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1 Efficient sampling designs to assess biodiversity
2 spatial autocorrelation : should we go fractal ?

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6 **Abstract**

7 1. Evaluating the autocorrelation range of species distribution in
8 space is necessary for many applied ecological questions like im-
9 plementing protected area networks or monitoring programs. The
10 autocorrelation range can be inferred from observations, based on
11 a spatial sampling design. However, there is a trade-off between
12 estimating the autocorrelation range of a species distribution and
13 estimating fixed effects affecting the mean species abundance or oc-
14 cupancy among sites. The random sampling design is considered as a
15 good heuristic to estimate autocorrelation range, for it contains con-
16 trasted pairwise distances that cover a wide array of possible range
17 values. The grid design is viewed as a better choice for estimat-
18 ing fixed effects, for it eliminates small pairwise distances that are
19 more prone to pseudo-replication. Mixing random and grid ('hybrid'
20 designs) has been presented as a way to navigate between both con-
21 flicting objectives. We postulated that fractal designs — which have

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22 a self-similarity property and well-identified scales — could make a
23 compromise, for they preserve some regularity reminiscent of grid at
24 each scale, but also browse a wide array of possible autocorrelation
25 range values across scales.

26 2. We used maximum likelihood estimation within an optimal design of
27 experiments approach to compare the accuracy of hybrid and fractal
28 designs at estimating the fixed intercept and the autocorrelation
29 range of a spatial field of values.

30 3. We found that hybrid designs were Pareto-optimal intermediary
31 strategies between grid and random for small autocorrelation range
32 values only, while classic grid design should always be preferred when
33 autocorrelation is large. Fractal designs yielded Pareto-optimal stra-
34 tegies specifically good at estimating small autocorrelation ranges.
35 However, they were generally not Pareto-optimal for higher values
36 of autocorrelation range. At last, when the surveyed area could be
37 changed, random designs were sufficient to reach the Pareto front in
38 any context.

39 4. Fractal designs seemed relevant when specifically aiming at improv-
40 ing the estimation of small autocorrelation ranges in a fixed surveyed
41 area with a limited sampling budget, which is a quite circumscribed
42 scenario. However, they may prove more clearly advantageous to
43 analyse biodiversity patterns when covariates are included in the
44 analysis and ecological processes differ among spatial scales.

45 **Keywords:** beta-diversity; distance-decay; fractal; maximum likelihood;
46 model-based inference; optimal design; sampling design; spatial autocorrelation

47 Introduction

48 Autocorrelation has a double status in the study of biodiversity patterns (Leg-
49 endre, 1993). It is often seen as a nuisance, generating biases in regression
50 models that seek to link covariates to spatial patterns of biodiversity (Lennon,
51 2000). Many techniques to control these undesirable effects are available, and
52 now well popularized among ecologists (Dormann et al., 2007). However, spa-
53 tial autocorrelation may also be viewed as the signature of endogeneous process
54 driving biodiversity patterns (McGill, 2010). In particular, it is often interpreted
55 through the prism of limited dispersal. For instance, auto-regressive modelling
56 of species occupancy in metapopulation ecology (ter Braak et al., 1998; Bardos
57 et al., 2015; Prugh, 2009; Ranius et al., 2010) or isolation by distance patterns
58 on neutral markers in population genetics (Ouborg et al., 1999; Vekemans and
59 Hardy, 2004; Manel and Holderegger, 2013) are often used to draw conclusion
60 on species colonization or dispersal abilities. From this perspective, the accu-
61 rate assessment of autocorrelation range has important implications in terms of
62 conservation biology, especially to assess the functional connectivity of habitat
63 networks (Tischendorf and Fahrig, 2000) or build efficient biodiversity monitor-
64 ing strategies (Rhodes and Jonzén, 2011).

65 Few studies focused on efficient designs to accurately estimate autocorrela-
66 tion range of biodiversity. In a simulation study, Bijleveld et al. (2012) showed
67 that a grid design was the best choice to estimate spatial or temporal trends on
68 the mean of a target field of values while random design was better at estimating
69 autocorrelation parameters. The authors further showed that a hybrid strategy,
70 mixing randomly chosen sites with a grid, stood as a Pareto-optimal solution
71 on the trade-off between the conflicting objectives (i.e. changing to other de-
72 signs necessarily generated performance loss on either objective). Following a
73 distinct line of research, Marsh and Ewers (2013) suggested that fractal sam-

74 pling designs may be an efficient option to study the distance-decay pattern of
75 β -diversity (Nekola and White, 1999), which can be seen as way to assess the
76 autocorrelation range of species composition among communities. Fractal de-
77 signs are characterized by a self-similar property (Mandelbrot, 1983; Falconer,
78 2003): sub-parts of the design look like a contraction of the total design, and
79 natural spatial ‘scales’ can thus be distinguished (see Fig. 1A). Thanks to this
80 property, a single fractal design can cover contrasted spatial scales with a low
81 sampling effort compared to other sampling strategies, which may offer a prac-
82 tical way to studying autocorrelation over a broad set of possible ranges. Based
83 on a non-parametric study of distance-decay patterns, the authors found that
84 fractal designs lead to estimating higher values of autocorrelation range than an
85 intensive control design, while other classic strategies (regular grid and random
86 design) tended to yield lower values of autocorrelation range than the control.
87 These results suggest that fractal designs have distinct properties, but precise
88 conclusions are hindered by the fact that the model used by Marsh and Ew-
89 ers (2013) to generate the data is a complex mixture of ecological scenarios
90 that does not have a well-defined statistical formulation, which impeded a clear
91 definition of estimation errors.

92 Here, we aimed at comparing fractal designs with random, grid and hybrid
93 strategies with respect to their ability to quantify autocorrelation range ver-
94 sus fixed effects on the mean of a spatial random field. We turned towards
95 the framework of optimal design of experiments (Müller et al., 2012), which
96 has been repeatedly used to build and compare designs of temporal (Archaux
97 and Bergès, 2008) or spatio-temporal [see (Hooten et al., 2009) and references
98 therein] biodiversity surveys. However, it has quite rarely been applied to the
99 specific problem of quantifying spatial autocorrelation. A noticeable exception
100 on that matter is the study by Müller (2007), which focused on the problem of

101 detecting autocorrelation with a test using Moran index (Moran, 1950). How-
102 ever, they did not quantify the corresponding range. Here, we focused on esti-
103 mation error when simultaneously estimating the mean (i.e. a fixed intercept)
104 and the autocorrelation range of a spatial field. We specifically considered the
105 maximum likelihood estimation framework which offers a powerful heuristic to
106 theoretically explore the estimation accuracy of sampling designs through the
107 analysis of the inverse Fisher matrix (Abt and Welch, 1998). Zhu and Stein
108 (2005) used this approach to numerically search for sampling designs able to
109 recover autocorrelation parameters. They found that designs showing the best
110 global performance at estimating autocorrelation parameters differ from random
111 design, and tend to conciliate aggregated points at the center of the surveyed
112 area with points scattered close to the frontier. Such designs might be viewed
113 as harbouring distinct scales and might be well approached by fractal designs,
114 hence reinforcing the interest of explicitly assessing fractal design performance.

