

Effect sizes and standardization in neighborhood models of forest stands

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Running head: effect sizes and standardization

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1 **Abstract** Effects of conspecific neighbors on growth and survival of trees have been
2 found to be related to species abundance. Both positive and negative relationships may
3 explain observed abundance patterns. Surprisingly, it is rarely tested whether such
4 relationships could be biased or even spurious due to influences of spatial aggregation,
5 distance decay of neighbor effects and standardization of effect sizes. To investigate potential
6 biases, we simulated communities of 20 identical species with log-series abundances but
7 without species-specific interactions. We expected no relationship of conspecific neighbor
8 effects with species abundance. Growth of individual trees was simulated in random and
9 aggregated spatial patterns using no, linear, or squared distance decay. Regression
10 coefficients of statistical neighborhood models were unbiased and unrelated to species
11 abundance. However, variation in the number of conspecific neighbors was positively or
12 negatively related to species abundance depending on spatial pattern and type of distance
13 decay. Consequently, effect sizes and standardized regression coefficients were also
14 positively or negatively related to species abundance depending on spatial pattern and
15 distance decay. We argue that tests using randomized tree positions and identities provide the
16 best bench marks by which to critically evaluate relationships of effect sizes or standardized
17 regression coefficients with tree species abundance.

18

19 **Keywords** community dynamics; multiple regression; neighborhood model; population
20 dynamics; tropical forest.

21

1 **1 Introduction**

2 Whether or not conspecific negative density dependence (CNDD) at small
3 neighborhood scales shapes species abundances in tropical tree communities at larger scales
4 is far from resolved and we probably should not even expect the answer to be simple. In
5 principle, there are several possibilities. First, the strength of CNDD is unrelated to
6 abundance. Second, the strength of CNDD is negatively related to abundance (strong CNDD
7 for abundant but weak for rare species). This would prevent abundant species to become even
8 more abundant and competitively exclude other species. Moreover, it would confer a rare-
9 species advantage and possibly lead to a community compensatory trend (CCT, Connell et al.
10 1984). Third, the strength of CNDD is positively related to abundance (strong CNDD for rare
11 but weak for abundant species). This would explain the rarity and low abundance of the
12 species with strong CNDD and the high abundances of species with weak CNDD (Comita et
13 al. 2010). There remain, though, two further possibilities, *viz.* that a mix of positive and
14 negative processes is operating, or the observed relationships are simply spurious (i.e. the
15 result of a statistical artefact).

16 Recently published experimental results showed that negative density dependence
17 caused by fungal pathogens and insect herbivores was greatest for the species that were most
18 abundant as seeds (Bagchi et al. 2014). In contrast, positive relationships between a species'
19 average abundance and its negative density dependence (Comita et al. 2010) could be
20 explained if the causality is reversed and lower negative density dependence leads to
21 increased abundance. Moreover, small seeds are likely to be more vulnerable to natural
22 enemies, and small seeds are produced in greater numbers. Thus, differences in seed size may
23 reconcile Bagchi and colleagues' results with previous work (Muller-Landau 2014).

24 We investigated relationships between the strength of CNDD and abundance using a
25 simple, spatially explicit and individual-based model simulating identical species without any

1 species-specific interactions. Thus, we would not expect any relationships between the
2 strength of CNDD and abundance in communities simulated under these assumptions.
3 Nevertheless, relationships do emerge because of interfering effects of spatial patterns or
4 distance decay (i.e. the functional form relating neighbor effects to distance from focal trees,
5 Fig. 1) and, perhaps most importantly, due to the common practice of scaling input variables.
6 For example, if rare species have higher variance in the number of conspecifics in their local
7 neighborhoods compared to common species, scaling is expected to increase effect sizes (or
8 standardized partial correlation coefficients) of rare relative to common species, possibly
9 leading to spurious positive relations between the strength of CNDD and abundances. Scaling
10 or standardization is usually recommended (e.g., Schielzeth 2010) and applied especially in
11 hierarchical Bayesian modeling to speed up or even ensure numerical convergence (e.g.,
12 Gelman and Hill 2007).

