailed description of input
279 parameters and simulation output is provided in the file named growth_files.rtf.

280 **Appendix B**

281 Relationships of variability in local neighbourhoods with species abundances in different
282 competitive scenarios, spatial patterns and various distance decays.

283

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319

319 TABLE 1. Average best fitting radii \pm standard deviation (SD) for bigger conspecifics in
 320 neighbourhood models (Eq. 3) across 20 species with identical initial size distributions
 321 and log-species abundances and random or aggregated spatial patterns.

Distance decay	Spatial pattern			
	random		aggregated	
no	20.0	\pm 0.0	19.8	\pm 0.4
linear	19.6	\pm 0.5	19.1	\pm 1.0
squared	15.9	\pm 2.6	14.5	\pm 3.2

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Figure legends

Figure. 1. Distance decay of neighbourhood effects. In the cut-off model (dashed), the sizes of bigger neighbours with a distance $<$ cut-off are summed. In the linear distance decay (black), the sizes of bigger neighbours are weighed by $1/\text{distance}$. This is similar to an exponential distance decay (red), which, however, gives somewhat more weight at intermediate distances. A decay of $1/\text{distance}^2$ (blue) yields a very rapidly decreasing function. Beyond 20, all three functions give essentially zero weights.

Figure. 2. Regressions of conspecific effects (regression coefficient, β_3 in Eq. 1) on individual survival, variability in number of conspecific neighbours within neighbourhood radius ($r = 20$), and standardized regression coefficients (b_3) against species abundances (number of individuals at plot level). Twenty species with identical initial size distributions and log-series abundances were simulated in a random spatial pattern. Note that in the panels of the bottom row, the number of neighbours was log-transformed. Data points are means (± 1 SD) from five replicate simulations. The simulated input value of β_3 (dotted lines) was -0.05 (top left) and -1.3 (bottom left). Continuous lines indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

Figure. 3. Frequency distributions of number of conspecific neighbours within neighbourhood radius r (20 m) for individuals of rare ($n = 132$) and common ($n = 2827$) species in simulated communities with random spatial patterns. Note that the x-axis in the panels of the top row have identical scales. This is also true for the panels of the bottom row. Moreover, the number of conspecific neighbours was log-transformed in the panels of the bottom row. SD indicates the standard deviation of each distribution.

349 Figure. 4. Regressions of conspecific negative density dependence (regression coefficient, β_3
350 in Eq. 3) and species abundances (plot level basal area). Twenty species with identical initial
351 size distributions and log-series abundances were simulated without, linear (1/distance) or
352 squared (1/distance²) distance decay of conspecific neighbour effects within 20 m radius in
353 random or aggregated spatial patterns. Data points are means (± 1 SD) from five replicate
354 simulations. The simulated input value of β_3 was -0.2 (green line).

355

356 Figure. 5. Regressions of variation in conspecific neighbour density (expressed as SD in basal
357 area of bigger conspecifics, ba_{CON} within 20 m) and species abundances (plot level basal
358 area). Twenty species with identical initial size distributions and log-series abundances were
359 simulated with random or aggregated spatial patterns without, linear (1/distance) or squared
360 (1/distance²) distance decay of conspecific neighbour effects. Data points are means (± 1 SD)
361 from five replicate simulations. Continuous lines indicate significant ($P < 0.05$) negative (red)
362 or positive (blue) regressions.

363

364 Figure. 6. Regressions of effect sizes (squared partial correlation coefficients of β_3 in Eq. 3)
365 and species abundances (plot level basal area). Twenty species with identical initial size
366 distributions and log-series abundances were simulated with random or aggregated spatial
367 patterns without, linear (1/distance) or squared (1/distance²) distance decay of conspecific
368 neighbour effects within 20 m radius. Data points are means (± 1 SD) from five replicate
369 simulations. Continuous lines indicate significant ($P < 0.05$) positive (blue) or negative (red)
370 regressions.