115 When comparing random, grid, hybrid and fractal designs, we had two
116 expectations grounded on the literature previously cited: (i) hybrid designs
117 should constitute a continuous set of intermediary Pareto-optimal designs be-
118 tween grid and random designs, meaning that when the proportion of random
119 points increases from 0 (grid design) to 1 (random design), the accuracy of
120 the mean estimate of the random field should decrease while the accuracy of
121 the autocorrelation range estimate should increase; (ii) fractal designs should
122 be better than other designs at estimating small autocorrelation ranges when
123 they are built to harbour contrasted scales, hence creating new Pareto-optimal
124 solution focused on autocorrelation range estimation.

125 Methods

126 Spatial sampling designs

127 All spatial sampling designs harboured $N = 27$ sampling points (the effect of
128 larger N is discussed later on). Sampling points are spread within an area of
129 study shaped as an equilateral triangle with a side length of $L = \sqrt{3}$ distance
130 units. Random designs were generated by sampling each plot independently
131 within the triangle with a homogeneous spatial density. Grid designs were ob-
132 tained by first generating a triangular grid matching the area of study with mesh
133 size equal to $L/6$ distance units, hence obtaining 28 sampling points, and then
134 removing one point at random. Hybrid designs were characterized by a param-
135 eter p , the proportion of sites that are randomly positioned in the area of study.
136 A hybrid design was obtained by building a grid design, selecting Np sites at
137 random within it and resampling their new position at random in the area of
138 study. Note that $p = 0$ yields the grid design while $p = 1$ yields the random
139 design. Here we consider the $N + 1 = 28$ values of $p \in \{0, 1/N, 2/N, \dots, 1\}$.

140 Following Marsh and Ewers (2013), we simulated fractal designs using an
141 iterated function systems (Falconer, 2003) based on three similarities of the
142 complex plane: $S_k(z) = \rho z + (1 - \rho)e^{\frac{2ik\pi}{3} - \frac{i\pi}{6}}$ for $k \in \{0, 1, 2\}$. A sampling
143 design is obtained by iterating three times the system starting from a seed at
144 the center of the area, hence yielding a sampling design with $N = 3^3 = 27$
145 plots. We varied the parameter ρ across designs. The parameter ρ drives the
146 ratio between the size of a part of the design and the size of the larger, auto-
147 similar set of plots it belongs to. The values of ρ considered in the study are :
148 $\rho = x\sqrt{3}/(2 + \sqrt{3})$ with 240 distinct x values evenly spaced on a log-scale from
149 $x = 10^{-1.5}$ to $x = 1$. We call x the ‘contraction parameter’ of fractal design
150 below. Note that $x > 1$ would generate a sampling design with overlapping
151 sub-components, which we considered as an undesirable property. The largest

152 value $x = 1$ yields a sampling design that is a subsample of the regular grid

153 with mesh size of c.a. $L/10$.

154 Examples of designs are presented in figure 1.

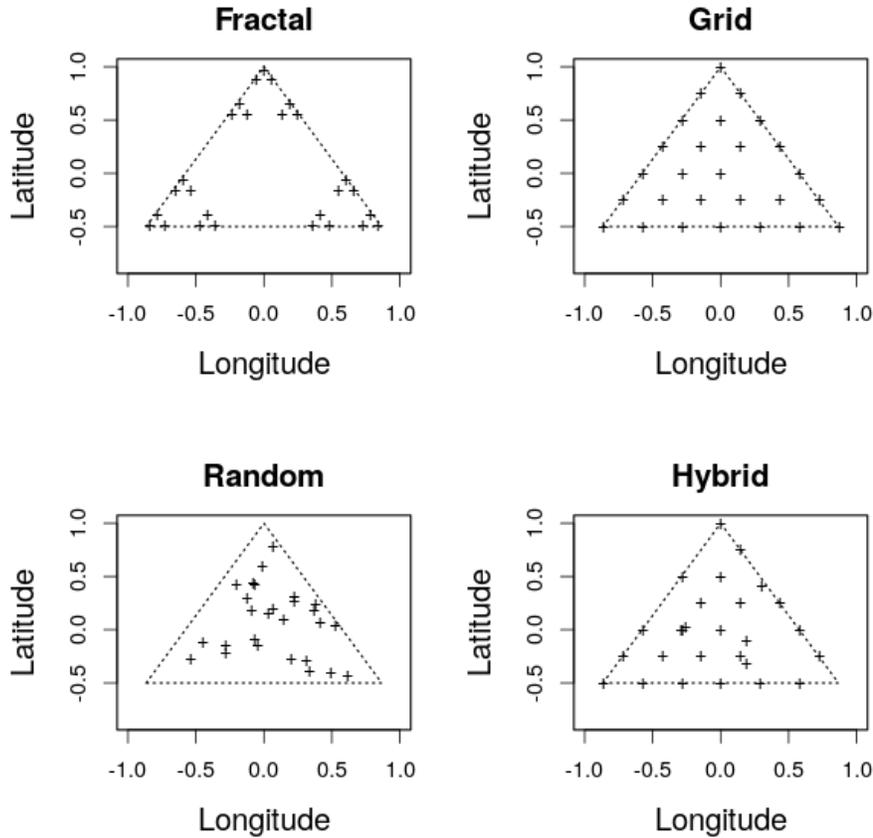


Figure 1: Examples of the four types of design considered in our study. The triangle dashed area is the area of study. Crosses show the position of the 27 sampling points. The fractal design presented here is generated with a contraction coefficient $x = 2/3$. The hybrid design is generated using a proportion of random sites $p = 5/27 \approx 0.19$.

155 **Gaussian random field model**

156 To study the error of estimation associated to each type of design depicted
157 above, we assumed that the vector of observations at each sampling points
158 $\mathbf{Z} = (Z_1, \dots, Z_N)$ is taken from a Gaussian random field with an exponential
159 variogram (Cressie, 1993) without nugget effect. Formally, it means that there
160 exist $\mu \in \mathbb{R}$ and $\sigma, a_s \in \mathbb{R}^{+*}$ such that:

$$\begin{aligned} \forall i \in \{1, \dots, N\}, Z_i &\sim \mathcal{N}(\mu, \sigma^2) \\ \forall i, j \in \{1, \dots, N\}^2, \mathbb{E}[(Z_i - Z_j)^2] &= 2\sigma^2 \left(1 - e^{-\frac{d_{ij}}{a_s}}\right) \end{aligned} \quad (1)$$

161 where d_{ij} is the distance between sampling points i and j and $\mathbb{E}[\cdot]$ denotes
162 the expectation of a random variable. The covariance between Z_i and Z_j is
163 $\text{Cov}[Z_i, Z_j]$, is:

$$\text{Cov}[Z_i, Z_j] = \sigma^2 e^{-\frac{d_{ij}}{a_s}} \quad (2)$$

164 which renders the simulation of \mathbf{Z} straightforward.