13 Our initial motivation to investigate relationships between the strength of CNDD and
14 abundance using simulations was two-fold. First, we were puzzled by a consistent negative
15 relationship between the strength of CNDD (i.e. effect sizes derived from statistical
16 neighborhood models) and abundance (total basal area of species) in randomization tests of
17 our own results (Newbery and Stoll 2013). Second, a positive relationship between the
18 strength of CNDD and abundance was found by Comita et al. (2010). Such contrasting
19 results are very interesting if they relate to different underlying biological mechanisms
20 operating on different species in different localities, but we should first try to rule out any
21 differences that might be caused by statistical methods.

22

1 **2 Materials and Methods**

2 We simulated a completely neutral forest without any species-specific effects. Initial
3 size distributions of individuals (basal area, ba) were log-normal with mean 2 and standard
4 deviation 1. Individuals of 20 identical species with log-series abundances (i.e. 2827, 1408,
5 935, 699, 557, 462, 395, 344, 305, 273, 248, 226, 208, 192, 179, 167, 157, 147, 139, 132)
6 were placed on plots (200 x 400 m) either randomly or with aggregated spatial patterns. The
7 aggregated pattern was realized by dispersing individuals around ‘parent trees’ (assigned
8 random locations according to a homogeneous Poisson process), using a Gaussian dispersal
9 kernel with mean 0 and standard deviation 3 m. Thus the species distributions were modeled
10 as a Thomas cluster process, which in turn is a special case of a Neyman-Scott cluster process
11 (Neyman and Scott 1952), and this method means species are spatially independent of one
12 another. For each individual, one single growth increment (absolute growth rate, agr) was
13 simulated for trees within a border of 20 m using the following multiple regression equation:

$$15 \log(agr) = \beta_0 + \beta_1 \log(ba) + \beta_2 \log\left(1 + \sum_r ba_{HET} / w\right) + \beta_3 \log\left(1 + \sum_r ba_{CON} / w\right) + error \quad (1)$$

16
17 with $w = 1$ (no distance decay), $w = \text{distance}$ (linear distance decay) or $w = \text{distance}^2$
18 (squared distance decay, Fig. 1). The neighborhood terms (ba_{HET} and ba_{CON}) summed the
19 basal areas of bigger heterospecific (HET) or bigger conspecific (CON) neighbors within a
20 neighborhood radius (r) of 20 m. The random error term was $N(0, 0.3)$. Regression
21 coefficients were $\beta_0 = -0.1$, $\beta_1 = 0.3$ and $\beta_2 = \beta_3 = -0.2$. To verify the simulations, test runs
22 with random errors set to $N(0,0)$ were performed. The simulations were realized using C++
23 (computer code is given in Appendix A of the supplementary material).

24 Neighborhood models (as in Stoll and Newbery 2005) were then fitted to the simulated
25 data over all possible combinations of radii for HET and CON neighbors using R (R

1 Development Core Team 2012) and parameter estimates taken from those models yielding
2 the highest adjusted R^2 -values. Five runs with different seeds were performed and estimates
3 of regression coefficients from best fitting neighborhood models, effect sizes (Cohen 1988;
4 Nakagawa and Cuthill 2007) or standardized regression coefficients (e.g., Warner 2012)
5 averaged across the five runs. Effect sizes (i.e. squared partial correlation coefficients, $t^2 / [t^2 +$
6 residual degrees of freedom], $t = t$ -value) and standardized regression coefficients ($b = \beta$'s
7 obtained from regressions with all input variables standardized by subtracting their mean and
8 dividing by their standard deviation) were then correlated with species abundances (i.e. plot
9 level basal area, BA, log transformed). Standardized regression coefficients can be calculated
10 from unstandardized β 's as $b = \beta * SD_X / SD_Y$. A positive correlation implies that less
11 abundant, rare species have stronger CON effects – β is more negative – (as in Comita et al.
12 2010), whereas a negative relationship implies more abundant species have stronger CON
13 effects (as in Newbery and Stoll 2013).