371

372 Figure. 7. Regressions of standardized regression coefficients (b_3) and species abundances
373 (plot level basal area). Twenty species with identical initial size distributions and log-series

374 abundances were simulated with random or aggregated spatial patterns without, linear
375 (1/distance) or squared (1/distance²) distance decay of conspecific neighbour effects within
376 20 m radius. Data points are means (\pm 1 SD) from five replicate simulations. Continuous
377 lines indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

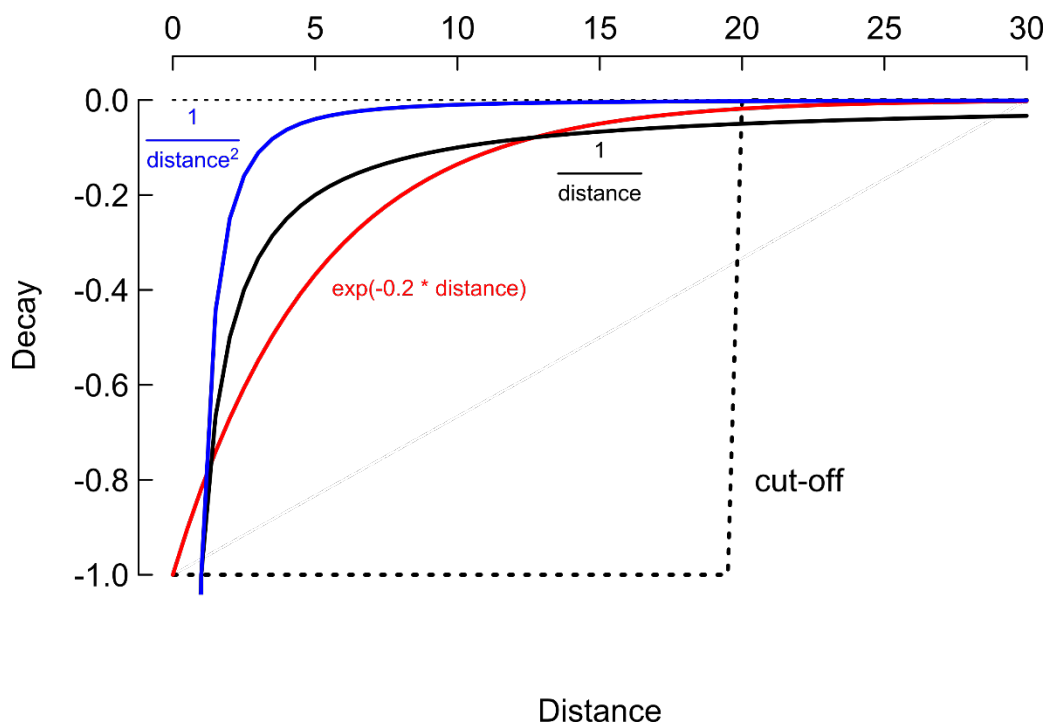


FIG. 1.

