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7

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23 **Abstract**

24 Spatial indicators are widely used to monitor species and are essential to management
25 and conservation. In the present study, we tested the ability of 11 spatial indicators to quantify
26 changes in species' geographic patterns: (1) spatial displacement of a patch of biomass
27 ('shift'), (2) a spatial decrease in a patch, accompanied either by a loss of biomass ('shrink0')
28 or (3) a relocation of the same biomass ('shrink1'), and (4) splitting of a patch into smaller
29 patches ('split'). The geographic changes were simulated by manipulating the spatial
30 distributions of the demersal species (observed during bottom trawl surveys). Hence, the
31 spatial distributions of the latter being used as input data on which the manipulations were
32 done. Additionally, other aspects of the indicators affecting the responses to the geographic
33 changes were also tested, (1) homogeneous increase in biomass throughout the patch and (2)
34 different sample sizes.

35 The center of gravity (defined by latitude and longitude) was the only indicator that
36 accurately detected the 'shift' in biomass. The index of aggregation identified a decrease in
37 the area and biomass of the main biomass patch ('shrink0'), while the Gini index, equality
38 area and spreading area were accurately identified a decrease in the area of the main biomass
39 patch when total biomass did not decreased ('Shrink1'). Inertia and isotropy responded to all
40 geographic changes, except for those in biomass or distribution area. None of the indicators
41 successfully identified 'split' process. Likewise, one of the indicators were sensitive to a
42 homogeneous increase in biomass or the type of spatial distribution. Overall, all indicators
43 behaved similarly well when sample sizes exceeded 40 stations randomly located in the area.
44 The framework developed provides an accessible and simple approach that can be used to
45 evaluate the ability of spatial indicators to identify geographic processes using empirical data

46 and can be extended to other indicators or geographic processes. We discuss perspectives of
47 the development of spatial indicators especially within the application of EU's Marine
48 Strategy Framework Directive.

49 **Keywords:** spatial metrics; monitoring; marine conservation; fisheries management;

50 1. Introduction

51 All life in Earth is both product and contributor to its place in space and time (David
52 Attenborough, launch of 'Our Planet', 2019). Spatial indicators have been developed to
53 represent and summarize species spatial patterns and their dynamics. They are often used in
54 management (e.g. assess the state of species and ecosystems) (Bock et al., 2005; Greenstreet
55 et al., 2012; Modica et al., 2016; Piet and Jennings, 2005; Rochet and Trenkel, 2009), and in
56 ecology (e.g. to understand a species' relationship with its environment, in face of habitat and
57 climate change (Persohn et al., 2009; Yalcin and Leroux, 2017). Thus, the ability of indicators
58 to identify an underlying geographic process accurately is crucial for their appropriate use in
59 practical situations.

60 Selecting indicators from the large list of those available is not straightforward and
61 usually only a few indicators can be used. Previous studies have attempted to identify a small
62 set of indicators that identified most of the spatial patterns observed and have better statistical
63 properties (e.g. robust to outliers and changes in the distribution, regardless of abundance,
64 Bock et al., 2005). Further, most indicators' results are often highly statistically correlated
65 with each other, and thus may be redundant. For example, Rufino et al. (2018) suggested
66 grouping indicators into three categories that, reflect the main ecological patterns of species
67 spatial distribution: occupancy, aggregation and quantity. Doing so would reduce the number
68 of indicators to only three, each representing one category.

69 Another important aspect of indicators that can influence their selection is their ability
70 to identify spatial or geographic change. To our knowledge, one aspect of sampling design
71 that has been poorly addressed when using empirical data is the number of samples required
72 to identify a change in species distribution. However, Rindorf and Lewy (2012) analyzed the
73 properties of several indicators analytically and by simulating abundance-occupancy
74 relationships, in response to changes in species distribution and sample size.

75 The aim of the current study was to determine the ability of several spatial indicators to
76 identify changes in geographic patterns of demersal species, when the species main biomass
77 patch moves (shift), when a larger patch splits into smaller ones (split) or when the area of
78 highest biomass decreases (shrink, with a decrease in or relocation of biomass). The
79 indicators were also assessed at higher levels of biomass (two and five times as high) and
80 multiple sample sizes (20-160 stations). Conclusions are then drawn about management
81 applications, especially in the European Union's Marine Strategy Framework Directive
82 (2008/56/EC) (MSFD), which requires that species and ecosystems be monitored using
83 indicators that are operational and have clearly defined targets.

84 2. Materials and Methods

85 2.1. Data used

86 The data analyzed came from a bottom trawl fishery survey (EVHOE)(Evaluation
87 Halieutique de l'Ouest Européen, EVHOE cruise, RV Thalassa, IFREMER, Leaute and
88 Pawlowski, 2015) that was performed in Autumn 2015 in the Bay of Biscay and the Celtic
89 Seas. The survey covered a bathymetric range 20 up to 700 m deep and consisted of 148
90 randomly stratified sampling stations (Fig. 2). The distribution of the biomass of 29 demersal
91 species (Supplementary material 1) was interpolated onto a grid with 15 km × 15 km

92 resolution that covered all species distributions, using ordinary kriging (see further details in
93 Rufino et al., 2019). This interpolated area was the input data manipulated and from which the
94 indicators were calculated.