14

15

3 Results

16 There were no significant regressions of negative conspecific density dependence
17 (regression coefficient β_3 in Eq. 1) and species abundance (plot level basal area) regardless of
18 distance decay or spatial pattern (Fig. 2). Variation in parameter estimates was largest for
19 squared distance decay and random spatial pattern. Best fitting radii for bigger conspecific
20 neighbors were unbiased in neighborhood models without distance decay and random spatial
21 pattern (Table 1). However, in the aggregated pattern and with linear distance decay they
22 were slightly underestimated. With estimates (mean \pm SD) of 15.9 ± 2.6 in the random spatial
23 pattern and 14.5 ± 3.2 , the underestimation was more pronounced with squared distance
24 decay.

1 Variance in local conspecific neighbor density (within 20 m) varied depending on
2 distance decay and spatial pattern (Fig. 3). A strong negative regression with abundance
3 emerged without distance decay in both spatial patterns. With linear distance decay, the
4 regression was not significant with random spatial pattern but still negative in the aggregated
5 pattern. With squared distance decay, the regression switched to positive in the random
6 pattern, but it was not significant in the aggregated pattern.

7 As a consequence of variation in local conspecific neighbor density, effect sizes (Fig.
8 4) and standardized regression coefficients (b_3 , Fig. 5) showed various relations with
9 abundance depending on distance decay and spatial pattern. Without distance decay both
10 effect sizes and standardized regression coefficients were positively related with abundance,
11 regardless of spatial pattern. This was also the case for effect sizes and linear distance decay,
12 whereas standardized regression coefficients were not significantly related with abundance in
13 random spatial pattern but still positively related with abundance in the aggregated pattern.
14 For squared distance decay, both effect sizes and standardized regression coefficients were
15 negatively related with abundance in random spatial patterns but unrelated in aggregated
16 patterns. Apparently, the squared distance decay canceled the effect of aggregation.

17

18 **4 Discussion**

19 Our simulations and neighborhood analyses showed that estimates of regression
20 coefficients were unrelated to species abundances independent of spatial pattern and distance
21 decay — as expected based on the simulations of identical species without species-specific
22 interactions. However, variation in local density of conspecifics showed various relationships
23 with species abundances depending on degree of spatial pattern and form of distance decay.
24 As a consequence, relationships between effect sizes, or standardized regression coefficients,
25 and species abundances were either non-significant, positive or negative.

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

14 We wondered, though, whether the specific scale and distribution of the priors used by
15 Comita et al. (2010) might have introduced additional critical information that determined in
16 part the estimation of their coefficients, in a similar way as standardization did in our
17 simulations, and may also have done for Lin et al. (2012). Gelman and Hill (2007), for
18 example, discuss the use of the inverse Wishart distribution in some detail. They highlight in
19 particular the need to confirm that Bayesian priors were indeed non-informative across the
20 same ranges of independent variables that resulted in the posterior probabilities. Similarly,
21 Dennis (1996) discussed more general and fundamental issues concerning the use of non-
22 informative priors and Bayesian analysis in ecology.

23 We are aware that our results dealt with effects of conspecific neighbors (as large tree
24 abundance) on the growth of small trees, whereas those of Comita et al. (2010) concerned
25 conspecific neighbor effects (as either seedling density or tree abundance) on survival of

1 seedlings. Their interesting result would be more generally important if it could be shown to
2 be fully robust. It might then contribute to the notion (Uriarte et al. 2004 ab, Newbery and
3 Stoll 2013) that fundamentally different DD processes are most likely operating at the
4 seedling as opposed to the small tree stage in tropical forest dynamics.

5 Because of conceptual similarities of neighborhood analyses of Comita et al. (2010)
6 and those of others (e.g., Lin et al. 2012; Uriarte et al. 2004ab), our analysis here could be
7 more widely relevant. Since standardization can lead to spurious relationships between
8 CNDD and species abundances — as we have shown here, its potential influence needs to be
9 carefully considered when interpreting relationships of small-scale effects of conspecific
10 neighbors on larger scale abundance patterns within diverse tree communities. Similarly, care
11 should be taken when specifying prior information in hierarchical Bayesian analyses. Our
12 recommendation, following from Newbery and Stoll (2013), is that tests that randomize tree
13 positions and identities indeed provide the best benchmark by which to critically evaluate and
14 judge relationships between effect sizes, or standardized regression coefficients, and tree
15 species abundances.