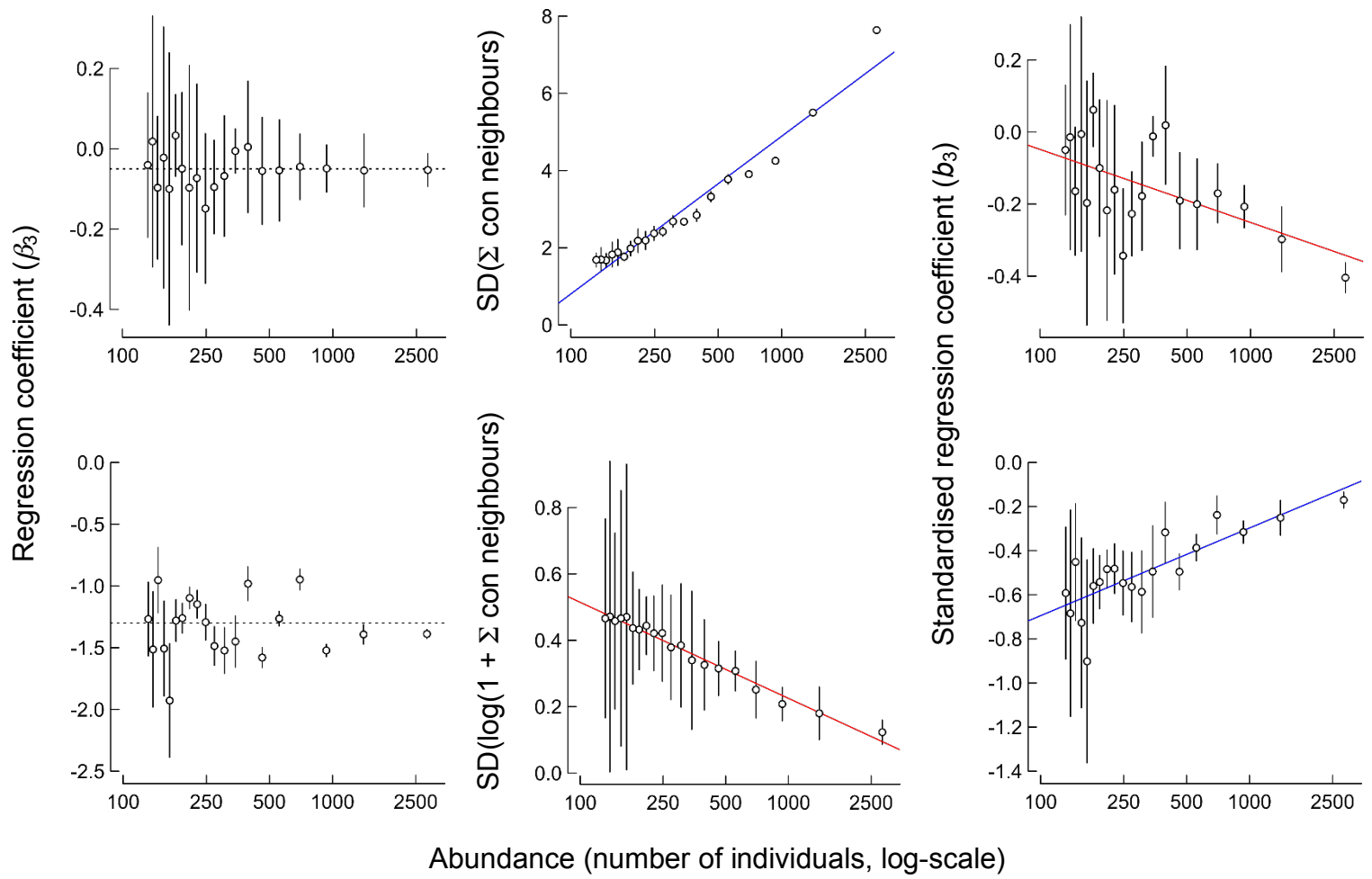


FIG. 2

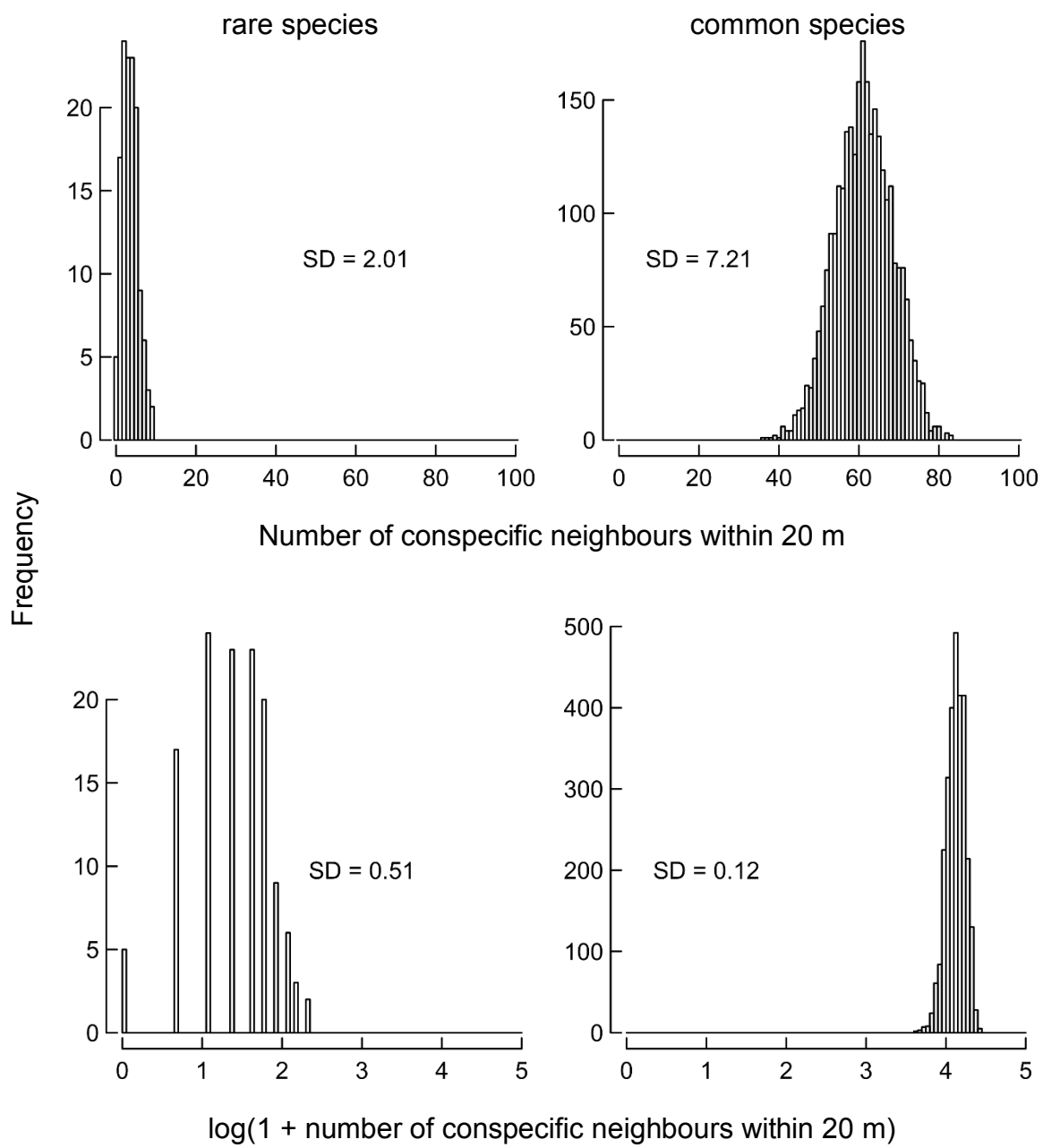