165 Parameter a_s corresponds to a characteristic length of the autocorrelation,
166 and we call it ‘autocorrelation range’ below. The parameter μ corresponds to
167 the mean of the random field. Although one could include effects of covariates
168 on this parameter, we followed previous studies [e.g. (Zhu and Stein, 2005)] and
169 considered a simple fixed-intercept model, where the mean is a single parameter
170 constant across space that one wants to accurately estimate it.

171 We considered 160 distinct a_s values evenly spaced on a log-scale between
172 10^{-3} and $10^{2.5}$. As we will show below, the values of μ and σ did not affect
173 estimation errors considered in our analysis, and we could therefore set $\mu = 0$
174 and $\sigma = 1$ without loss of generality.

175 **Estimation variance of maximum likelihood estimates**

176 We assimilate the problem of assessing autocorrelation range to accurately esti-
177 mate a_s and the problem of assessing the mean of the field of values to accurately
178 estimating $\alpha = e^\mu$. We considered the exponential mean to compare estimation
179 error of parameters that are defined on the same domain \mathbb{R}^{+*} . Estimation error
180 on a parameter θ ($= \alpha$ or a_s) is quantified through the relative root mean square
181 error:

$$RRMSE(\theta) = \sqrt{\mathbb{E}[(\hat{\theta} - \theta)^2]}/\theta$$

182 The statistical model used to estimate a_s and α matches the one used to generate
183 the data (i.e. we assume no error on model specification):

$$\mathbf{Z} = \mu\mathbf{1} + \mathbf{E}$$

184 where $\mathbf{1}$ is a N -dimensional vector with all coordinates equal to 1, and \mathbf{E} is
185 a N -dimensional gaussian vector with mean $\mathbf{0}$ and variance-covariance matrix
186 Σ following the exponential model presented in (2). Parameters of this model
187 can be summarized in a vector $\boldsymbol{\theta} = (\alpha, \sigma, a_s)$. We focused on the maximum
188 likelihood estimate $\hat{\boldsymbol{\theta}} = (\hat{\alpha}, \hat{\sigma}, \hat{a}_s)$ of $\boldsymbol{\theta}$.

189 In the context of stationary Gaussian random fields without nugget, it is
190 known that the diagonal terms of $\mathcal{I}(\boldsymbol{\theta})^{-1}$, where $\mathcal{I}(\boldsymbol{\theta})$ is the Fisher informa-
191 tion matrix of the model with true parameters $\boldsymbol{\theta}$, yield a qualitatively good
192 approximation of the quadratic error on parameters in $\boldsymbol{\theta}$. By ‘qualitatively’,
193 we mean that it allows to correctly rank designs according to their accuracy,
194 even for moderate sample sizes (Abt and Welch, 1998; Zhu and Stein, 2005).
195 We therefore use the diagonal terms of $\mathcal{I}(\boldsymbol{\theta})^{-1}$ as a theoretical approximation
196 of quadratic error of $\hat{\boldsymbol{\theta}}$ below.

197 **Results**

198 **Derivation of Fisher information matrix and predicted er-**
 199 **rors**

200 The Fisher information matrix associated to parameters $\boldsymbol{\theta} = (\alpha, \sigma, a_s)$ in model
 201 (1) is [see Article S1 in Supporting Information, section 1; Zhu and Stein (2005);
 202 Müller (2007)]:

$$\mathcal{I}(\boldsymbol{\theta}) = \begin{pmatrix} \frac{1}{\alpha^2} \mathbf{1}' \Sigma^{-1} \mathbf{1} & 0 & 0 \\ 0 & \frac{N}{2\sigma^4} & \frac{1}{2\sigma^2} \text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s}) \\ 0 & \frac{1}{2\sigma^2} \text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s}) & \frac{1}{2} \text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s} \Sigma^{-1} \frac{\partial \Sigma}{\partial a_s}) \end{pmatrix} \quad (3)$$

203 From equation (3), one obtains the relative root mean squared error associated
 204 to \hat{a}_s and $\hat{\alpha}$ (see Article S1 in Supporting Information, section 1):

$$\begin{aligned} \text{RRMSE}(\alpha) &= \frac{1}{\sqrt{\mathbf{1}' \Sigma^{-1} \mathbf{1}}} \\ \text{RRMSE}(a_s) &= \frac{1}{a_s} \sqrt{\frac{2}{\text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s} \Sigma^{-1} \frac{\partial \Sigma}{\partial a_s}) - \frac{1}{N} \text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s}) \text{tr}(\Sigma^{-1} \frac{\partial \Sigma}{\partial a_s})}} \end{aligned} \quad (4)$$

205 Equation (4) implied in particular that RRMSEs did not depend on α (or
 206 μ), hence justifying that we set $\alpha = 1$ throughout the study without loss of
 207 generality. Recalling that we also set $\sigma = 1$, equation (4) shows that $\text{RRMSE}(a_s)$
 208 did not depend on σ but that $\text{RRMSE}(\alpha)$ was proportional to σ , which implies
 209 that quantitative predictions on $\text{RRMSE}(\alpha)$ should vary when changing the
 210 value of σ . However, we were mostly interested in the ranking of designs, which
 211 should remain identical up to a multiplicative constant. Therefore, setting $\sigma = 1$
 212 did not imply any loss of generality on our results either.

213 Theoretical analysis of asymptotic errors

214 **When $a_s \rightarrow 0$** Our theoretical analysis (see Article S1 in Supporting Informa-
215 tion, section 2) yielded that $\text{RRMSE}(a_s)$ should increase towards $+\infty$ as a_s be-
216 comes small, irrespective of considered design. The increase is quite abrupt, pro-
217 portional to $a_s/d_{\min} \times \exp(d_{\min}/a_s)$ where d_{\min} is the smallest distance among
218 two distinct sampling points. Although the proportionality constant depends on
219 the sampling design, the feature of designs with strongest effect on $\text{RRMSE}(a_s)$
220 when a_s becomes arbitrarily small is d_{\min} : designs with smaller d_{\min} should
221 yield markedly smaller $\text{RRMSE}(a_s)$. The grid design tends to maximize d_{\min}
222 for a given sampling effort N (see Article S1 in Supporting Information, section
223 3) and should thus yield consistently higher $\text{RRMSE}(a_s)$ than other designs as
224 $a_s \rightarrow 0$. Fractal design can harbour arbitrarily small d_{\min} values by decreasing
225 contraction parameter x . As a result, there should exist a threshold on x below
226 which fractal designs yield lower $\text{RRMSE}(a_s)$ than hybrid sampling designs, and
227 thus become Pareto-optimal.

228 In the meantime, $\text{RRMSE}(\alpha)$ should converge to σ/\sqrt{N} irrespective of the
229 sampling design. This corresponds to the expected standard error on the mean
230 when sampling points are independent. When $\sigma^2 = 1$ and $N = 27$, this yields
231 $\text{RRMSE}(\alpha) \approx 0.19$.

232 Both results suggest that fractal design with low contraction parameters may
233 exclude hybrid designs from the Pareto front, since the accuracy at estimating
234 autocorrelation range should become the major difference among designs.

