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1 Threshold and weighted-distance methods: A combined
2 multiscale approach improves explanatory power of forest
3 carabid beetle abundance in agricultural landscape

4

5 Benjamin Bergerot¹, Pierre-Gilles Lemasle¹, Hugues Boussard², Julie Betbeder^{3,4},
6 Olivier Jambon¹, Romain Georges¹, Solène Croci⁵, Françoise Burel¹ & Jacques
7 Baudry²

8

9 ¹ Univ Rennes, CNRS, ECOBIO - UMR 6553, F-35042 Rennes, France

10 ² INRAe, UMR BAGAP, F-35042 Rennes, France

11 ³ Forêts et Sociétés, Univ Montpellier, CIRAD, F-34398 Montpellier, France

12 ⁴ Ecosystems Modelling Unity, Forests, Biodiversity and Climate Change Program,
13 Tropical Agricultural Research and Higher Education Center (CATIE), Turrialba,
14 Cartago, Costa Rica

15 ⁵ CNRS, Université Rennes 2, UMR 6554 LETG, F-35043 Rennes, France

16

17 **Correspondence:** Benjamin Bergerot, Tel. + 33 223235616

18 Email: benjamin.bergerot@univ-rennes1.fr

19 Address: UMR CNRS 6553 ECOBIO, Université de Rennes 1, Bât 14B, porte 117, Avenue du
20 Général Leclerc, 35042 Rennes Cedex, France

21

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32 manuscript.

33 **Abstract**

34

35 *Context.* To analyze the scales at which landscape structure influences ecological processes, two
36 approaches with different underlying ecological assumptions exist; the usual threshold method and
37 the weighted-distance method.

38

39 *Objectives.* We used abundance of species to test if the combination of weighted-distance and
40 threshold approaches improves the explained variance of landscape metrics.

41

42 *Methods.* We developed a workflow using the two approaches to calculate metrics computed at
43 multiple scales. The latter was developed using weighted metrics based on different weighted-
44 distance functions, and one metric could be selected for more than one spatial scale. Then, we tested
45 the explained variance of species distribution (the activity-density of *Abax parallelepipedus*) by
46 these two approaches applied independently and then together in modeling a specific ecological
47 response.

48

49 *Results.* The combination of metrics computed at multiple scales calculated by both weighted-
50 distance and threshold method improved the predictive performance of the models. More precisely,
51 adding metrics derived from the weighted-distance method to the threshold method significantly
52 increased the explained variance when using the same environmental variables. The mean R^2 values
53 of the selected model for the threshold method was 0.34 ± 0.10 , 0.49 ± 0.11 with the weighted-
54 distance method, and reached 0.71 ± 0.07 with the two methods combined. These results demonstrate
55 the importance of combining metrics using the weighted-distance method and the threshold method.
56 In addition, activity-density was better explained by metrics selected at multiple scales.

57

58 *Conclusions.* This study highlights the importance of combining threshold and weighted-distance
59 method at several scales to improve the explanation of ecological responses based on species
60 abundance.

61

62 *Keywords:* *Abax parallelepipedus*, multiscale approach, weighted distance, landscape metric

63

64 **Introduction**

65 Many studies aim to elucidate the scale at which environmental variables explain the
66 abundance and diversity of species (Jackson and Fahrig 2015; Chandler and Hepinstall-Cymerman
67 2016). To incorporate landscape effects in models and the scale at which landscape effects occur,
68 landscape metrics are generally computed within buffers around sampling points (Miguet et al.
69 2016). As the evidence for a relation between the scale of effect and movement (Desrochers et al.
70 2010; Stuber et al. 2018), the buffers tend to be circular when there is no *a priori* information about
71 the movement capacity of species in the studied landscape. Metrics are calculated at different scales
72 according to the known or estimated dispersal abilities of species (Bertrand et al. 2016; Serckx et al.
73 2016).

74 To characterize landscape structure within buffers, maps of relevant landscape elements are
75 required (Burel and Baudry 2003). Based on landscape ecology theory (Burel and Baudry 2003;
76 Tschardt et al. 2012), landscapes have two main components: composition and configuration
77 (Fahrig et al. 2011). Composition defines the proportion of different landscape elements, while
78 configuration represents spatial organization of these elements. In each buffer, landscape metrics
79 are then computed using the composition or configuration of landscape features (e.g., Bertrand et al.
80 2016). The final step defines the “best” scale at which the effect of landscape metrics on
81 biodiversity is highest based on model selection processes and criteria based methods (e.g.,
82 correlation coefficient, regression slopes, Akaike Information Criterion, model averaging or
83 posterior probability; Burnham et al. 2011; Jackson and Fahrig 2015; Stuber and Gruber 2020).