FIG. 3

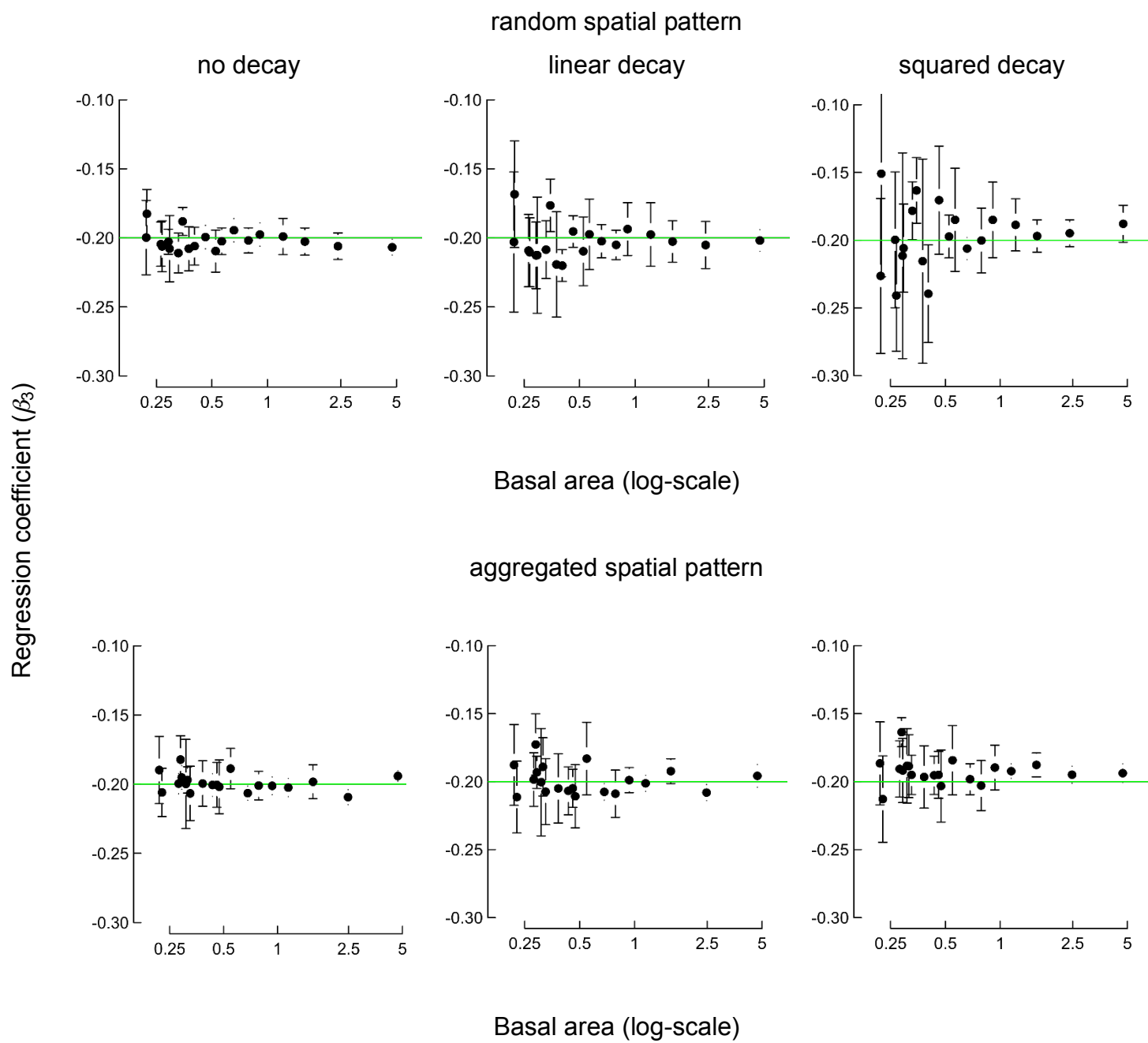


FIG. 4.