235 **When $a_s \rightarrow +\infty$** $\text{RRMSE}(a_s)$ converges towards $\sqrt{2N/(N-1)}$ (≈ 1.44 when
236 $N = 27$), irrespective of the sampling design (see Article S1 in Supporting
237 Information, section 2). In the meantime, $\text{RRMSE}(\alpha)$ converges to σ ($= 1$ in
238 our example), irrespective of the sampling design. This is the expected result for
239 a single observation, hence illustrating the fact that all the sampling points are

240 perfectly correlated. Both results suggest that all the sampling designs should
 241 converge towards very similar performance as $a_s \rightarrow +\infty$, hence rendering their
 242 ordination impossible.

243 **Numerical analysis of Pareto fronts for hybrid designs**

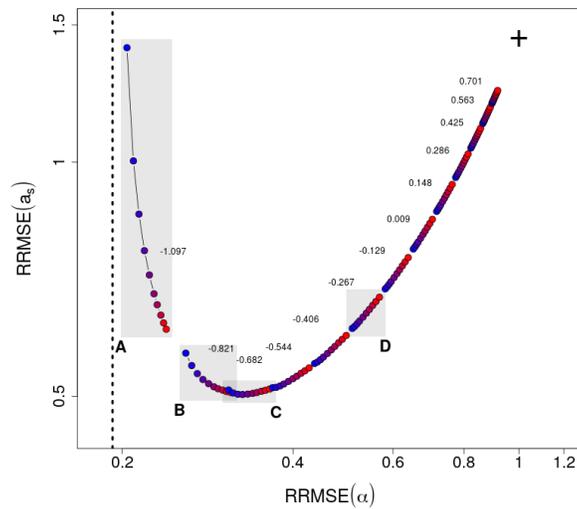


Figure 2: Relative root mean square error of estimation of exponential mean (α) and autocorrelation range (a_s) for hybrid designs along a gradient of a_s values. For each a_s value, we present a line of dots showing the RRMSEs for the 28 hybrid designs. Dots color indicates the value of p , increasing from blue ($p = 0$; grid design) to red ($p = 1$; random design). The lines of dots shift towards the right as a_s increases, following a U-shaped global pattern. We presented results for 13 values a_s out of the 160 values explored, for readability. Those values are reported above each line of dots. The vertical dotted line shows the predicted asymptote when $a_s \rightarrow 0$, the cross shows the predicted limit when $a_s \rightarrow +\infty$. We obtained the same qualitative pattern when assessing the quadratic error of estimation through a Monte-Carlo approach (see Article S1 in Supporting Information, section 4). The four grey rectangles show the lines of hybrid designs that are further considered in fig. 3.

244 In line with the asymptotic study when $a_s \rightarrow 0$ detailed above, the predicted
 245 RRMSE(a_s) of hybrid designs rapidly increased at the lower margin of explored

246 a_s values. It exceeded standard numerical precision of computers and software
247 when considering designs with high d_{\min} (e.g. grid design). Below, we focused
248 our analysis on the range of a_s values for which $\text{RRMSE}(a_s)$ could be computed
249 for all designs. This led us to ignore a_s values smaller than $10^{-2.101}$ (26 values
250 out of the 160 initially considered).

251 Some patterns were common to all hybrid designs (fig. 2). The $\text{RRMSE}(\alpha)$
252 increased with the autocorrelation range, starting from the expected value of
253 0.19 towards the predicted value upper limit of 1. This increase was quite
254 expected : stronger autocorrelation increases pseudo-replication and makes the
255 mean of the field harder to estimate. The $\text{RRMSE}(a_s)$ showed a non monotonic
256 profile first decreasing from infinity, then increasing again towards the expected
257 limit of 1.44.

258 Increasing the degree of randomness p within hybrid designs consistently
259 increased the $\text{RRMSE}(\alpha)$ along the gradient of a_s (see fig. 2). By contrast, the
260 ordination of $\text{RRMSE}(a_s)$ among hybrid designs with various degree of random-
261 ness p changed as a_s increased. For small a_s values ($a_s \leq 10^{-0.786}$), increasing p
262 decreased the $\text{RRMSE}(a_s)$. Therefore, any hybrid design along the gradient of p
263 was a Pareto-optimal strategy (see figs. 3A, 3B, 4A). For intermediate a_s values
264 ($10^{-0.752} \leq a_s \leq 10^{-0.579}$), the $\text{RRMSE}(a_s)$ harboured a U-shaped pattern as p
265 increased. Therefore, there existed a threshold on a_s above which increasing p
266 too much did not lead to Pareto-optimal strategies anymore (see figs. 3C, 4A).
267 For larger a_s values ($a_s \geq 10^{-0.544}$), the $\text{RRMSE}(a_s)$ increased with p , making
268 grid design ($p = 0$) the only Pareto-optimal strategy among hybrid designs (see
269 also figs. 3D, 4A). We retrieved those three types of patterns for small, inter-
270 mediary and large values of a_s when estimating RRMSEs from simulations in a
271 Monte-Carlo approach (see Article S1 in Supporting Information, section 4).

272 Considering the intermediate range of a_s values where the effect of p grad-

273 ually changes from all hybrid designs being Pareto-optimal to grid design only,
274 we observed that it contained the a_s value corresponding to the mesh size of
275 the grid design ($\sqrt{3}/6 \approx 10^{-0.540}$). In practice, the transition might therefore
276 occur when the autocorrelation range reach values close to the mesh size of the
277 grid design. For simulated RRMSEs, the three ranges of a_s values associated to
278 distinct patterns seemed to be positioned later on the autocorrelation gradient
279 (see Article S1 in Supporting Information, section 4), but the rule of thumb
280 that transition occurs for autocorrelation range values close to mesh size was
281 not rejected.

282 **Numerical comparison of fractal designs to the Pareto front** 283 **of hybrid designs**

284 For small a_s values ($a_s \leq 10^{-1.893}$), fractal designs with intermediate to high
285 contraction parameter ($10^{-0.969} \leq x \leq 1$; fig. 4B) excluded all the hybrid de-
286 signs from the Pareto front except the pure grid design ($p = 0$; fig. 4A), which
287 remained the most efficient design to estimate the mean of the field. We had
288 the theoretical conjecture — derived from our theoretical analysis of asymp-
289 totic errors above — that fractal designs with low contraction parameters x
290 could become unilaterally better than hybrid designs at small autocorrelation
291 range, because the performance of all designs at estimating α should become
292 similar while fractal design with low x should be better at estimating a_s . The
293 observed exclusion of most hybrid designs can be seen as a result of this process.
294 However, the conjecture was not fully verified over the range of a_s values ex-
295 plored: first fractal designs with very low contraction parameters ($x < 10^{-0.969}$)
296 were not Pareto-optimal among fractal designs, second grid design still persisted
297 as a Pareto-optimal option. Maybe smaller a_s values would have matched the
298 theoretical conjecture better, but as explained above, they could not be explored

