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14

15   **Abstract**

16   The Maximum Entropy Theory of Ecology (METE) predicts patterns of species abundance, size,

17   and spatial structure. The spatial component of the theory successfully predicts diversity patterns

18   across scales, but has focused on patterns that ignore inter-site spatial correlations. We developed

19   a semi-recursive version of METE's spatially explicit predictions for the distance decay of

20   community similarity and compared it to empirical data. The version of METE we examined

21   successfully captured the general form of the distance decay relationships, a negative power

22   function, but over-predicted the degree and rate of species turnover. Our results suggest that

23   while METE accurately predicts species occupancy and the species-area relationship, its semi-

24   recursive form does not accurately characterize spatially-explicit patterns of correlation. These

25   results also suggest that tests of spatial theories using only the species-area relationship may

26   yield good fits despite significant deviations in important aspects of spatial structure.

27

28   **Introduction**

29   The Maximum Entropy Theory of Ecology (METE) is a unified theory of biodiversity

30   that simultaneously predicts distributions of species abundance, body size, and spatial structure

31   (Harte et al. 2008, 2009, Harte 2011). One of METE's central assumptions is that ecological

32   communities are characterized by their most likely state given a set of constraints which can be

33   solved for using a Maximum Entropy modeling approach. METE has no free parameters and

34   only requires information on total community area, total number of individuals, total number of

35   species, and total metabolic rate of all individuals to generate its predictions.

36   There is strong empirical support for METE's predictions for the species abundance

37   distribution and patterns related to the spatial distribution of individuals and species (Harte et al.

38   2008, 2009, Harte 2011, White et al. 2012a, Xiao et al. 2013, McGlinn et al. 2013, Newman et al.

39   in review). Specifically, METE has been successful at predicting spatially implicit patterns of

40   community structure such as the species spatial abundance distribution and the species-area

41   relationship (Harte et al. 2008, 2009, McGlinn et al. 2013). It has even been proposed that the

42   METE spatial predictions yield a widely applicable universal species-area relationship (Harte et

43   al. 2009, 2013, but see Šizling et al. 2011, 2013). However all of METE's spatial predictions that

44   have been tested focus on spatially implicit patterns that ignore spatial correlations. As a result

45   the theory has not been evaluated using one of the core components of spatial structure. This is

46   due in part to the fact that METE's spatial correlation predictions have not been fully derived.

47   The most commonly studied ecological pattern that relies on these spatial correlations is

48   the distance decay relationship (DDR) in which the similarity of species composition decreases

49   with distance (Nekola and White 1999). This pattern is observed in almost all taxonomic groups,

50   at least at some spatial scales (Green et al. 2004, Soininen et al. 2007). The DDR provides a

51 spatially-explicit, community-level characterization of intra-specific aggregation patterns

52 including correlations in space (Plotkin and Muller-Landau 2002, Palmer 2005, Morlon et al.

53 2008, McGlinn and Palmer 2011). Despite the generality of the DDR there are only a small

54 number of simple models that attempt to predict the DDR from first principles (Chave and Leigh

55 2002, Condit et al. 2002, Zillio et al. 2005, Harte 2007, 2011, Nekola and McGill 2014), and

56 predicting this pattern is an important area of future development for METE because the DDR is

57 necessary to accurately extrapolate community patterns to unsampled areas (Harte 2011).

58   METE has thus far been used to derive the probability that a random cell on a landscape

59 will be occupied by a given number of individuals (i.e., the intra-specific spatial abundance

60 distribution). Predictions for this distribution have been based either on recursively subdividing

61 an area in half or on predicting species abundances directly at smaller scales (Harte 2011,

62 McGlinn et al. 2013). In addition to the spatial abundance distribution, the DDR requires a

63 prediction for the correlations in abundance among neighboring cells, which has proved difficult

64 to derive for METE (Harte 2011).