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5 Supplementary Materials

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Appendix A

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

22

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19

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

4

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

5

6

1 **Figure legends**

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

8
9 Figure. 2. Regressions of conspecific negative density dependence (regression coefficient, β_3
10 in Eq. 1) and species abundances (plot level basal area). Twenty species with identical initial
11 size distributions and log-series abundances were simulated without, linear (1/distance) or
12 squared ($1/\text{distance}^2$) distance decay of conspecific neighbor effects within 20 m radius in
13 random or aggregated spatial patterns. Data points are means (± 1 SD) from five replicate
14 simulations. The simulated input value of β_3 was -0.2 (green line).

15
16 Figure. 3. Regressions of variation in conspecific neighbor density (expressed as SD in basal
17 area of bigger conspecifics, ba_{CON} within 20 m) and species abundances (plot level basal
18 area). Twenty species with identical initial size distributions and log-series abundances were
19 simulated with random or aggregated spatial patterns without, linear (1/distance) or squared
20 ($1/\text{distance}^2$) distance decay of conspecific neighbor effects. Data points are means (± 1 SD)
21 from five replicate simulations. Continuous lines indicate significant ($P < 0.05$) negative (red)
22 or positive (blue) regressions.

23
24 Figure. 4. Regressions of effect sizes (squared partial correlation coefficients of β_3 in Eq. 1)
25 and species abundances (plot level basal area). Twenty species with identical initial size

1 distributions and log-series abundances were simulated with random or aggregated spatial
2 patterns without, linear ($1/\text{distance}$) or squared ($1/\text{distance}^2$) distance decay of conspecific
3 neighbor effects within 20 m radius. Data points are means (± 1 SD) from five replicate
4 simulations. Continuous lines indicate significant ($P < 0.05$) positive (blue) or negative (red)
5 regressions.

6

7 Figure. 5. Regressions of standardized regression coefficients (b_3) and species abundances
8 (plot level basal area). Twenty species with identical initial size distributions and log-series
9 abundances were simulated with random or aggregated spatial patterns without, linear
10 ($1/\text{distance}$) or squared ($1/\text{distance}^2$) distance decay of conspecific neighbor effects within 20
11 m radius. Data points are means (± 1 SD) from five replicate simulations. Continuous lines
12 indicate significant ($P < 0.05$) positive (blue) or negative (red) regressions.