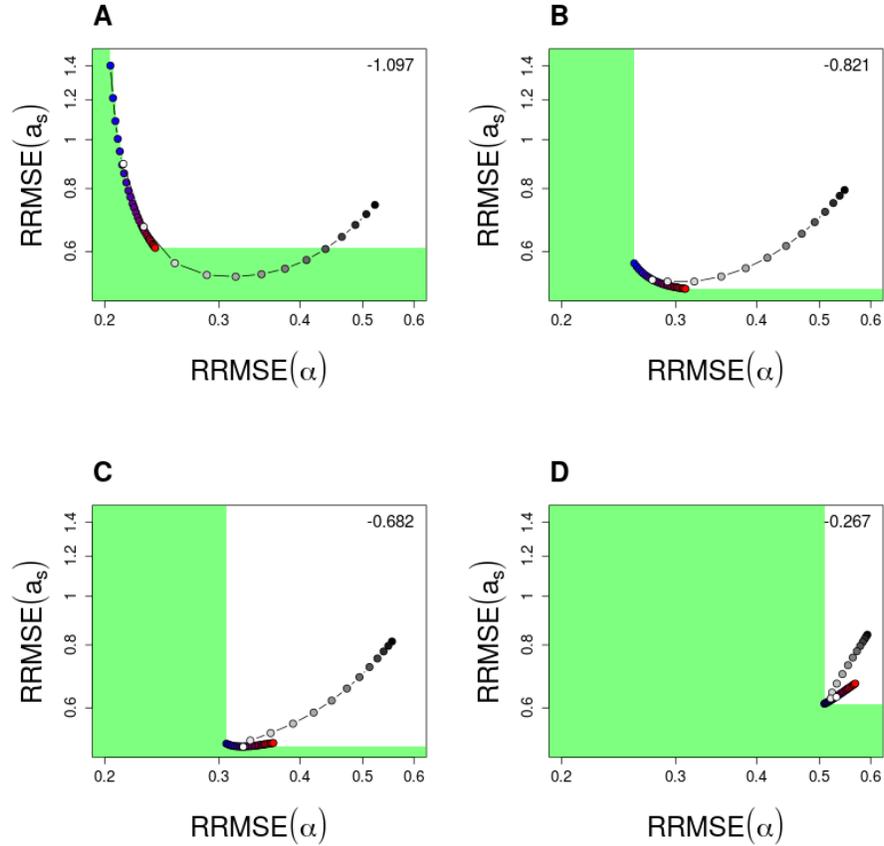


Figure 3: Comparing the relative root mean square errors of fractal designs to the Pareto front of hybrid designs in four typical situations. Panels *A*, *B*, *C* and *D* correspond to increasing values of a_s (values of $\log_{10}(a_s)$ are reported at the upper right corner). They were identified as grey rectangles in figure 2. In each panel, the RRMSEs of fractal designs are presented as a line of grey dots. The grey level of dots indicates the value of the contraction parameter x , increasing from black ($x = 10^{-1.5}$) to white ($x = 1$). Only a sub-sample of the 240 explored values on x were presented, to improve readability. RRMSEs of hybrid strategies are presented using the same caption as in figure 2 with blue-to-red gradient. The Pareto front associated to hybrid designs is presented as a green polygon. When fractal designs reach the green area, they offer a new Pareto-optimal design compared to hybrid strategies.

299 because the theoretical prediction of grid design error on a_s parameter exceeded
300 computer limits.

301 Then we observed a narrow range of a_s values ($10^{-1.858} \leq a_s \leq 10^{-1.513}$)
302 where all the hybrid designs gradually came back to the Pareto front as a_s
303 increased, starting from pure random design ($p = 1$; fig. 4A). Nearly simulta-
304 neously, as a_s increased above $10^{-1.789}$, fractal designs within a range of inter-
305 mediary contraction parameter values x became excluded from the Pareto front
306 by hybrid designs. The range of excluded x values initiated at $x = 10^{-0.306}$ and
307 expanded while shifting towards high x values, until encompassing the higher
308 end of the range ($x = 1$; fig. 4B). Fractal designs with high contraction param-
309 eters ($x > 10^{-0.1}$) could sporadically become Pareto optimal again at larger a_s
310 values but, in those cases, they were quantitatively very close to hybrid design
311 in terms of error (see for instance the fractal design with $x = 1$ in fig. 3C).

312 By contrast, fractal designs with lower x values (e.g. $x < 10^{-0.306}$) were
313 not excluded from the Pareto front when a_s increased above $10^{-1.789}$ (fig. 4B),
314 and remained Pareto-optimal over a larger range of a_s values. These designs
315 came as an extension of — rather than in competition with — the Pareto front
316 associated to hybrid designs. They were associated to lower error on a_s but
317 higher error on α (as illustrated in fig. 3A). However, when a_s values increased
318 above $10^{-0.924}$, this type of Pareto-optimal fractal strategies based on accurate
319 a_s estimation were excluded by hybrid designs, as illustrated by the transition
320 between fig. 3A and fig. 3B.

321 For larger a_s values ($a_s > 10^{-0.682}$), fractal designs became excluded from
322 the Pareto front by hybrid designs, irrespective of x value (figs. 3D, 4B).

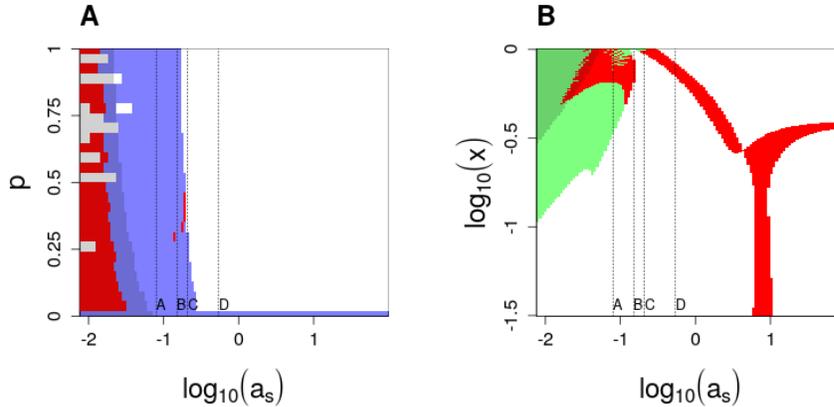


Figure 4: Intersection between Pareto fronts associated hybrid and fractal designs. Panel A presents the impact of fractal designs on the Pareto front of hybrid designs. Colored pixels (either blue or red) show, for each explored a_s value, the values of the proportion of random observations (p) that lead to a Pareto-optimal hybrid design. White ‘holes’ on the left side of the graph are artifacts due to limits in the numerical precision at very high errors on a_s . Among those Pareto-optimal values of p , red pixels show which values are not Pareto-optimal anymore when adding fractal designs, while blue pixels show the p values that remain Pareto optimal. Panel B presents the impact of hybrid designs on the Pareto front of fractal designs. Colored pixels (either green or red) show, for each explored a_s value, the values of the contraction parameter (x) that lead to a Pareto-optimal fractal design. Among those Pareto-optimal values of x , red pixels show which values are not Pareto-optimal any more when adding hybrid designs, while green pixels show the x values that remain Pareto optimal. In both panels, the shaded area (left on panel A, upper-left on panel B) shows designs where the $\text{RRMSE}(a_s)$ is above 2. Vertical dotted lines show the positions of examples detailed in figure 3.