95 2.2. Geographical manipulation

96 To determine whether the indicators were sensitive to the main geographic changes in
97 species distributions, four types of naive spatial manipulation were performed: 1) shift; 2)
98 shrink0 3) shrink1 and 4) split (Fig. 1). With this objective, an area was selected within the
99 geographic distribution of each species and then manipulated to simulate the four geographic
100 changes. More precisely, a rectangular area was extracted from the total area interpolated for
101 all 29 species. The geographic range of this rectangular area was -10.482 to -7.145 in latitude
102 and 48.289 to 51.439 in longitude, represented as 23 rows \times 14 columns, on a grid with 15 km
103 \times 15 km resolution) (Supplementary material 1, Fig. S1, S2).

104 These raster grids were subjected to an initial treatment in which the biomass in a target
105 area of nine rows in the center was left unchanged, while those in the remaining rows at the
106 top and bottom were replaced with randomly generated values close to zero (i.e. mean equal
107 to the 10% quantile of the biomass of the target area) and low variability (half the standard
108 deviation of the target area). This treatment was performed to remove any patterns present in
109 the top and bottom sections of the species distributions and to ensure that any differences in
110 the indicators would be due only to the geographic changes simulated. Thus, the target area
111 corresponded to nine contiguous rows with the highest biomass (Fig. S3). This area was then
112 subjected to the four geographic manipulations: shift, split and shrink (with and without a
113 decrease in biomass) (Fig. 2, Fig. S4).

114 The 'shift' process illustrates when the center of a species distribution moves in a
115 certain direction, without a change in biomass (e.g., as expected under climate change). This

116 is not a change in the species distribution but simply reflects that the biomass has relocated.
117 For this process, starting from the initial state, the target area was successively shifted,
118 towards the bottom of the rectangle (south), by one row seven times (to the bottom of the
119 raster rectangle). Each shift of one row corresponded to a $\sim 4\%$ shift in the species
120 distribution.

121 The 'split' manipulation mimics the process in which a larger patch with higher biomass
122 is broken into smaller patches, without changing the total biomass. For this, starting from the
123 initial state, the target area was split into thirds, and the three top and bottom rows were
124 shifted successively towards the top and bottom of the rectangle, respectively five times.

125 The 'shrink' process reflects a decrease in species distribution, (i.e. when a large
126 biomass patch decreases in size). For this, starting from the initial state, the two edge rows of
127 the target area were successively replaced with randomly low values four times, until only
128 one row of the target was left. Two shrink processes were considered: (1) total biomass
129 decreases due to the decrease in the distribution areas (shrink.0, i.e. some of the population
130 emigrated) and (2) the biomass of the reduced areas was randomly distributed in the complete
131 area (shrink.1), representing relocation of the same population.

132 2.3. Spatial indicators

133 Eleven spatial indicators were calculated for each manipulated spatial distribution
134 (Table 1). The indicators selected were not intended to be exhaustive, but rather to represent
135 the three main categories identified by Rufino et al., (2018). Since the data were interpolated
136 on a regular grid, the areas of influence of each data point were set to 1 for simplicity. Thus,
137 indicators representing an area were expressed as a number of grid cells rather than in units of
138 surface area. We denoted $x_i, i = 1, \dots, N$ the geographic location of data points. In two

139 dimensions, this corresponds to $(longitude_i, latitude_i)$. Fish biomass was denoted $z(x_i) =$
140 $z_i, i = 1, \dots, N$.

141 **Center of Gravity** also called center of mass, indicates the mean spatial location of the
142 population (Bez and Rivoirard, 2001)(Supplementary material 2). Given the manipulations
143 performed, we considered longitude and latitude of the center of gravity separately:

$$144 \quad CG. lon = \frac{\sum_{i=1}^N z_i longitude_i}{\sum_{i=1}^N z_i}$$

$$145 \quad CG. lat = \frac{\sum_{i=1}^N z_i latitude_i}{\sum_{i=1}^N z_i}$$

146

147 This indicator is sensitive to the spatial locations of data points.

148 The **Gini index** is defined as the two times the area between the 1:1 line and the Lorenz
149 curve (Supplementary material 2). It is considered a measure of statistical concentration since
150 it is not sensitive to the spatial location of the data points (Petitgas, 1998, 1997; Reuchlin-
151 Hugenholtz et al., 2015) . When applied to fish density, the x-axis of Lorenz curve represents
152 the area occupied by cumulative fish densities (ranked by increasing density) while the y-axis
153 represents the corresponding percentage of the total population biomass. For fish density
154 equally distributed among the samples, the Lorenz curve follows the 1:1 line. As the
155 distribution of fish density becomes increasingly uneven (i.e., more concentrated) the Lorenz
156 curve deepens. Gini index ranges from 0-1, the higher its value, the more concentrated the
157 biomass is in fewer samples.

158 The **level of aggregation** (Bez and Rivoirard, 2001) is calculated as follows:

$$159 \quad L_{agg} = \frac{\sum_{i=1}^N z_i^2}{\sum_{i=1}^N z_i}$$

160

161 It corresponds to the mean fish density at the location where an individual fish is randomly
162 sampled from the population. This index is not sensitive to the spatial location of the data
163 points.