65   Here we explore one approach to making DDR predictions using METE by building on

66 the Hypothesis of Equal Allocation Probabilities (HEAP, Harte et al. 2005, Harte 2007) using an

67 approach that combines elements of both the non-recursive and recursive versions of METE.

68 We test those predictions using data from 16 spatially explicit plant communities and compare

69 METE's performance to the classic Random Placement Model (RPM) in which individuals are

70 randomly placed on the landscape (Coleman 1981). Additionally because METE can predict the

71 pattern of species abundances independently of its spatial predictions, we compared the METE

72 DDR using both the observed and predicted species abundances.

Methods

Developing METE's Spatially Explicit Predictions

METE's spatial predictions depend on two conditional probability distributions which are computed using independent applications of MaxEnt:

1) the species abundance distribution (SAD), $\Phi(n \mid S_0, N_0)$, the probability that a species has abundance n in a community with S_0 species and N_0 individuals, and

2) the intra-specific spatial abundance distribution, $\Pi(n \mid A, n_0, A_0)$, the probability that n individuals of a species with n_0 total individuals are located in a random quadrat of area A drawn from a total area A_0.

The METE prediction for Φ is calculated using entropy maximization with constraints on the average number of individuals per species (N_0/S_0) and the maximum number of individuals N_0 for a given species, which yields a truncated log-series abundance distribution (Harte et al. 2008, Harte 2011). The spatially implicit Π distribution is solved for using entropy maximization with constraints on the average number of individuals per unit area (n_0/A_0) and the maximum number of individuals n_0 of a given species. Although METE requires information on total metabolic rate to derive its predictions, this variable can be ignored when solving for Φ and Π (Harte et al. 2009, Harte 2011).

Previous studies have downscaled (or upscaled) METE's predictions using recursive and non-recursive approaches. Here we develop a spatially explicit approach to downscaling METE's predictions that combines elements of both approaches and builds off an existing theoretical framework for modeling the DDR. With the recursive version of METE, Φ and Π are solved for at each successive halving or bisection of A_0 until the area of interest is reached. After each bisection, Φ and Π are calculated and used to derive predicted values of average S and N at

96   that scale which provide updated constraints for the next bisection (Harte et al. 2009).

97   Alternatively, a non-recursive approach can be used in which, Φ and Π at the spatial grain of

98   interest can be solved for directly from the constraints placed at A_0 (Harte et al. 2008). A semi-

99   recursive approach is also possible in which Π is recursively downscaled but Φ is not. The semi-

100 recursive predictions of METE have not been previously examined but this model builds directly

101 on the existing theoretical derivations of the DDR by Harte (2007) for the Hypothesis of Equal

102 Allocation Probabilities (HEAP). In Appendix A, Fig. A1 we examine how the semi-recursive

103 formulation of METE differs from a previous examination of the METE recursive and non-

104 recursive SARs (McGlinn et al. 2013), and in Appendix B we develop the analytical derivations

105 of the semi-recursive formulation of the DDR.

106   In the semi-recursive formulation of the DDR, multi-cell correlations emerge from the

107 spatially nested application of a recursive bisection scheme in which individuals are randomly

108 placed in the left or right half of a cell at each bisection (Fig. 1). Biologically, this can be thought

109 of as a sequentially dependent colonization rule in which individuals randomly choose to occupy

110 the left or right side of an area depending on the existing number of individuals in each half

111 (Harte et al. 2005, Harte 2007, and Conlisk et al. 2007). Our version of METE predicts that for a

112 single bisection there is an equal likelihood for every possible spatial configuration of

113 indistinguishable individuals (Eq. B1). Multi-cell spatial correlations emerge from this approach

114 because the two cells that are formed from a common parent cell are adjacent to one another and

115 are likely to be more similar in abundance than other cells on the landscape (Fig. 1). This

116 approach has three important and inter-related limitations: 1) At each stage in the bisection

117 algorithm, information about the cells surrounding the parent cell is ignored when determining

118 allocations within the parent cell, 2) between-cell distance is defined in reference to an artificial

119 bisection scheme which does not have a one-to-one correspondence with physical distance, and 3)

120 the correlation between cells does not decrease smoothly with physical distance. Alternative

121 approaches have been proposed for deriving the DDR for METE based on computing the single-

122 cell Π distribution at two or more scales and then using the scaling of this marginal distribution

123 to infer the probabilities of a given spatial configuration of abundance (Harte 2011). However,

124 these approaches have yet to yield predictions for the DDR.