323 **Theoretical analysis of changing the size of the surveyed** 324 **area or the sampling effort**

325 In this section, we used the shorthand notations $E_a(a_s, L, N)$ [resp. $E_\alpha(a_s, L, N)$]
 326 for the $\text{RRMSE}(a_s)$ [resp. $\text{RRMSE}(\alpha)$] when true autocorrelation range is a_s ,
 327 surveyed area side length is L and sample size is N .

328 **Surveyed area** Until now, we considered the problem of sampling within
329 a fixed triangular area constraining designs to cover the whole surface. We
330 relaxed this assumption and allowed the side length L of the surveyed area to
331 vary as a free parameter. A re-scaling argument (see Article S1 in Supporting
332 Information, section 5) yielded that:

$$E_a(a_s, \lambda L, N) = E_a(a_s/\lambda, L, N)$$
$$E_\alpha(a_s, \lambda L, N) = E_\alpha(a_s/\lambda, L, N)$$

333 where $\lambda > 0$ is the dilatation factor applied to side length. In words, changing
334 the size of the area, through dilatation or contraction, is exactly equivalent to
335 changing the value of a_s while keeping the size of the area to its original value.
336 Therefore, when the surveyed area can freely change, Pareto fronts of sam-
337 pling strategies can be obtained directly through merging RRMSEs previously
338 obtained at distinct a_s values, and computing the Pareto front of the pooled
339 dataset. By doing so, we can compare hybrid and fractal sampling strategies
340 and see their respective contributions to a global Pareto front (fig. 5A).

341 Grid design was never a Pareto-optimal design (fig. 5A). It was consistently
342 excluded from the front by other hybrid designs including some degree of ran-
343 domness and by fractal designs. By contrast pure random designs alone reached
344 a Pareto front very similar if not identical to the Pareto front of all hybrid de-
345 signs, suggesting that when the size of the area can be adapted it may not be
346 useful to add regular elements within the random design. Fractal and random
347 designs showed quantitatively very close Pareto fronts, which both contributed
348 to the global Pareto front. Fractal designs seemed slightly more performant
349 when seeking intermediary error levels on the mean and the autocorrelation
350 range, but we reckoned that the magnitude of the difference was too reduced
351 to justify a deep interpretation. Focusing on random designs ($p = 1$), the tran-
352 sition from designs oriented towards estimating the mean to designs oriented

353 towards estimating the autocorrelation range occurred when L decreased from
 354 $L = 100a_s$ to $L = 10a_s$ (fig. 5B).

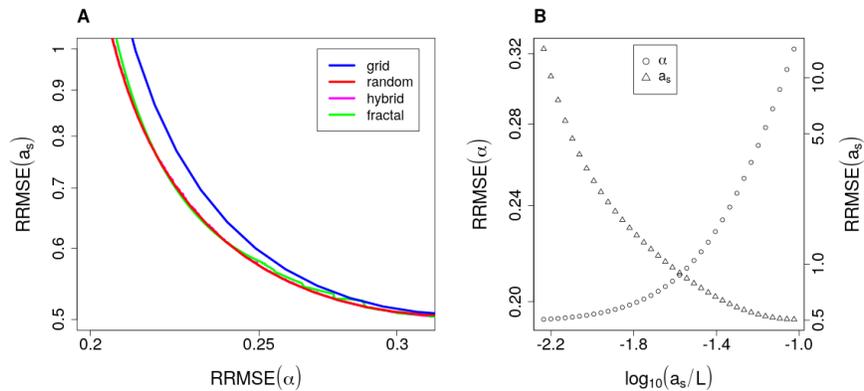


Figure 5: Pareto front of relative root mean square error of estimation of exponential mean $\text{RRMSE}(\alpha)$ and autocorrelation range $\text{RRMSE}(a_s)$ for four sampling strategies when allowing to change surveyed area, hence removing the dependence on a_s . The ‘hybrid’ Pareto front corresponds to considering all the values of p simultaneously (hence encompassing grid and random designs as particular cases). The ‘fractal’ Pareto front corresponds to considering all the values of x simultaneously. Hybrid (pink) and random-only (red) Pareto fronts are nearly exactly super-imposed. Panel A shows the Pareto fronts for the different types of design. Panel B relates the position on the random-only Pareto front to the value of $\log_{10}(a_s/L)$, where L is the length of the side of the triangular area.

355 **Sampling effort** We now theoretically explore the implication of increasing
 356 sample size N by a factor $\eta = 3^q$ with $q \in \mathbb{N}^*$. For fractal designs, the increase
 357 of sample size is done by further iterating q times the iterating function system
 358 depicted in methods. For hybrid designs, the increase of sample size is done by
 359 increasing the density of sampling points by a η factor. We propose the following
 360 approximation for a design i (see Article S1 in Supporting Information, section

361 5 for a justification):

$$E_a^{(i)}(a_s, L, \eta N) \approx \eta^{-\frac{1}{2}} E_a^{(i)}(a_s \times \eta^{\frac{1}{\delta_i}}, L, N)$$

$$E_\alpha^{(i)}(a_s, L, \eta N) \approx \eta^{-\frac{1}{2}} E_\alpha^{(i)}(a_s \times \eta^{\frac{1}{\delta_i}}, L, N)$$

362 where δ_i is known as the ‘fractal dimension’ of the design i , equal to 2 for hybrid
363 designs and to $-\log(3)/\log(\rho)$ for fractal designs (always strictly lower than 2).

364 The first effect of increasing sample size should thus be to decrease RRMSEs by
365 a factor $\eta^{-\frac{1}{2}}$, irrespective of the design, which should not change the ordination

366 of designs, and suggest considering rescaled RRMSEs to discuss the question of
367 ordination :

$$\eta^{\frac{1}{2}} E_a^{(i)}(a_s, L, \eta N) \approx E_a^{(i)}(a_s \times \eta^{\frac{1}{\delta_i}}, L, N)$$

$$\eta^{\frac{1}{2}} E_\alpha^{(i)}(a_s, L, \eta N) \approx E_\alpha^{(i)}(a_s \times \eta^{\frac{1}{\delta_i}}, L, N)$$

368 These rescaled RRMSEs suggest that the effect of increasing sampling effort on
369 designs ordination is equivalent to increasing a_s . The equivalent increase on a_s
370 depend on the fractal dimension, it is larger for fractal designs than for hybrid
371 designs.