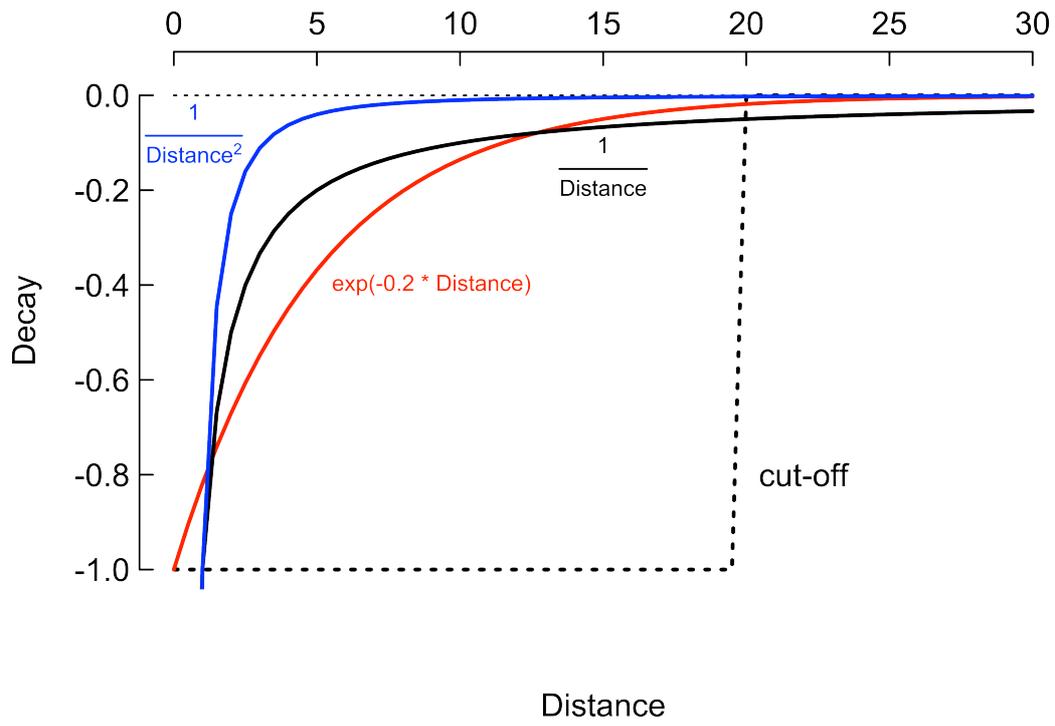


FIG. 1.

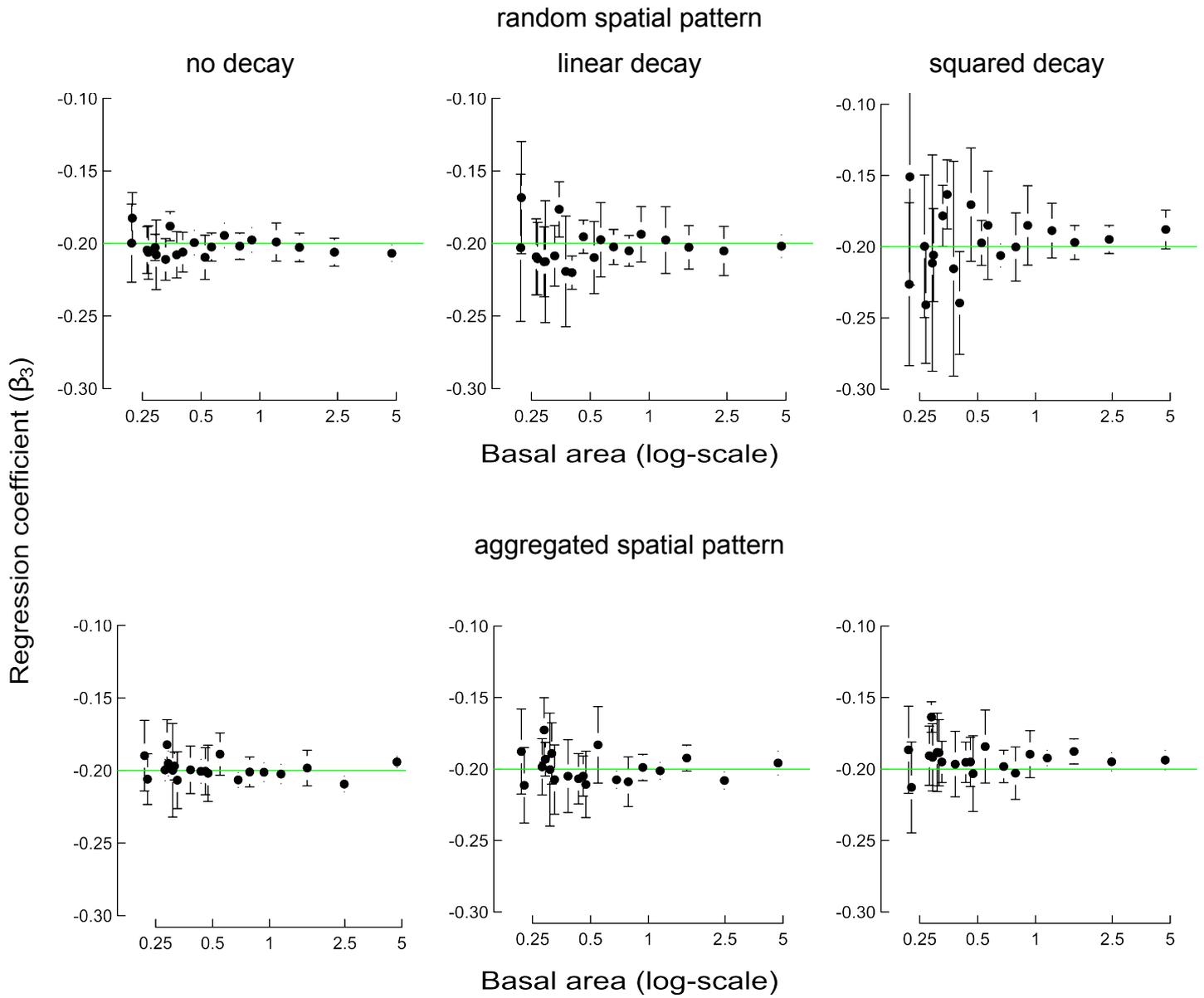


FIG. 2.