125   The analytical forms of the semi-recursive formulation (Appendix B) are time-intensive

126 to compute due to the multiple levels of recursion, ignore patterns of abundance (i.e., are

127 formulated only in terms of presence-absence), and are not exact. An alternative approach to

128 deriving semi-recursive METE predictions for the DDR is to use a spatially-explicit simulation.

129 *Spatially Explicit METE Simulation*

130   To simulate semi-recursive METE's spatial predictions the equal probability rule (Eq. B1)

131 that METE predicts when total area is halved is recursively applied starting at the anchor scale A_0

132 and progressively bisecting the area until the finest spatial grain of interest is achieved (Fig. 1).

133 Abundance in the simulation model can be parameterized using an observed SAD or using a

134 random realization of the METE SAD given the values of S_0 and N_0. Once the abundances of the

135 species are assigned, each species is independently spatially distributed. Because the equal

136 probability rule requires that there is an equal probability of 0 to n_0 individuals occurring on the

137 left or right side of the total area A_0, the number of individuals in the left side can be set as a

138 draw from a discrete random uniform distribution between 0 and n_0 and the remaining number of

139 individuals are placed on the right hand side.

140   *Datasets*

141   We used a database of 16 spatially explicit and contiguous community datasets compiled

142   by McGlinn et al. (2013) to evaluate the DDR predictions of recursive METE (Table 1). All of

143   the sites were terrestrial, woody plant communities with the exception of the serpentine grassland

144   dataset which covered a terrestrial, herbaceous plant community. In the woody plant

145   communities, all stems were recorded that were at least 10 mm in diameter at breast height (i.e.,

146   1.4 m from the ground) with the exception of the Oosting and Cross Timbers sites where the

147   minimum diameter was 20 and 25 mm respectively. Recursive METE only generates predictions

148   for bisections of total area; therefore, we restricted our analysis to square or rectangular areas

149   with a length-to-width ratio of 2:1. Two of the sites had irregular plot designs: Sherman and

150   Cocoli. At these sites we partitioned the datasets into two 2:1 rectangles and analyzed each half

151   independently and then averaged the results (see Supplemental Information: Fig. S1 in McGlinn

152   et al. 2013). See McGlinn et al. (2013) for additional information on site selection criteria, and

153   in particular their Supplemental Table 1, which provides a more complete description of the

154   datasets used in our analysis.

155   *Data Analysis*

156   We compared the fit of METE with and without the observed SAD and the random

157   placement model (RPM) to the empirical DDRs. The METE predictions represented averages of

158   the abundance-based Sørensen index across 200 simulated communities. The abundance-based

159   RPM predictions were generated by distributing the observed number of individuals of each

160   species randomly in space and then computing the average abundance-based Sørensen index

161   across 500 permutations (Morlon et al. 2008).

162   The DDR is sensitive to the choice of the spatial grain of comparison (Nekola and White

163   1999); so, we examined the DDR at several spatial grains for each dataset. We examined spatial

164   grains resulting from 3-13 bisections of A_0. To ensure that the samples at a given grain were

165   square we only considered odd numbers of bisections when A_0 was rectangular and even

166   numbers of bisections when A_0 was square. To ensure the best possible comparison between the

167   observed data and METE and to avoid detecting unusual spatial artefacts in the METE predicted

168   patterns we employed the "user rules" of Ostling et al. (2004) such that samples were only

169   compared if they were separated by a specific line of bisection (i.e., a given separation order, Fig.