372 We previously observed that $\text{RRMSE}(\alpha)$ tended to increase with the degree
373 of randomness p of hybrid designs (fig. 2) irrespective of a_s value. Because
374 hybrid designs all have the same fractal dimension, this pattern should persist
375 as sampling effort increases. The effect of increasing sampling effort on the
376 ordination of $\text{RRMSE}(a_s)$ among hybrid design is harder to predict since the
377 variation of $\text{RRMSE}(a_s)$ along the a_s gradient is non-monotonic. However, using
378 previous results (fig. 2), one expects that when sampling effort has increased
379 enough to ensure that the mesh size of grid sampling design has become lower
380 than autocorrelation range a_s , the grid design would become the best hybrid
381 design with respect to $\text{RRMSE}(a_s)$, and therefore the unique Pareto-optimal
382 design among hybrid designs.

383 Combining the facts that (i) grid design consistently outperformed fractal
 384 designs on $\text{RRMSE}(\alpha)$ at the same a_s value (e.g. fig. 4A), (ii) fractal designs
 385 have higher ‘equivalent’ a_s than hybrid designs when sampling effort increases
 386 and (iii) $\text{RRMSE}(\alpha)$ of fractal designs increased with a_s (fig. 6A), one can
 387 expect that increasing sampling effort preserves grid design as the best design
 388 among all with respect to $\text{RRMSE}(\alpha)$. When the autocorrelation range a_s is
 389 higher than the mesh size of grid sampling design, $\text{RRMSE}(a_s)$ of fractal designs
 390 increases with a_s (fig. 6B). This tends to suggest that when sampling effort has
 391 increased enough to ensure a mesh size of grid sampling design lower than a_s ,
 392 the grid design may also outperform fractal designs with $x > 10^{-1.5}$ in terms of
 393 $\text{RRMSE}(a_s)$, and thus be the unique Pareto-optimal design among all designs.

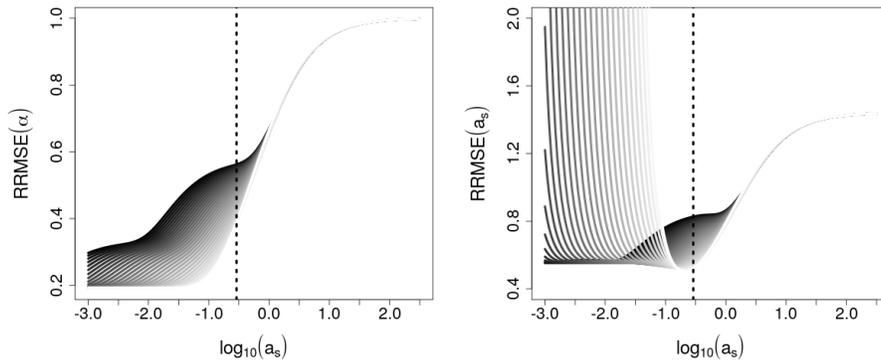


Figure 6: RRMSEs of fractal designs as a function of autocorrelation range a_s . Panel A shows $\text{RRMSE}(\alpha)$, panel B shows $\text{RRMSE}(a[s])$. In both panels, the vertical dotted line shows the grid design mesh size. The grey level of curves indicates the value of the contraction parameter x , increasing from black ($x = 10^{-1.5}$) to white ($x = 1$). Only a sub-sample of the 240 explored values on x were presented, to improve readability.

394 Discussion

395 **Within a fixed surveyed area, hybrid designs are not always inter-**
396 **mediary Pareto-optimal strategies between grid and random designs**

397 For autocorrelation range smaller than the grid mesh size, we retrieved the ex-
398 pected continuum of Pareto-optimal hybrid designs between grid and random
399 designs. In this context, pairwise distances among sampling points smaller than
400 the grid mesh size were needed to accurately estimate the autocorrelation range,
401 and such smaller distances were provided by the introduction of random points.
402 Increasing the degree of randomness in designs thus lead to a gradual shift in the
403 accuracy from estimating the mean of the field to estimating the autocorrela-
404 tion range. For larger autocorrelation ranges, we obtained less expected results:
405 adding too much randomness could depart from the Pareto front of designs and
406 become sub-optimal. The upper threshold of acceptable randomness decreased
407 with autocorrelation range and, for large autocorrelation ranges, the grid design
408 stood as the unique best strategy among hybrid designs to estimate both the
409 mean and the autocorrelation range of the field.

410 In practice, choosing among hybrid designs thus relies on *a priori* knowledge
411 about the order of magnitude of the autocorrelation range for the quantity of
412 interest. Let us consider the practical case where one wants to define a strategy
413 to position 27 sampling plots in a forest of about 3600ha in order to study the
414 distribution of saproxylic beetles species living in hollow trees. The mesh size
415 of a regular grid spread over the forest would then be of c.a. 1500m (with fluc-
416 tuations depending on the geometry of both forest and the chosen shape of the
417 mesh). A previous studies based on auto-regressive occupancy models [Ranius
418 et al. (2010), fig. 1] suggested that cavicolous beetles often harbour a spatial
419 autocorrelation with range below 1000m. One thus expects the mesh size to be
420 larger than autocorrelation range in this example. If estimating the autocorre-

421 lation range were a strong priority of the study, random sampling should thus
422 be preferred. If one rather looked for a compromise between mean and auto-
423 correlation range estimation, truly hybrid strategies should be preferred. In the
424 latter case, the shape of the Pareto front seems to be convex when autocorre-
425 lation is smaller than mesh size (fig. 2), suggesting that the pay-off of adding
426 randomness decreases as the proportion of random points increase. Therefore,
427 a choice for a low degree of randomness [e.g. $p = 0.1$; Bijleveld et al. (2012)]
428 could be appropriate.

429 Bijleveld et al. (2012) had already identified that the relative performance
430 of designs depended on the level of the underlying autocorrelation range. For
431 instance, they found that the bias when estimating autocorrelation range was
432 minimized by random design for small autocorrelation ranges, but minimized by
433 hybrid strategy with $p = 0.1$ at higher autocorrelation level. However, because
434 they averaged the performance of designs out across autocorrelation levels and
435 intersample distances explored in their analysis, the authors further concluded
436 that, overall, there was a Pareto front of hybrid designs between grid and ran-
437 dom. Our findings discourage averaging across autocorrelation ranges, because
438 the magnitude of errors on autocorrelation estimation rapidly increases as the
439 autocorrelation range decreases. Global averaging thus tends to give too much
440 of weight to scenarios with small autocorrelation range compared to intersample
441 distance, and may lead to over-generalizing patterns that are in fact specific to
442 small autocorrelation range values. Diverging magnitude of error at the lower
443 end autocorrelation range raises the same problem for all metrics of performace
444 integrating over an interval of autocorrelation ranges. For instance, Zhu and
445 Stein (2005) mentioned that minimax or average metrics of estimation error
446 across the autocorrelation range considered in their study were very unstable
447 and hard to optimize, probably due this phenomenon. For this reason, we chose

448 not to derive global metrics in our study but focused on the qualitative analysis
449 of Pareto fronts.