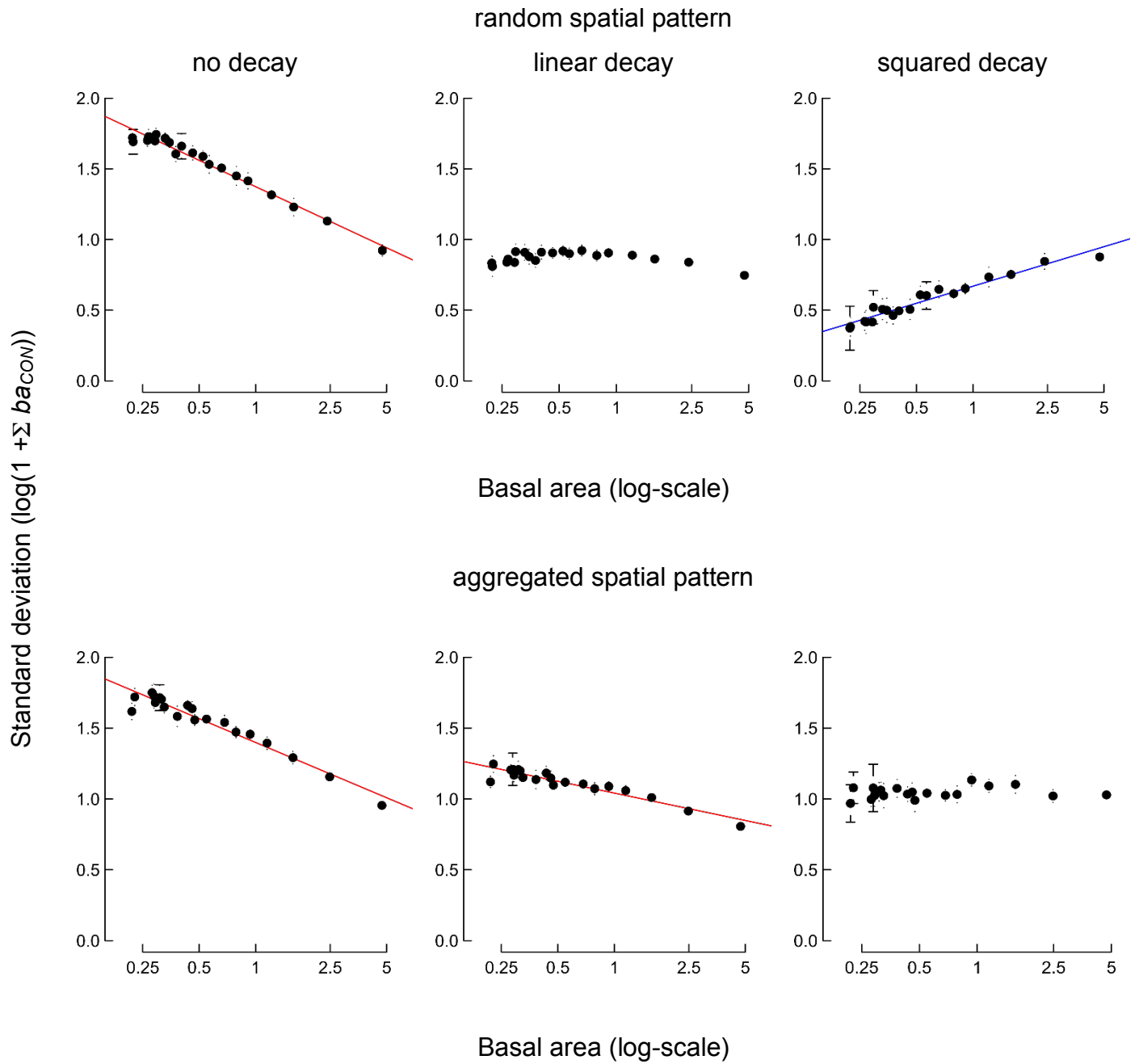


FIG. 5.