170   1 and Appendix A, Fig. A2). This approach was taken rather than the standard method of

171   constructing the DDR from all possible pairwise sample comparisons without reference to an

172   imposed bisection scheme. For the Crosstimbers study site we were not able to examine the DDR

173   based on the METE SAD because of difficulty in generating random realizations of the METE

174   SAD needed for the community simulator when S_0 is less than approximately 10.

175   We used weighted least squares (WLS) regression for estimating the intercept and slope

176   of power and exponential models of the DDR to account for differences in the number of

177   pairwise comparisons at different spatial lags. We examined the power model and exponential

178   models because they are the simplest statistical models of the DDR that tend to fit well (Nekola

179   and White 1999, Nekola and McGill 2014).

180   We checked that our results were consistent with the results provided in previous studies

181   (Harte 2007, Fig. 6.7 and 6.8, 2011, Fig. 4.1), and that the DDR generated by the community

182   simulator closely agreed with the analytical solution Eq. B5 (Appendix B, Fig. B1). The code to

183   recreate the analysis is provided as Appendix D and at the following publicly available

184   repository: https://github.com/weecology/mete-spatial.

185 **Results**

186   In general, the semi-recursive METE distance decay relationship (DDR) provided a poor

187 fit to the empirical DDR (Figs. 2 and 3). While the METE DDRs exhibited the general functional

188 form of the empirical DDRs, an approximately power-law decrease in similarity with distance,

189 they typically had lower intercepts and steeper slopes than the empirical DDRs (Fig. 2, Appendix

190 A, Fig. A3 and A4). Both the empirical and METE predicted DDR were better approximated by

191 power rather than exponential models (Appendix A, Fig. A4). METE converged towards

192 reasonable predictions at fine spatial grains; however, this is to be expected because at these

193 scales similarity in both the observed and predicted patterns must converge to zero due to low

194 individual density (grey points in Fig. 3A,B). This is because when individual density is low the

195 probability of samples sharing species decreases rapidly simply due to chance. The RPM is

196 known to be a poor model for distance decay because it does not exhibit a decrease in similarity

197 with distance. However, it fit the empirical DDR slightly better than METE (Figs. 2 and 3).

198   The METE DDR was not strongly influenced by the choice of using the observed or the

199 METE SAD (Figs. 2 and 3A,B). The METE SAD typically yielded a DDR with a slightly lower

200 intercept with the exception of the four tropical sites where it produced DDRs with slightly

201 higher intercepts. In general, we did not observe strong consistent differences between the

202 habitat types (Fig. 2, Appendix A, Fig. A5).

203   Our formulation of a semi-recursive METE produced SARs that generally agreed (i.e.,

204 within the 95% CI) with the recursive and non-recursive formulations of METE (Harte et al.

205 2009); however, it did appear that the semi-recursive approach systematically deviated towards

206 lower richness at fine spatial scales which is consistent with predicting stronger patterns of

207 spatial aggregation compared to the other formulations of METE (Appendix A, Fig. A1).

208   **Discussion**

209   The semi-recursive METE distance decay relationship (DDR) was well approximated by

210   a decreasing power function, and thus consistent with the general form of empirical DDRs, but it

211   provided a poor fit to empirical data. Specifically, the slope and the intercept of this power

212   function deviate substantially from empirical data resulting in a poor fit. These deviations

213   contrast with a number of studies showing that the theory successfully predicts both the Π

214   distribution and the SAR (Harte et al. 2008, 2009, Harte 2011, McGlinn et al. 2013, but see

215   Šizling et al. 2011). Both Π and the SAR are influenced by the spatially explicit pattern of

216   intraspecific aggregation but neither pattern reflects inter-quadrat correlations and therefore they

217   represent coarse metrics of spatial structure. The combination of a well fit SAR and a poorly fit

218   DDR suggests that the current version of METE accurately characterizes average occupancy, but

219   fails to characterize the spatial relationships among cells (McGeoch and Gaston 2002, Storch et

220   al. 2003, McGlinn and Hurlbert 2012, Nekola and McGill 2014).