164 The **index of aggregation** is calculated by standardizing the level of aggregation by Q
165 the total biomass (Bez and Rivoirard, 2001). While the areas of influence of each sample have
166 been set to 1:

$$167 \quad I_{agg} = \frac{L_{agg}}{Q} = \frac{\sum_{i=1}^N z_i^2}{N(\sum_{i=1}^N z_i)^2} = \frac{1}{eqarea}$$

168 From this equation, the **equivalent area** represents the area covered by a population with
169 constant density equal to the level of aggregation (Bez and Rivoirard, 2001).

170 **Spreading area** measures whether the positive fish biomasses are statistically concentrated
171 around their mean (Wuillez et al., 2007; Supplementary material 2). It is the Gini index of the
172 positive sample and thus related to the Gini index.

173 **Inertia** represents the spatial dispersal of the population around its center of gravity, i.e. the
174 mean square distance between individual fish and the center of gravity (Bez and Rivoirard,
175 2001; Supplementary material 2).

$$176 \quad Inertia = \frac{\sum_{i=1}^N z_i \cdot (x_i - CG)^2}{\sum_{i=1}^N z_i}$$

177
178 **Isotropy/anisotropy** represents the shape (symmetry) of the inertia, i.e. round or ellipsoid, and
179 equals the ratio of the two principal axes of inertia (Supplementary material 2).

180 The **index of dispersion** and **coefficient of dispersion** also called variance-to-mean ratio
181 ($\sigma^2:\mu$) or relative variance, measure the aggregation of individuals (Taylor, 1961).

182 2.4. Procedure

183

184 To determine whether the indicators were sensitive to a homogeneous increase in
185 biomass (e.g. to represent a year with good environmental conditions overall, in which
186 biomass increases proportionally at all points), the geographically manipulated raster was
187 multiplied by two and five before the geographic manipulation (biomass effects, three levels,
188 1, 2 and 5) and the indicators were estimated again.

189 To determine whether the indicators were sensitive to sample size (i.e. the number of
190 samples required to detect the geographic changes), 20 -160 random samples (in steps of 20)
191 were taken from each of the manipulated raster's (sample size effect, nine levels), and the
192 indicators were estimated again using these data.

193 Thus, the indicators differed as a function of the initial state, (1) the geographic
194 manipulation (shift, split or shrink), (2) the level of biomass, and (3) the sample size. The
195 difference in indicator value between the initial state and each configuration was calculated
196 for each species and summarized (mean and 95% confidence interval estimated by bootstrap).
197 Thus, a total of 3132 simulations were performed (29 species distribution \times 4 manipulations \times
198 3 biomass levels \times 9 sample sizes).

199 All analysis and plotting were performed using R software (R Core Team, 2014).
200 Indicators were estimated using the RGeostats (Renard et al., 2017) and ineq (Zeileis, 2014)
201 packages of R, while rasters were manipulated using the raster package (Hijmans, 2016).

202 3. Results

203 The latitude of the center of gravity accurately identified the southward shift of the
204 species biomass, although its relative change was smaller than that of the corresponding
205 number of grid rows shifted (i.e. a 20% shift in latitude, for a 30% shift in rows, i.e. 7 out of
206 23 in the target area). No change was detected for the shrink or split processes (Fig. 3; Table

207 1). The longitude of the center of gravity did not change for the shift and split processes, but
208 did changed slightly (by 0.02) for both shrink processes (shrink0 and shrink1), especially at
209 higher levels of shrinkage (target area decreased by >50%, by 2-4), thus independent of total
210 biomass.

211 The Gini index, did not change for the shift or split processes, but progressively
212 increased by up to 20% as the species distribution main occupied area decreased, when total
213 biomass was redistributed (shrink.1) (Fig. 3; Table 1). However, when the biomass of the
214 reduced area was lost (shrink0), the Gini index decreased slightly and then increased slightly
215 (by ~5%) as the level of shrinkage increased. A similar but opposite pattern was observed for
216 the equivalent area and spreading area.

217 The index of aggregation showed an opposite pattern, increasing progressively up to
218 0.03 units (shrink0) but not when the total biomass was maintained (shrink1) (Fig. 3; Table
219 1).

220 The inertia and isotropy decreased progressively with an increasing level of each
221 geographic manipulation considered, although to a greater extent for the shrink1 and split
222 (Fig. 3; Table 1).

223 The index of dispersion, level of aggregation and the coefficient of dispersion all
224 responded mainly to the increase in total biomass in the rectangular area, and only slightly to
225 the geographic manipulations (Fig. 3; Table 1).

226 For most indicators the influence of sample size on the ability to identify the underlying
227 geographic manipulation was inconsistent when only 20 stations were considered (Fig. 4;
228 Table 1). The indicators showed a consistent response to changes in geographic patterns when
229 the sample size reached 40 stations, except for the level of aggregation, which required 80

230 stations. Only equivalent area and spreading area had increasing ability to identify changes as
231 the level of manipulation and sample size increased.