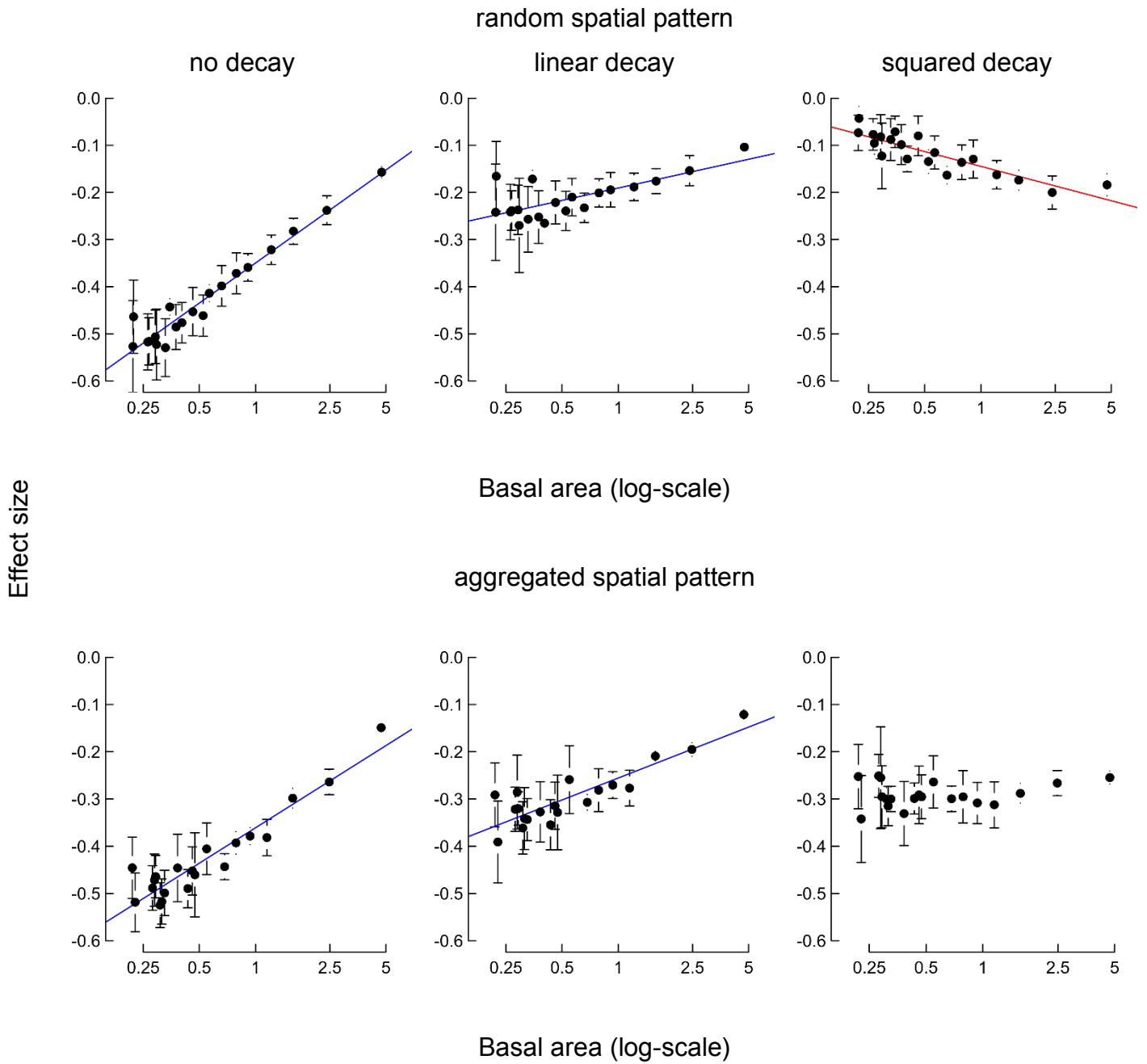


FIG. 6.