221   These results only apply directly to the particular HEAP-based semi-recursive version of

222   the spatial METE theory, which represents a middle ground in terms of approach between Harte

223   et al. (2008) and Harte et al. (2009). Other approaches to deriving the METE DDR may perform

224   better than the semi-recursive approach if they can be developed. It has been suggested that there

225   is no *a priori* reason to prefer one version of the theory and that the best way to choose among

226   the different versions is empirically (Haegeman and Etienne 2010, Harte 2011). However, the

227   traditionally defined recursive and non-recursive versions of METE have shortcomings with

228   respect to how their assumptions and predictions are scaled, and the semi-recursive approach we

229   defined is limited by its dependence on an artificial bisection scheme. Specifically the recursive

230   approach predicts that the SAD has the same functional form, a truncated log-series, at all scales.

231 This is problematic because SADs are typically not scale-invariant if, as METE predicts, species

232 display intraspecific spatial aggregation (Green and Plotkin 2007, Šizling et al. 2009). The non-

233 recursive approach does not suffer from this problem because the SAD is only solved for at the

234 anchor scale; however, Haegemann and Etienne (2010) found that the non-recursive predictions

235 for a multi-cell generalization of the Π distribution were scale-inconsistent. The semi-recursive

236 approach does not suffer from this shortcoming because its multi-cell form (see Eq. 2.2 in

237 Conlisk et al. 2007) is only defined over the set of bisections that are consistent with a landscape

238 in which n_0 individuals are distributed (see Appendix C for proof). However, the set of bisections

239 is artificial and multi-cell correlations only emerge from this approach in reference to bisection

240 distance rather than directly to physical distance between cells such that cells have equal

241 magnitude of correlation regardless of their physical distance if they have equivalent separation

242 orders (see Conlisk et al. 2007 for a critique of distances defined by separation indices). An

243 important future direction for METE is to attempt to develop spatial multi-cell predictions using

244 approaches that avoid these shortcomings and the two approaches suggested by Harte (2011) for

245 deriving the METE DDR may provide a useful starting point for future development.

246   Our results suggest that semi-recursive METE differs from spatial patterns observed in

247 nature. This deviation could indicate that the emergent statistical approach to modeling spatial

248 structure is incorrect, with some set of specific biological processes such as dispersal limitation

249 or environmental filtering directly controlling spatial correlation (Condit et al. 2002, Gilbert and

250 Lechowicz 2004, Karst et al. 2005, Seidler and Plotkin 2006, Chase 2007, McGlinn and Palmer

251 2011). Alternatively it could mean that while the general idea underlying the theory is valid, the

252 specific formulation is wrong. For example it could be that the approaches outlined by Harte

253 (2011) that are more sophisticated in how they handle spatial correlations will be more

254   appropriate or that a generalized version of this kind of recursive approach like that developed by

255   Conlisk et al. (2007) in which the degree of aggregation is a tunable parameter will capture the

256   reality of biological systems more precisely. Although Conlisk et al. (2007) did not use MaxEnt

257   to derive their models, Haegeman and Etienne (2010) suggest that it may be possible to obtain

258   many reasonable models of the Π distribution using maximum entropy approaches.

259   Our results mirror those of Xiao et al. (2013) and Newman et al. (in review) evaluating

260   the non-spatial aspects of METE. All three studies show that when evaluating the theory using

261   multiple patterns simultaneously some of the predictions perform well and some perform poorly.