232 Inertia and isotropy were generally sensitive to all geographic manipulations, although
233 to a higher degree for shrink1 and split, and were not sensitive to changes in total biomass.
234 The shift manipulation was detected only by the respective coordinate of the center of gravity,
235 which was also relatively insensitive to a homogeneous increase in the biomass level. The
236 shrink manipulation, in which the main biomass patch decreased, was identified by the Gini
237 index, index of aggregation, equality area and spreading area. For shrink0, (i.e. total biomass
238 decreases), the index of aggregation was more effective. For shrink1 (i.e. biomass missing
239 from the decrease in the area is relocated over the entire area), the Gini index (increased),
240 equality area (decreased) and spreading area (decreased) were more effective; however, the
241 latter two were highly sensitive to smaller sample sizes. The ‘split’ manipulation was not
242 detected by any of the indicators.

243 Three indicators were not sensitive to any of the manipulations but did change with the
244 increase in total biomass: coefficient of dispersion, index of dispersion and level of
245 aggregation.

246 4. Discussion

247 A good suitable indicator should be calculated by a simple direct equation and clearly
248 interpret the underlying process (Baddeley et al., 2015). Although previous studies
249 recommend including multiple indicators (Petitgas and Poulard, 2009; Woillez et al., 2007b),
250 monitoring programs, such as the MSFD often require parsimonious and non-redundant
251 indicators. It is thus necessary to select few indicators, if possible, using objective criteria. We
252 tested the ability of several indicators to detect the main geographic processes that are

253 observed in species distributions and their sensitivity to changes in total biomass, and sample
254 size.

255 For the interpretation to remain unambiguous, each indicator should respond to only one
256 change. However, if only one indicator can be used, one that is sensitive to several geographic
257 changes can help identify spatial changes that can be investigated in detail in future studies.
258 the indicator can be used as a preliminary signal to indicate that a population experienced a
259 spatial change. For these situations, the inertia and isotropy indicators are the most adequate
260 since they responded to all of the geographic processes considered: shift, shrink and split,
261 although they did not respond to the level of biomass or the spatial distribution.

262 The center of gravity was the only indicator that responded only to the 'shift' process
263 (i.e. a patch of higher biomass moves in a certain direction without changing the total biomass
264 or range. It is widely recognized that species are modifying their distributions due to climate
265 change and other anthropogenic impacts (Hermant et al., 2010). Most previous studies on
266 biogeography, however, use presence/absence data, and thus measure only species
267 distributions. The center of gravity (through its coordinates) can accurately spot and quantify
268 a biomass geographic shift of a species, when the species distribution does not change.
269 Additionally, this indicator was not influenced by homogeneous changes in biomass.
270 Nevertheless, the center of gravity can be highly sensitive to the presence of other patches
271 within the sampled area or outliers and to non-homogeneous changes in biomass (data not
272 shown).

273 Four indicators responded only to the shrink process (i.e. a decrease in the size of the
274 main biomass patch). If biomass is lost along with the decrease in the area, (shrink0), the
275 index of aggregation should be used. However, if the biomass is relocated (i.e. total biomass

276 does not change), Gini index, equivalent area and spreading area were more effective,
277 although the latter two were highly sensitive to the sample size.

278 None of the indicators detected a split of the main biomass patch into smaller patches.
279 Other indicators, such as the number of patches or a geostatistical variogram model (through
280 its range parameter, also known as patch size) may do so. Nether was included in the current
281 study, however, because the former varies greatly depending on the parameters chosen for
282 calculation, while the latter had no spatial structure to analyze, since the distribution was
283 broken during manipulation. Additionally, it is difficult to identify a spatial model for many
284 distributions because they are not visible for some species or years. Nevertheless, this aspect
285 requires further study.

286 For simplicity, we studied a rectangular sampling area, however, this is rarely possible
287 in real world situations which are hindered by an irregular topography. For example, the areas
288 sampled in coastal surveys are often long and narrow, with extremely irregular shapes
289 (Brind'Amour et al., 2014; Rufino et al., 2017, 2010). In such cases, irregularities in the
290 sampling area can move the center of gravity outside the surveyed area and cause the inertia
291 and isotropy indicators to calculate non-real distances. Artificially dividing the sampling area
292 into several sub-areas may sometimes resolve this problem (Tableau et al., 2016).
293 Nevertheless, future studies are required to develop indicators that are for areas with irregular
294 shapes.

295 One approach to address the sampling area issue is to split study areas into smaller
296 spatial management units. When large areas, such as ocean, are sampled, several processes are
297 combined that are difficult to distinguish. In this case it becomes essential to divide the areas
298 into spatial management areas, which can then be monitored using indicators. For example,
299 several fishery surveys are conducted on an annual basis in European waters. If indicators are

300 to be used to monitor such a large area, spatial management areas are required. We
301 recommend that the scales of underlying processes be identified as well as the methods to
302 establish spatial management areas for relevant application of indicators.

303 Empirical data on species distribution was used instead of simulated data to avoid
304 making assumptions about factors, such as distribution parameters. Species distributions were
305 then manipulated to specify define the spatial changes studied. This approach is generalizable
306 to all indicators and case studies because it is simple, effective and available to all researcher.