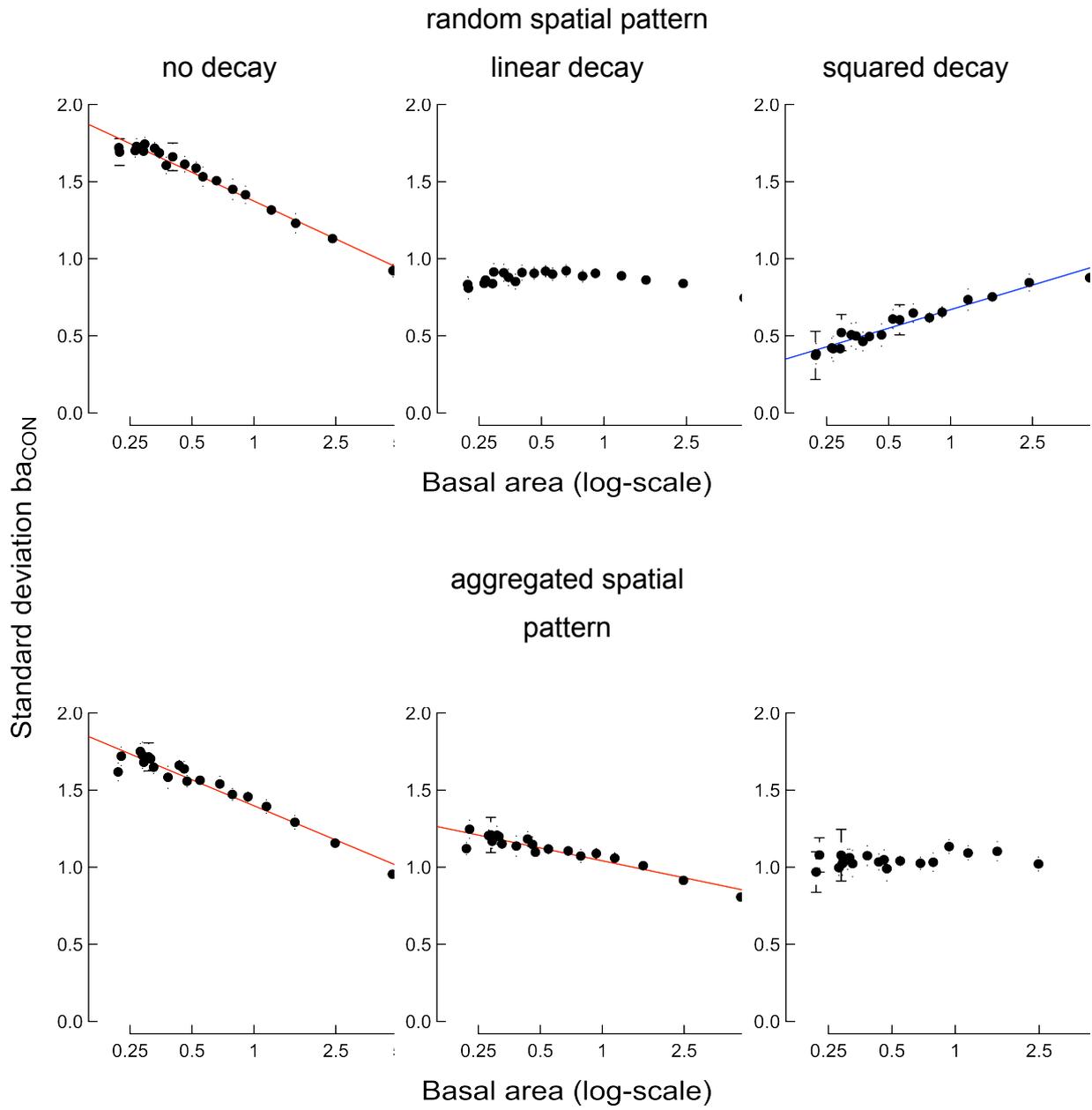


FIG. 3.