262   It is inherently difficult for theories to predict large numbers of patterns simultaneously, which is

263   why evaluating theory in this way provides stronger tests than evaluating single patterns (McGill

264   2003, McGill et al. 2006). General theories like METE that make multiple predictions are

265   therefore both easier to evaluate and also more broadly useful since they allow a large number of

266   patterns to be predicted from a relatively small amount of information. Because there are many

267   patterns to evaluate it is also more likely that deviations from theory will be identified (White et

268   al. 2012b). In some cases these deviations may indicate that the theory is fundamentally unsound,

269   but in others it may suggest modifications to the theory to address the observed deviations

270   (White et al. 2012b). Whether METE can be modified to address the observed deviations from

271   empirical data remains to be seen. In the case of the DDR, despite its generality, there are a

272   limited number of models that attempt to predict the DDR from first principles (Chave and Leigh

273   2002, Condit et al. 2002, Zillio et al. 2005, Harte 2007, 2011, Nekola and McGill 2014), which

274   means that it may be worth pursuing the METE approach further.

275   METE is one of several general theories in ecology that make many predictions for many

276   aspects of ecological community structure based on only a small amount of information. Our

277   analysis of the semi-recursive formulation of METE's spatially explicit prediction for the DDR

278   suggests that this form of the theory over-predicts the strength of spatial correlation. These

279   results coupled with studies of the species-area relationship suggest that semi-recursive METE

280   accurately predicts the scaling of species occupancy but not spatial correlation. More generally,

281   our results demonstrate that tests of spatial theories that focus solely on the species-area

282   relationship and related patterns are only evaluating part of the spatial pattern, the distribution of

283   occupancy among cells. Evaluating these theories using the DDR in addition to the SAR will

284   help identify cases where the theories are correctly identifying some aspects of spatial structure,

285   but not others, and thus yield stronger tests of the underlying theory. In some cases this will

286   require extending the theory to make additional predictions, but this effort will provide both

287   more testable and more usable theories.

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427

Tables:

Table 1. Summary of the habitat type and state variables of the vegetation datasets. The state variables are total area (A_0), total abundance (N_0) and total number of species (S_0). A_{min} and A_{max} are the finest and coarsest areas (m^2) examined. Data was collected on woody forest plants with the exception of the serpentine site which contained herbaceous grassland plants.

Site name	Habitat type	Ref	A_{min}	A_{max}	A_0	N_0	S_0
BCI	tropical	1-3	61.0	62500	500000	205096	301
Sherman	tropical	4	2.4	625	20000	7622.5	174.5
Cocoli	tropical	4	2.4	625	20000	4326	138.5
Luquillo	tropical	5	15.3	15625	125000	32320	124
Bryan	oak-hickory	6-8	2.1	534.8	17112.5	3394	48
Big Oak	oak-hickory	6-8	2.4	625	20000	5469	40
Oosting	oak-hickory	9	16	4096	65536	8892	39
Rocky	oak-hickory	6-8	3.5	900	14400	3383	37
Bormann	oak-hickory	6-8	4.8	1225	19600	3879	30
Wood Bridge	oak-hickory	6-8	1.2	315.1	5041	758	19
Bald Mtn.	oak-hickory	6-8	2.4	156.3	5000	669	17
Landsend	old field, pine	6-8	1.0	264.1	8450	2139	41
Graveyard	old field, pine	6-8	2.4	625	10000	2584	36
UCSC	mixed-evergreen	10	5.4	1406.3	45000	5885	31
Serpentine	serpentine	11	0.3	4	64	37182	24
Cross Timbers	oak woodland	12	9.8	2500	40000	7625	7
Ranges			0.3-61.0	4-62500	64-500000	669-205096	7-301

[1.] Condit (1998), [2.] Hubbell et al. (1999), [3.] Hubbell et al. (2005), [4.] Condit et al. (2004), [5.] Zimmerman et al. (1994), [6.] Peet and Christensen (1987), [7.] McDonald et al. (2002), [8.] Xi et al. (2008), [9.] Palmer et al. (2007), [10.] Gilbert et al. (2010), [11.] Green et al. (2003), [12.] Arévalo (2013)