307 The MSFD criterion associated with the spatial distribution of species (D1C4) requires
308 indicators that can identify two main processes: (i) species distribution range and, where
309 relevant, (ii) pattern within this range. We chose three geographic changes that likely match
310 the spatial processes highlighted in the MSFD. Hence, we suggest using the indicators that
311 respond to the geographic 'shift' to assess species distribution and using those that respond to
312 shrink (0 or 1) or split changes to assess the pattern within the species distribution. Based on
313 Rufino et al. (2018), who classified indicators into three categories we suggest that
314 'occupancy-related' indicators would correctly identify shift changes (i.e. distributional range)
315 and 'aggregation-related' indicators would correctly identify shrink and split changes (*i.e.*
316 pattern within the distribution).

317 In conclusion this approach is a simple and straightforward way to determine the ability
318 of indicators to identify certain spatial processes. Based on the indicators studied, the center
319 of gravity (for shift process), Gini index, index of aggregation (for a shrink process), with
320 more than 60 samples were the best indicators for options to identify the geographic processes
321 underlying. Inertia and isotropy were two indicators that were sensitive to all processes, so
322 can be used to trigger a spatial change in the species or community.

323

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457 **Table 1: Response of the spatial indicators to the handled distributions and biomass change (no change, vs. double and**
 458 **quintuple).**

Indicator	Description	Manipulation					
		Shift	Shrink.0	Shrink.1	Split	Biomass	Spatial distribution
		Migration of a species southward (without changing the species range)	Decrease in the area occupied and biomass	Decrease in the area occupied, with biomass relocated	Split of the main occupied area in three smaller areas		
	Expectations	Increase or decrease depending on the indicator	Increase or decrease depending on the indicator	Increase or decrease depending on the indicator	Increase or decrease depending on the indicator	No change	No change
Latitude of the centre of Gravity (CG.lat)	Mean geographic location of the population (lat/long coordinates).	Increase up to 20%	Stable	Stable	Stable	No influence	No influence
Longitude of the Centre of Gravity (CG.long)		Stable	Stable but increase variability	Stable but increase variability	Stable	No influence	Influence for RFO and TPS, in 'shrink'
Gini (Lorenz curve)	Represents the difference between the observed distribution and a distribution where every sample contains the same individuals [0-1].	Stable	Small decrease (<10%; stable)	Increased	Stable	No influence	Small influence only in 'shrink'
Equivalent area (eqarea)	The area that would be covered by the population if all individuals had the same density, equal to the mean density per individual [0-PosA](nmi ²)	Stable	Small increase (stable)	Decreased	Stable	No influence	Small influence only in 'shrink'
Spreading area (sparea)	Index related to the Gini index, but which has the advantage of having no contribution from zero values of density (nmi ²).	Stable	Small increase (stable)	Decreased	Stable	No influence	Small influence only in 'shrink'
Index of aggregation (Iagg)	Describes the level of aggregation independent of total abundance.	Stable	Decreased	Small increase (stable)	Stable	No influence	Small influence only in 'shrink'
Inertia	Describes the dispersion of the population around its center of gravity (nmi ²)	Decreased	Decreased	Decreased	Decreased	No influence	Small influence
Isotropy	Measures the elongation of the spatial distribution of the population. dispersion shape (symmetry) of the inertia around the center of gravity (i.e.	Decreased	Decreased	Decreased	Decreased	No influence	Small influence

	round or ellipsoid), and it is the ratio between the two inertia axes. [0-1]						
Index of dispersion (contagion)(MeVa)	Used to measure the distributional pattern within the range (MSFD)	Stable	Stable	Stable	Stable	Changed	Small influence only in 'shrink'
Level of aggregation (Lagg)	Mean density per individual, used to describe the level of aggregation.	Stable	Stable	Stable	Stable	Changed	Small influence only in 'shrink'
Coefficient of dispersion (σ^2 /mean ratio)(VaMe)	This index gives indications on over or under dispersion compared to a Poisson distribution.	Stable	Stable	Stable	Stable	Changed	Small influence only in 'shrink'

460 **FIGURE LEGENDS:**

461 Summary of the process used to evaluate spatial indicator's ability.

462 Figure 1: Mean response and respective bootstrap 95% confidence intervals of spatial
463 indicators as a function of three geographic manipulations Shift, Shrink, with biomass
464 decrease (0) or biomass relocation (1) and Split) and of a homogeneous increase in biomass
465 (0 no increase, 2 two times and 5 five times) of the area analysed. Spatial indicators (Table 1):
466 center of gravity latitude (CG.lat) and longitude (CG.long), Gini, equivalent area (earea),
467 spreading area (sparea), index of aggregation (Iagg), inertia, isotropy (iso), index of
468 dispersion (MeVa), level of aggregation (Lagg) and coefficient of dispersion (VaMe). The 'd.'
469 preceding the indicator's name means 'difference' from its value for the initial state.

470 Figure 2: Mean response and respective bootstrap 95% confidence intervals of the
471 spatial indicators as a function of three geographic manipulations manipulations (Shift,
472 Shrink, with biomass decrease (0) or biomass relocation (1) and Split). Indicators are defined
473 as in Figure 1.