84 The problem with this approach is that most landscape metrics are scale dependent and
85 often multi-scaled (Wu 2004; Ostapowicz et al. 2008; Cushman et al. 2008; Stuber and Gruber
86 2020), which might influence the results (Miguet et al. 2016). There is no single adequate scale for
87 all landscape metrics, with wrong scale identification generating misleading results. Consequently,
88 an optimal relation between ecological processes and landscape metrics is still being sought in
89 landscape ecology (Jackson and Fahrig 2015). This issue has led to the emergence of multi-scale

90 methods (Mayor et al. 2009; McGarigal et al. 2016) used to measure the different spatial scales at
91 which relations between landscape metrics and ecological processes are the most meaningful
92 (Gaucherel et al. 2007; Martin and Fahrig 2012; Miguet et al. 2017; Egerer et al. 2018; Remon et al.
93 2018).

94 Among the multi-scale analytical methods, two main approaches stand out that are based on
95 very different underlying biological assumptions: the classical threshold-based method and the
96 weighted-distance method (Jackson and Fahrig 2015; Miguet et al. 2016, 2017). The threshold
97 method is based on the computation of landscape metrics, and tests the relation between metric and
98 biodiversity variables using a statistical model at a variety of separate scales. This approach aims to
99 identify the scales at which the relation is meaningful. The main issue with this method is that it
100 assumes that the landscape metric has a constant effect up to the edge of the buffer, where it then
101 falls to zero (Miguet et al. 2017), which is biologically unrealistic (Jackson and Fahrig 2015). This
102 issue has led to the recent investigation of weighted-distance methods. These methods assume that
103 the landscape affects ecological process according to distance, following a predefined function
104 (Miguet et al. 2016, 2017). Computed landscape metrics are, thus, distance dependent from the
105 sampling site where the ecological response is measured. The distance weighted landscape variables
106 are obtained by weighting the spatial distribution of each metric by a decreasing function of the
107 distance from the point where the biological response is measured. However, this approach remains
108 primarily theoretical and under development; yet, recent developments in computing yield very
109 promising results (Peterson et al. 2011; Chandler and Hepinstall-Cymerman 2016; Miguet et al.
110 2017; Remon et al. 2018).

111 In this paper, we present a new workflow approach by combining landscape metrics
112 computed at multiple scales using the weighted-distance method and the more classical threshold
113 method. More precisely, we propose a general framework and reuse existing methodological tools
114 in order to adapt it to a plurality of ecological data. Specifically, we tested various metrics known to
115 affect the activity-density of a forest specialist carabid species, *Abax parallelepipedus*, and we

116 calculated the metrics using: i) the threshold method, and ii) the weighted-distance method and iii)
117 the threshold method combined with different weighted-distance functions. We compared the
118 results obtained using the metrics calculated only on the basis of the threshold method, the metrics
119 calculated only on the basis of the weighted-distance method, and the mix of the two.

120 A number of studies have been previously conducted on *A. parallelepipedus* (Work et al.
121 2011; Davies and Asner 2014; Müller et al. 2014), particularly in our study area (Charrier et al.
122 1997; Petit and Burel 1998a; Betbeder et al. 2015). In this study, we analyze if landscape metrics
123 calculated by the combination of the weighted-distance method and threshold method at multiple
124 scales could better explain the ecological response of *A. parallelepipedus* density-activity than the
125 threshold-based method or weighted-distance method alone (Jackson and Fahrig 2015; Miguet et al.
126 2016, 2017). We know that *A. parallelepipedus* prefers forest habitat and hedges (Niemela 2001;
127 Davies and Pullin 2007; Roume et al. 2011). Therefore, we expect that heterogeneity indices
128 (Niemelä et al. 1992; da Silva et al. 2008) and the micro-climatic effects of the woody elements
129 (Forman and Baudry 1984; Vannier et al. 2011; Baudry and Burel 2019) will influence carabid
130 density activity.

131

132 Methods

133 Study Area

134 This study was conducted in Brittany, Western France (Fig. 1A), in the ZAA (Zone Atelier
135 Armorique), which is a French Long Term Ecological Research site (LTER, Fig. 1C). The ZAA is
136 bordered by the sea (48° 36' N, 1° 32' W), and the climate is of oceanic temperate type, with mild
137 winters. The area is mainly agricultural, composed of small fields separated by a hedgerow network
138 called “bocage” (Baudry et al, 2000). Annual crops in this area are winter cereals and maize. In this
139 area, carabids are a key biodiversity component of long-term studies (Baudry and Burel 2019).

140

141 Biological model sampling

142 *A. parallelepipedus* is a nocturnal, polyphagous and flightless forest carabid of medium size. It is
143 often a dominant species in deciduous forest communities (Loreau 1985, 1990; Fournier and Loreau
144 1999). Its annual period of adult activity, from April to October, is one of the longest for carabid
145 beetles, and this species is characterized by a continuous reproduction so that hibernation can be
146 withstood by both adults and third larval instars (Loreau 1985). *A. parallelepipedus* has a great
147 longevity as some individuals have been found to be at least four years old in the field (Loreau
148 1990). *A. parallelepipedus* is a slow-moving species and is mostly carnivorous. It prefers woody
149 habitats, such as woodlots and hedgerows with a high density of tree vegetation and connectivity of
150 hedgerow network (Charrier et al. 1997; Petit and Burel 1998a). It prefers fine grain hedgerow
151 networks (Vannier et al, 2011). This species is an efficient natural control agent of slugs in
152 agricultural environments, particularly in fields bordered by hedges (Symondson and Liddell 1993;
153 Symondson 1994).