436 **Figures**

437
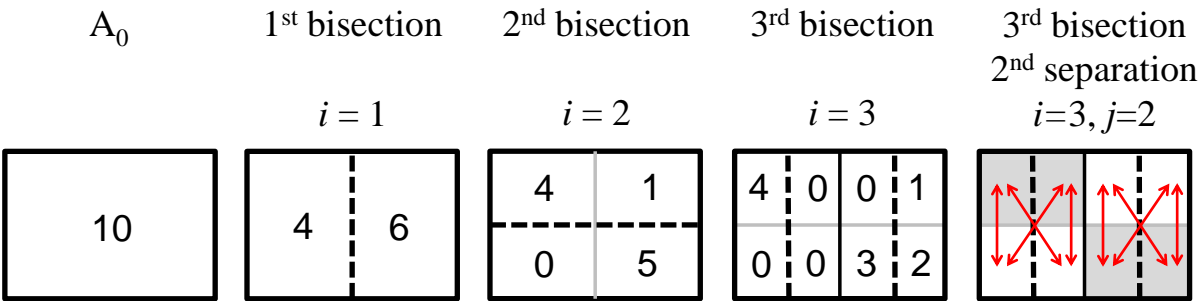
438 *Fig 1*. This diagram illustrates the "user rules" of how a landscape is bisected and how samples

439 are compared for a given separation order. In this specific example, three bisections are used to

440 generate a spatially explicit distribution of 10 individuals. In the last panel, the eight pairwise

441 comparisons (red arrows) at separation order of 2 for a scale of $A_0/2^3$ (i.e., $A_{i=3}$, $D_{j=2}$) are

442 illustrated. When simulating random bisections the number of individuals distributed to the left

443 or right of the bisection line is a random draw from a discrete uniform distribution.

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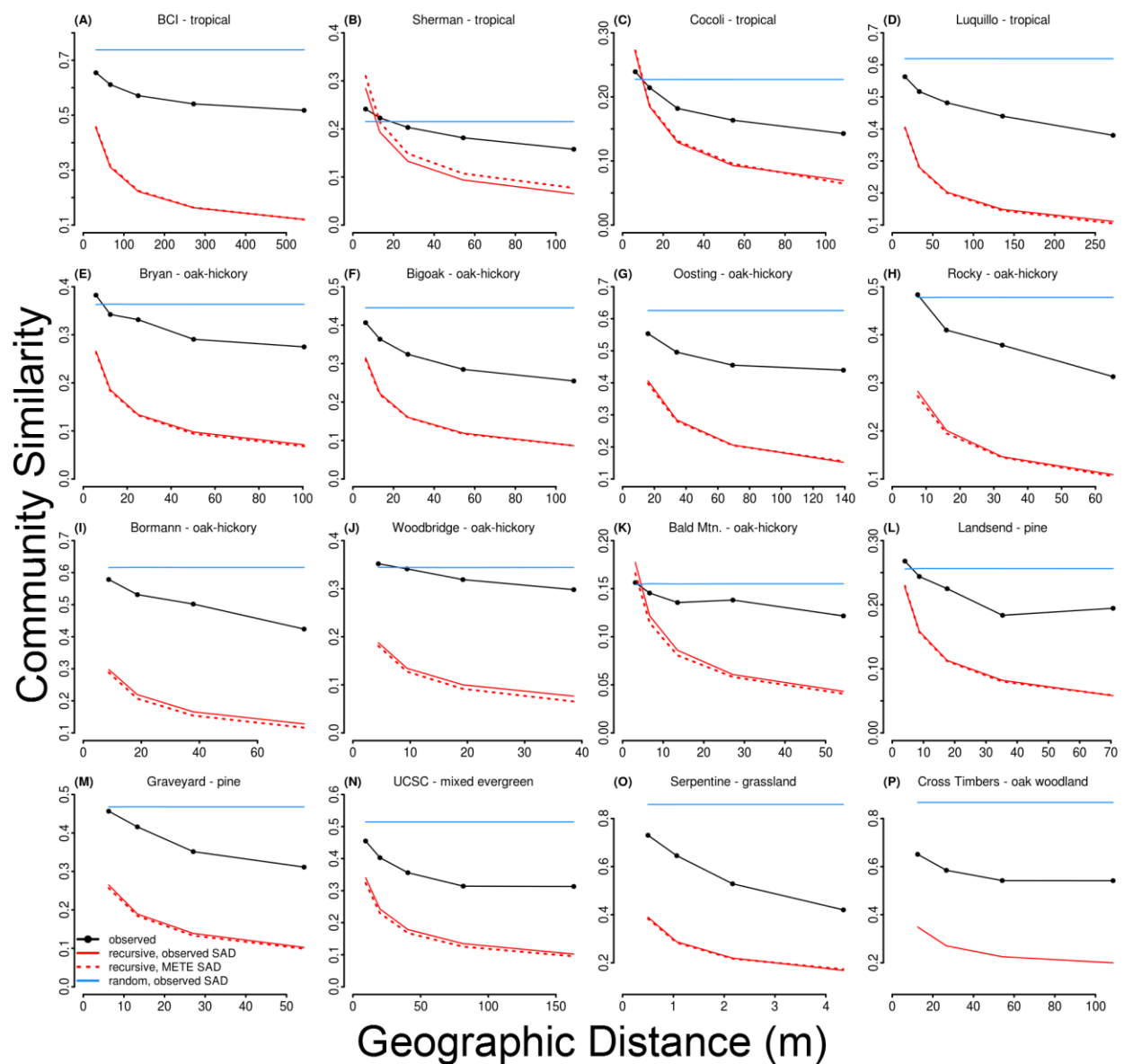
Fig 2. The observed and predicted distance decay relationships for each site at a single spatial