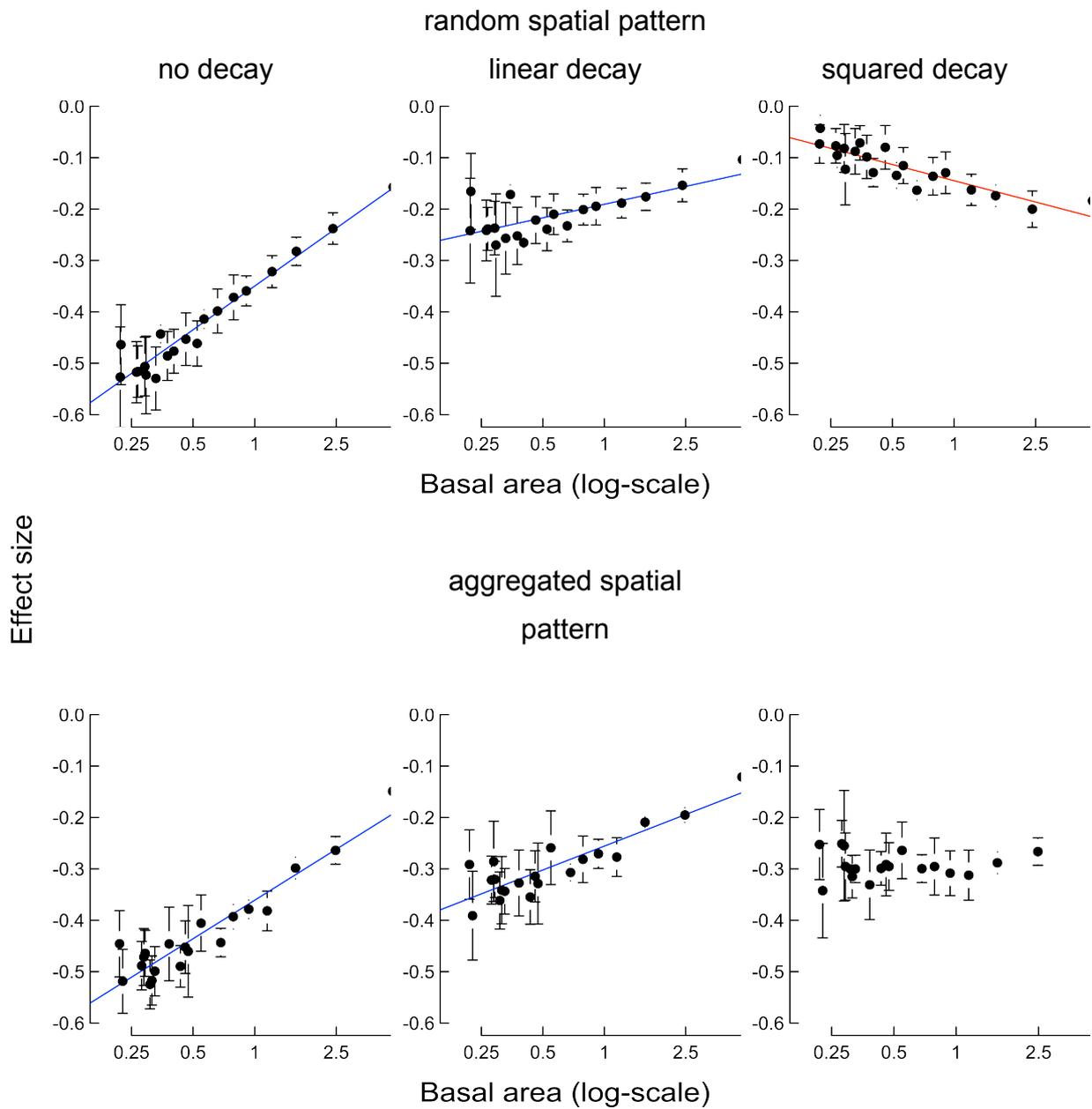


FIG. 4.