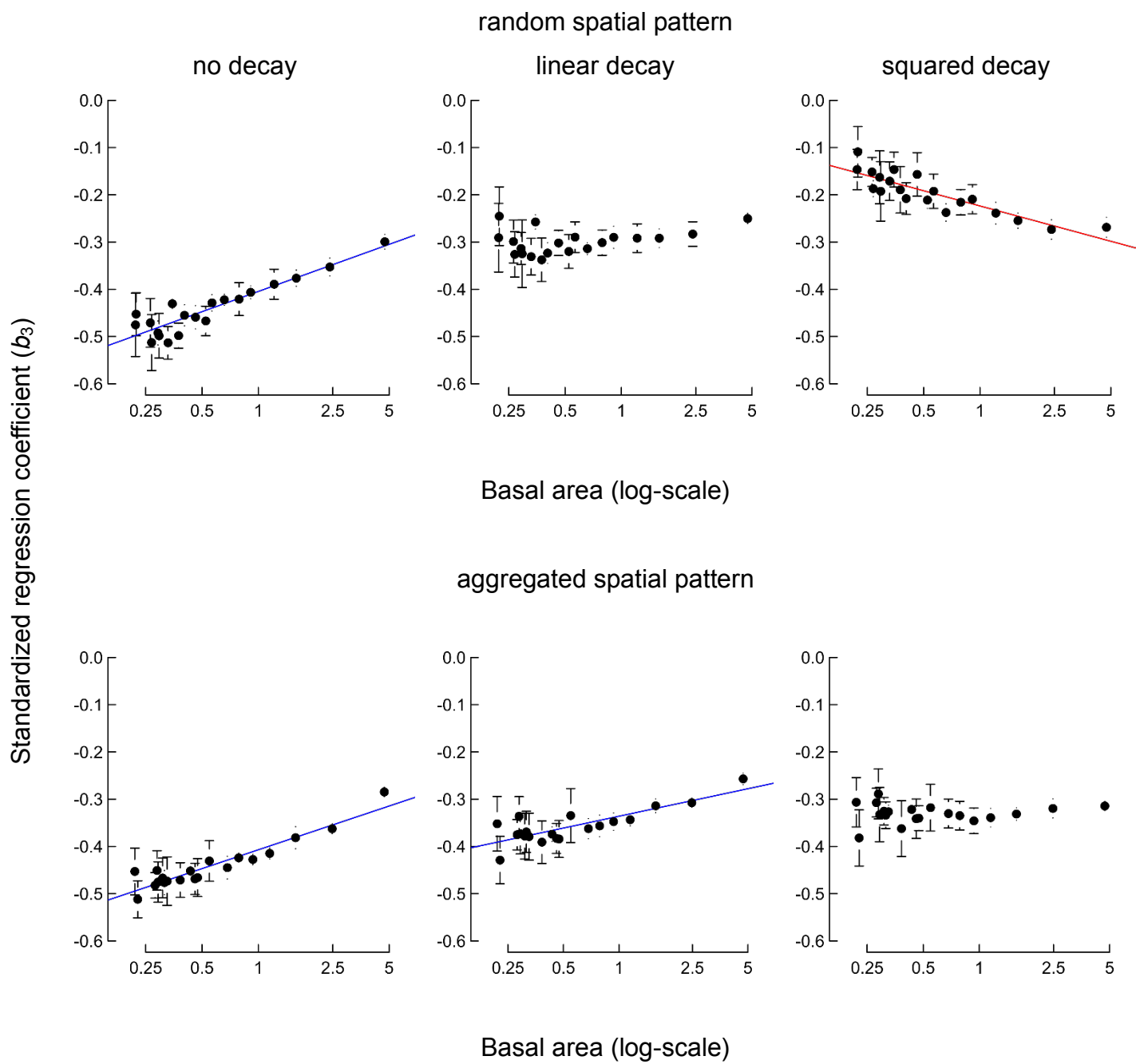


FIG. 7.