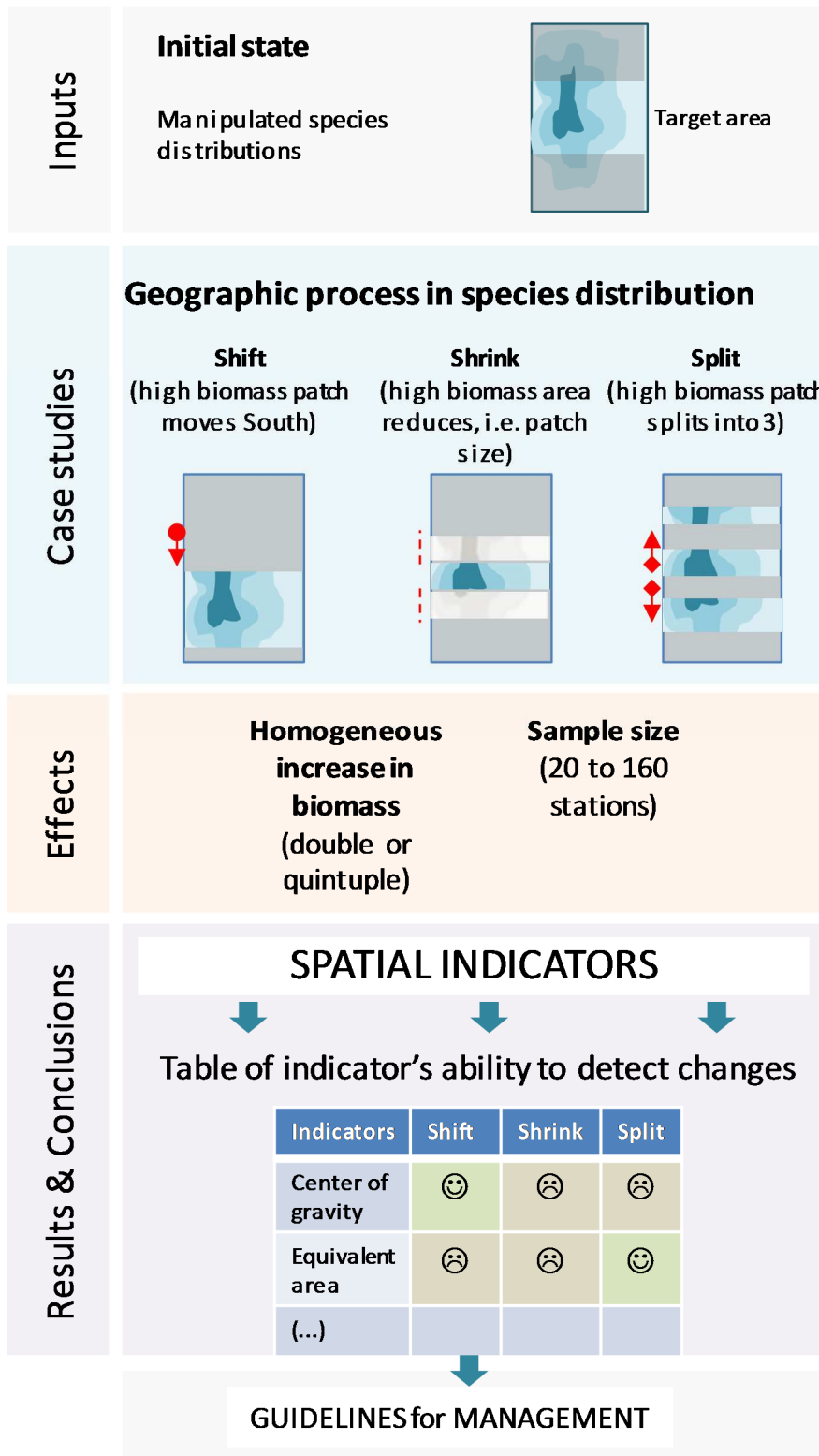
474 Figure 3: Mean response and respective bootstrap 95% confidence intervals of the
475 spatial indicators as a function of sample size (20-160) and three geographic manipulations
476 (Shift, Shrink, with biomass decrease (0) or biomass relocation (1) and Split). Indicators are
477 defined as in Figure 1.