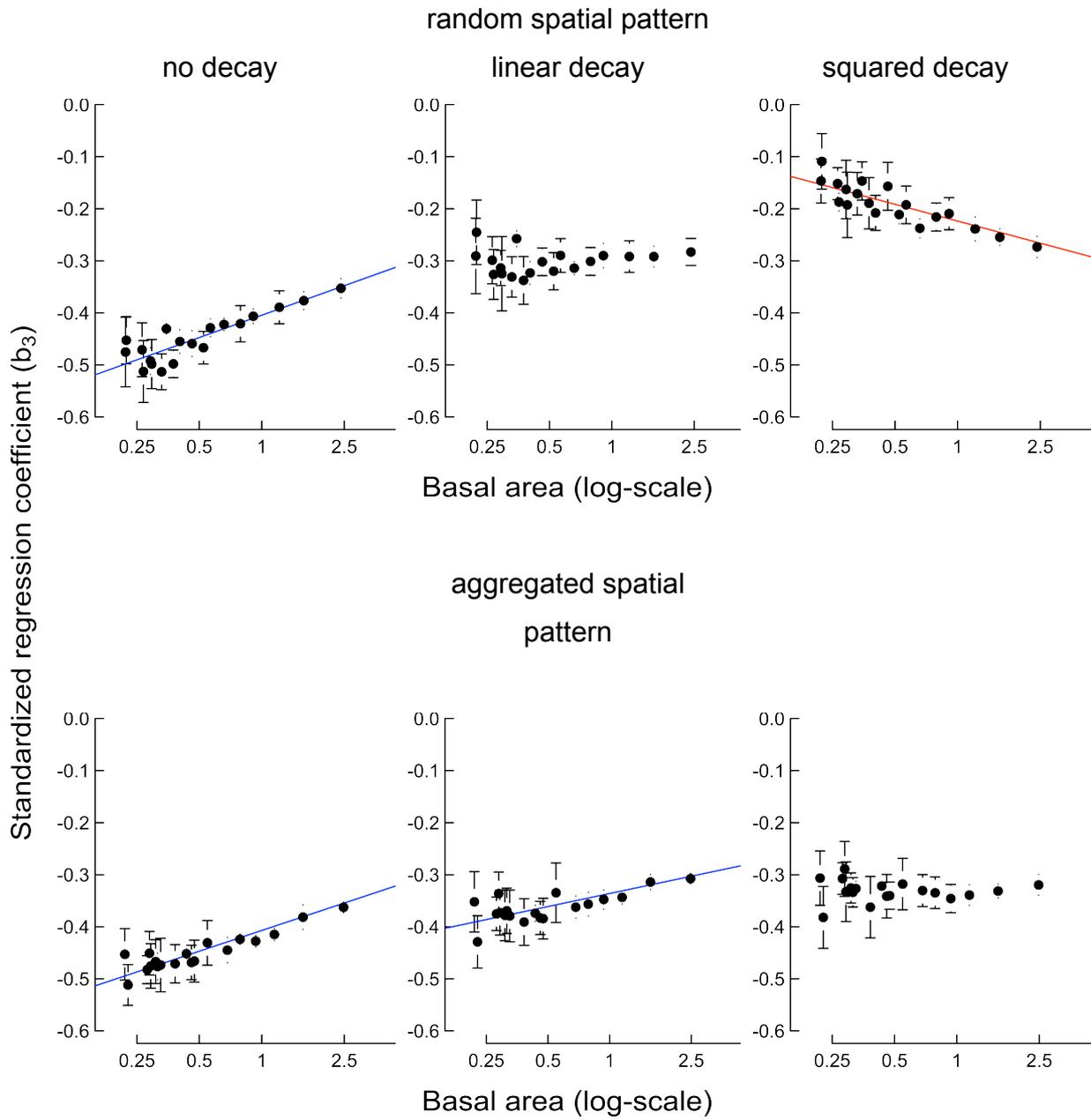


FIG. 5.