450 **Within a fixed surveyed area, fractal designs can be Pareto-optimal**
451 **strategy to estimate small autocorrelation ranges** At very small auto-
452 correlation ranges, all hybrid designs except grid were excluded by fractal de-
453 signs, i.e. the latter were more efficient at estimating both the autocorrelation
454 range and the mean. Fractal design with intermediate contraction parameter
455 seemed particularly interesting because the associated absolute level of error
456 on autocorrelation range remained moderate (see non-shaded area on fig. 4A).
457 These designs remained Pareto-optimal when autocorrelation range increased up
458 to values close to grid mesh size, because they extended the hybrid Pareto front
459 towards estimating autocorrelation range more accurately. In other words, they
460 offered a way to go further than the random design towards the aim of accurately
461 estimating the autocorrelation range while paying a cost on the estimation of
462 the mean. Coming back to the example of saproxylic beetles mentioned above, if
463 estimating the autocorrelation range were a strong priority of the study, fractal
464 designs with intermediate x may be even more interesting than random design.
465 Under the assumptions of our study, the figure 4B seems to suggest that taking
466 $x = 10^{-0.4} \approx 0.4$ is quite a robust choice. One may object that when accurately
467 estimating small autocorrelation ranges is a strong priority of a survey, it may
468 be relevant to combine the optimization of sampling design with the reduction
469 of the area of study. This specific point is discussed in the next section.

470 It should be noted that, in practice, the choice of contraction parameter to
471 build sampling design comes with sterical constraints when sampling units can-
472 not be too close one from another. This may happen when sampling units have
473 a large size (see our example below) or if sampling induces a disturbance than
474 would alter the outcome of sampling nearby (e.g. because of organisms have

475 large home range or because they are sensitive to the presence of observers), a
476 phenomenon akin to ‘interference among sampling unit’ in causal theory (Kim-
477 mel et al., 2021). Considering our example about saproxylic beetles, sampling
478 units could be circular plots of 1ha (a radius of c.a. 57m). Then the mini-
479 mal distance between two sampling units would have to be of at least 114m
480 to avoid overlapping. If one assumes that the forest under study (≈ 3600 ha)
481 has a diameter of c.a. 7km, building a triangular fractal design with 27 plots
482 implies that the largest distance between plots in the design is $114/\rho^2$ where
483 $\rho = x\sqrt{3}/(2+\sqrt{3})$. The constraint that this distance must be below 7km implies
484 that x cannot be lower than 0.27. Similarly, it is straightforward to show that
485 there could not be more than five scales in the triangular fractal sampling design
486 without generating overlapping of sampling units (i.e. sampling effort must be
487 lower than $N = 3^5 = 243$ plots). However, this threshold on sampling size could
488 be overcome by considering a more complex geometrical shape of the fractal.
489 More generally, the number of sampling sites can be modulated by combining
490 the choice of the geometrical shape with subsampling (Marsh and Ewers, 2013).

491 **If the size of surveyed area can be adapted or sampling effort in-
492 creased, fractal designs are outperformed by more classic options**

493 Assuming that the size of the area of study is not predetermined by exter-
494 nal constraints, random design was sufficient to reach — or get very close to
495 — the global Pareto front of designs explored in our study through adjusting
496 the size of the surveyed area. In this case, moving towards hybrid or random
497 designs seems adding complexity without subsequent payoff. The problem of
498 knowing the order of magnitude of autocorrelation range *a priori* is still present
499 though, for the size of the area has to be adapted to this quantity. For 27
500 sampling point, the typical dimension — side length in our case — of surveyed
501 area should be comprised between ten and a hundred times the target autocor-

502 relation depending on whether the main goal is autocorrelation range or mean
503 estimation, respectively. Our results about the effect of sampling effort suggest
504 that if the number of sampling points is increased e.g. fourfold, then the range
505 of side length values to consider for the surveyed area should be shifted upwards,
506 and approximately comprised between twenty and two hundred times the target
507 autocorrelation range.

508 However, there are several reasons in practice for which the area of study
509 may not be a real degree of freedom when building the study design. First,
510 the area open to sampling may be limited in space either for biological reasons
511 (e.g. a spatially-limited habitat, like a lake) or practical reasons (restricted
512 access, time of travel, etc.). This would prevent extending at will the area of
513 study and potentially limit the opportunities for improving the estimation of
514 the mean that way. Conversely, the area study cannot be freely reduced when
515 one aims at relating environmental covariates to target biodiversity patterns
516 (especially non-linear ones; Albert et al. (2010)), because the range of covariate
517 values has to be appropriately covered. This implies e.g. stratifying among
518 various type of soil cover (Yoccoz et al., 2001), or to span the full extent of an
519 environmental gradient (Field et al., 2009; Albert et al., 2010). Our study does
520 not include these constraints, for we did not consider a third criterion that would
521 be accurately estimating patterns along an environmental covariate. By taking
522 this simplified regression framework, we could easily adress the question of the
523 trade-off between estimating a fixed effect and estimating the spatial structure
524 of residuals. At that stage, we showed that fractal and random designs showed
525 very similar Pareto-fronts when freely adjusting the size of surveyed area (fig.
526 5A). Consequently, if fractal designs happened to better estimate the effect of
527 gradients by forcing the presence of large pairwise distances, they may exclude
528 random design from the Pareto front when including this third axis of evaluation.

529 Our choice of sampling effort $N = 27$ was done to reflect realistic settings
530 that one can observe in many research projects on biodiversity, ours included.
531 However, when data acquisition at a sampling point is not very demanding, it is
532 also frequent to observe larger designs. Sticking with the hollow trees example,
533 if one simply aims at describing features of the trees like tree-related microhab-
534 itats (Larrieu et al., 2018), which are proxys for saproxylic beetle biodiversity
535 (Bouget et al., 2014, 2013), but does not aim at sampling and identifying bee-
536 tles themselves, then the sampling budget can considerably increase. In this
537 case, our theoretical results tend to suggest that when the sampling budget is
538 sufficient for the mesh size of a grid design to become equivalent to or lower
539 than the anticipated magnitude of autocorrelation range, a grid design should
540 be preferred among the other strategies and fractal designs are excluded from
541 the Pareto-front.

542 Conclusions

543 In the context of our study, the main advantage of fractal designs occurred when
544 aiming at estimating short autocorrelation ranges while constrained on cover-
545 ing a large area of survey with a limited sampling budget. In other situations,
546 it seemed more efficient and less complicated to implement more classic de-
547 signs. The niche for fractal designs may thus appear quite limited. It should
548 nonetheless be noted that we evaluated designs on a simple scenario with a par-
549 simonious autocorrelation structure and no effect of covariates. The question of
550 jointly estimating the effects of covariates and the autocorrelation range should
551 now be further adressed, for it adds new axes to the trade-off among designs.
552 In particular, biological patterns often stem from heterogeneous drivers acting
553 at different scales (Thuiller et al., 2015; Ricklefs, 2008). Designs that harbour a
554 clear hierarchical structure — like fractal designs — may be particularly adapted

555 to capture such heterogeneity (Simpson and Pearse, 2021), provided that the
556 scales of variation induced by the hypothesized processed match the geometrical
557 constraint of self-similarity inherent to fractals.

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570 **Conflicts of interest**

571 The author has no conflict of interest to declare.

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