grain. Community similarity represents the average of the abundance-based Sørensen index for

each spatial lag. The spatial grain displayed was taken at either 8 or 9 bisections of the total area

depending on whether the total extent was a square or a rectangle respectively.
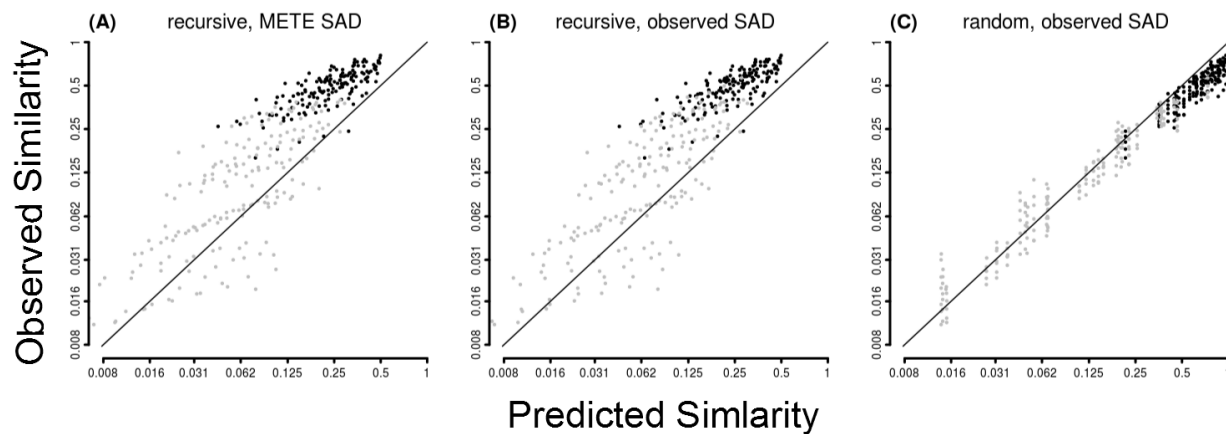
451

Fig 3. The log-log transformed one-to-one plots of the predicted and observed abundance-based

Sørensen similarity values for the three models across all distances and spatial grains. The solid

line is the one-to-one line. The grey points represent values from spatial grains in which the

average individual density was low (i.e., less than 10 individuals) and thus both the observed and

predicted similarities must be close to zero simply because of a sampling effect.