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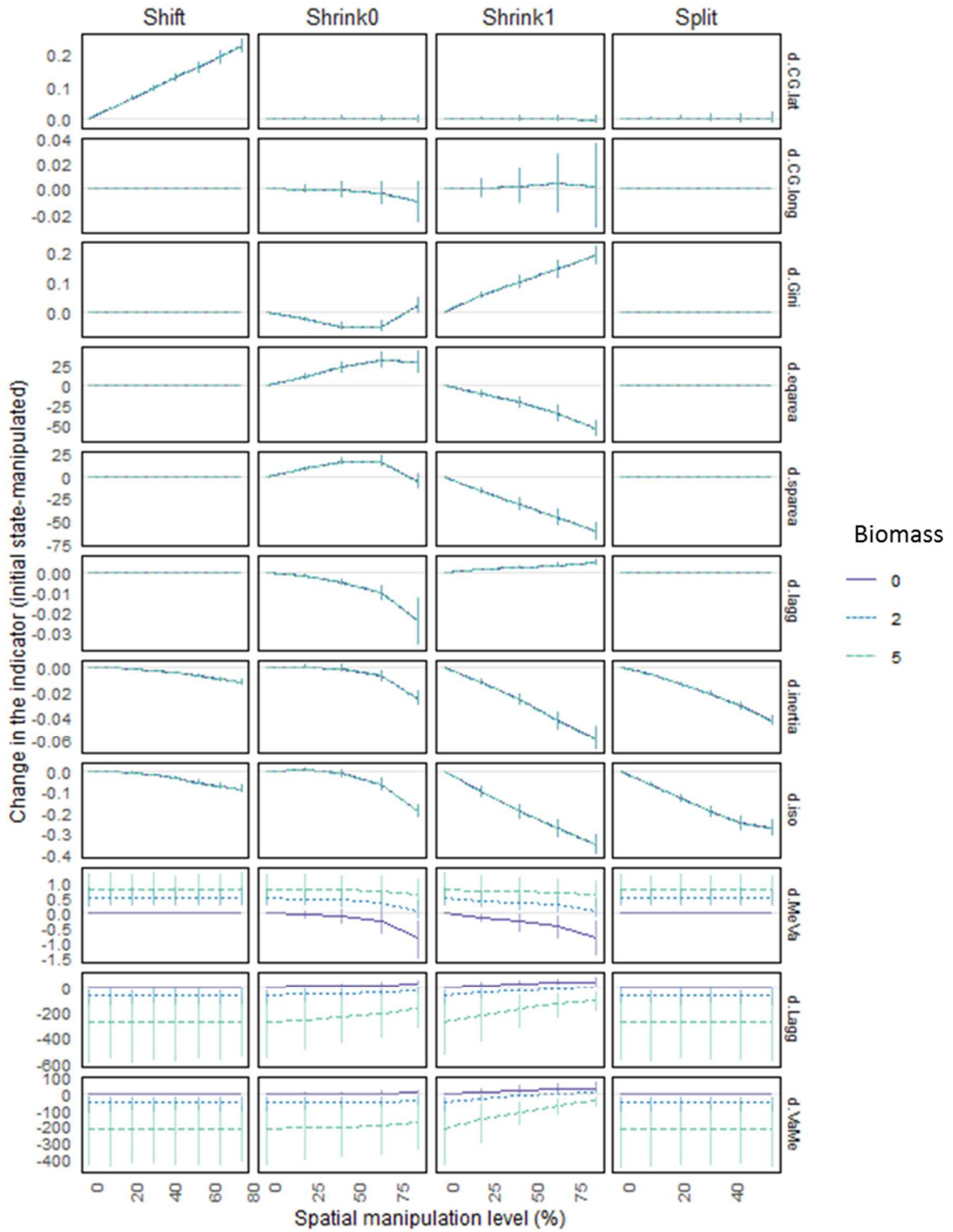
480 FIGURES:

481 Graphical abstract.



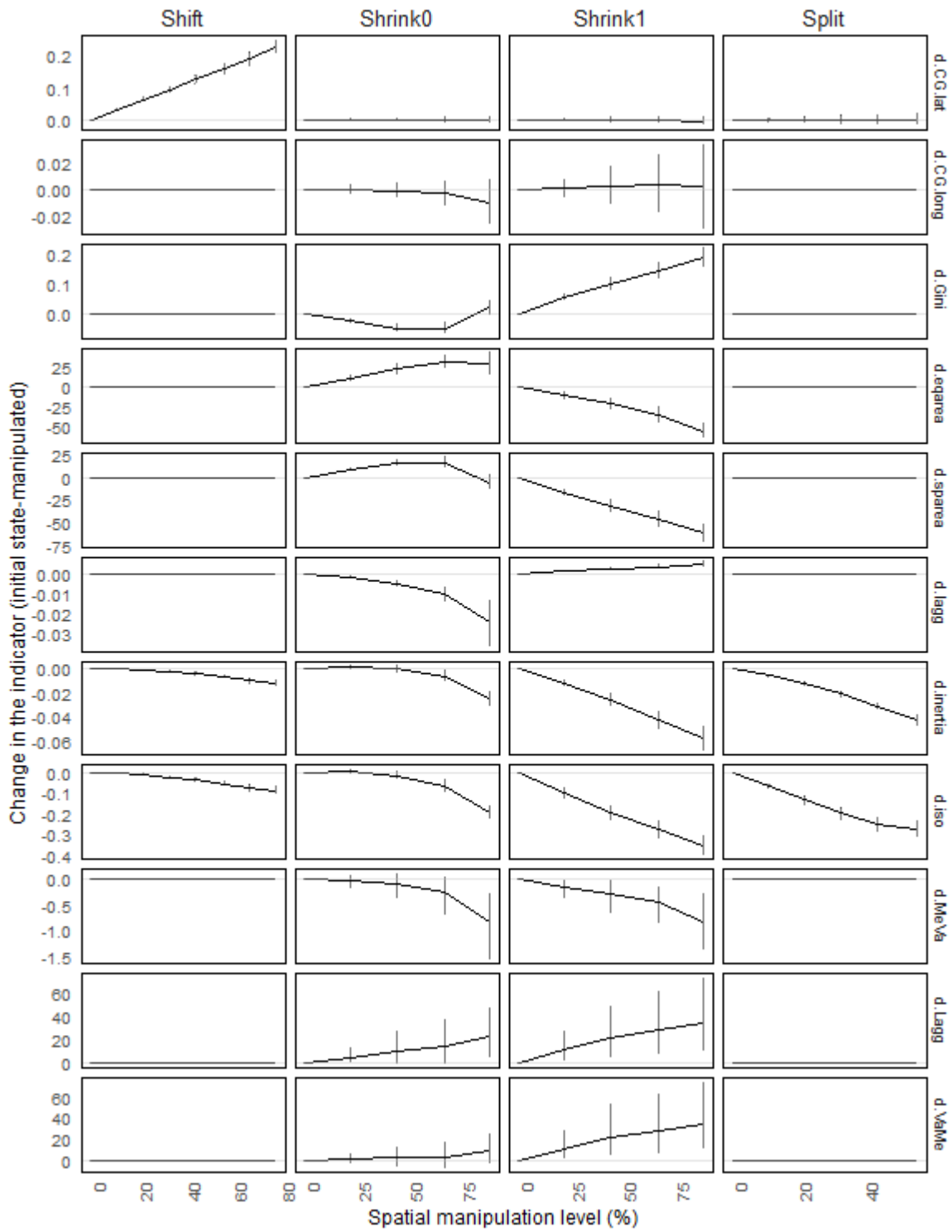
482

483 Figure 1: by biomass level



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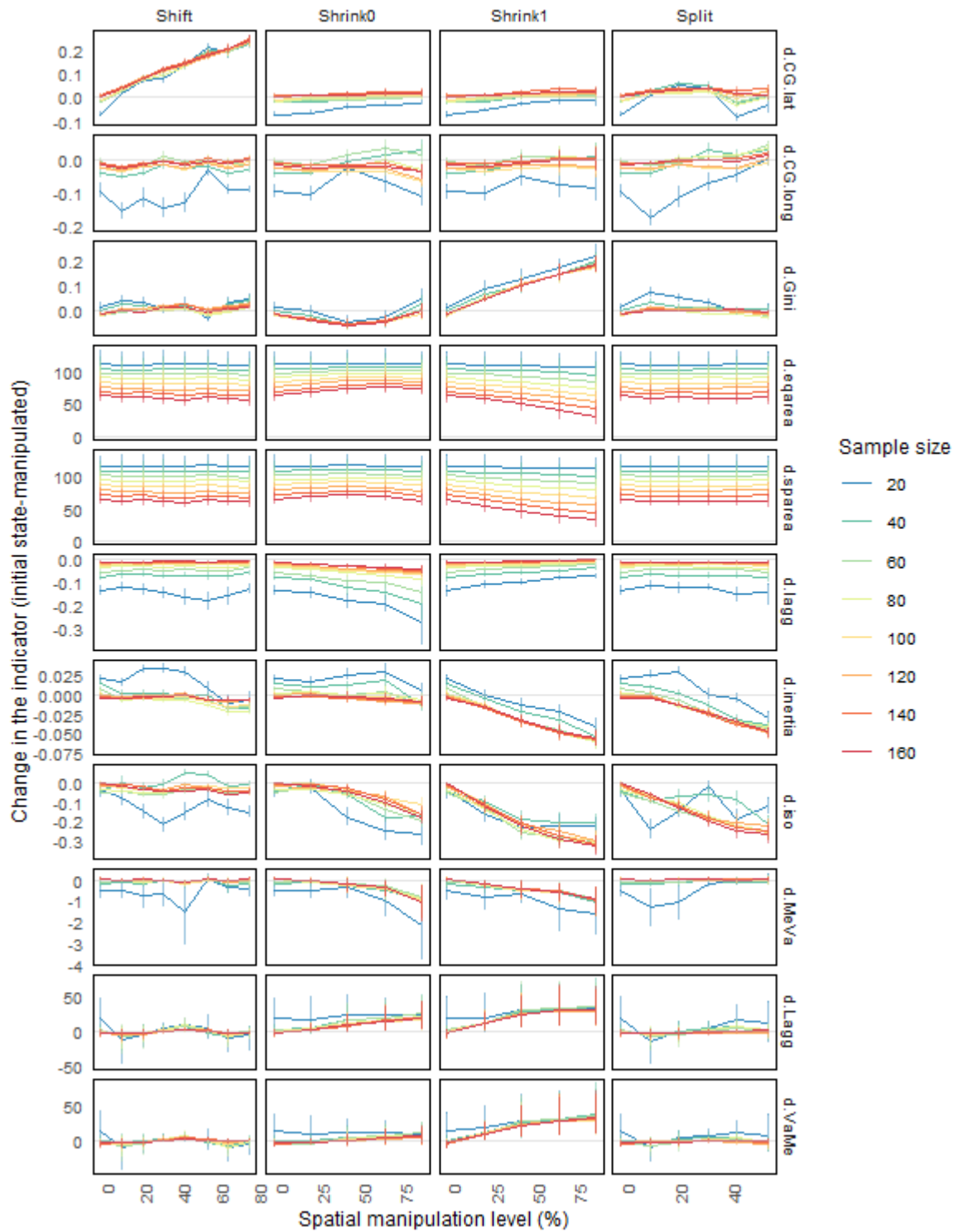
486 Figure 2: by method



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489 Figure 3: by sample size



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