154 *A. parallelepipedus* were sampled from 30 hedgerows in 2017 (Fig. 1C) using pitfall traps (i.e.,
155 plastic pitfall traps containing water, salt, and soap). A sample consisted of three pitfall traps placed
156 three meters apart per hedgerow. This method was easy to implement and produces high capture
157 rates (Luff 1975; Spence and Niemelä 1994). Traps were set up three times in 2017 (May 9, June 6,
158 and August 29) and were left open for 14 days. Catches by pitfall traps depend on both population
159 density and activity (Thomas et al. 1998), therefore, sampling is a measure of activity-density.
160 Activity-density is calculated as the mean value of catches in the three pitfall traps over the
161 sampling period. We selected the 30 hedgerows based on specific criteria. Specifically, they had to
162 be: (1) in landscape contexts covering a gradient of grain values (described in the metric section),
163 (2) at least 50 m long (to ensure that individuals sampled every 14 days come from this hedgerow),
164 (3) at least 400 m from another sampled hedgerow (to ensure the ecological independence of
165 sampling sites), and (4) with oak as the dominant tree species.

8

166

167 Maps

168 We used two raster maps with a resolution of $5\text{ m} \times 5\text{ m}$ to calculate landscape metrics (Online
169 Resource 1). A preliminary map that was defined by 11 land use categories (Table 1) was obtained
170 by the photo-interpretation of aerial photography generated by LETG (Littoral, Environnement,
171 Télédétection Géomatique laboratory, Rennes) in 2017. These categories were selected following
172 the preferences of the species according to the literature (Loreau and Nolf 1993; Symondson 1994;
173 Charrier et al. 1997; Petit and Burel 1998a,b; Fournier and Loreau 1999; Pichancourt et al. 2006). A
174 second, wooded features map (hedgerows, woodlots), was used to calculate the grain metric (i.e.,
175 MD metric, described in the metrics section). This map represented the canopy cover of trees
176 extracted from aerial photographs by KERMAP (a private company) in 2016.

177

178 Metrics

179 Seven classes of landscape metrics (Table 2) led to the calculation of twenty-four metrics. They
180 were computed using CHLOE software (Boussard and Baudry 2017). Specifically, we calculated
181 (1) abundance of the different types of land cover (NV), which represent eleven metrics (each
182 representing a type of land use); (2) abundance of the interfaces between the woods and the other
183 land cover types (NC), which represent eight metrics (each representing a possible interface with
184 woods); (3) number of heterogeneous types of adjacent pairs of pixels (NC hete), a landscape-level
185 metric; (4) land cover diversity measured from the Shannon diversity index (SHDI), a landscape-
186 level metric; and two landscape-level heterogeneity metrics computing Shannon Diversity based on
187 the number of pixel pairs of different types; specifically, (5) HET, which is the overall
188 heterogeneity; (6) HET-Frag, which is the heterogeneity of dissimilar interfaces; and (7) a grain
189 metric (MD), a landscape-level metric representing the micro-climatic effects of the woody
190 elements. These seven class of metrics were selected according to the ecological preferences of *A.*
191 *parallelepipedus*. NV metrics is a composition metric and NC metric is a mixture of composition

9

192 and configuration metric as it depends on how the land covers are distributed. These metrics were
193 selected knowing the influence of habitat and edge effect on carabids (Niemelä 2001; Davies and
194 Pullin 2007; Roume et al. 2011). NC metric is a mixture of composition and configuration metric
195 because it depends on how the land covers are distributed (Niemelä 2001; Davies and Pullin 2007).
196 The SHDI (used to measure the land cover diversity) and the two heterogeneity indices (HET and
197 HET-Frag, used to display the diversity of dissimilar interfaces) characterize the landscape
198 heterogeneity, which influences carabids (Niemelä et al. 1992; da Silva et al. 2008). The grain
199 metric (MD) represents micro-climatic effects of the woody elements, which are known to influence
200 the activity of the carabids. As mentioned in Betbeder et al. 2015, the grain metric integrates both
201 the density of hedgerows and the shape of the meshes of the network measured as the mean distance
202 to hedgerows (Forman and Baudry 1984, adapted by Vannier et al., 2011 for hedgerow networks).
203 Hedgerow networks have many discontinuities and, therefore, do not comprise “closed meshes”
204 (the space between hedgerows). The size of these meshes controls the local climate by reducing
205 wind speed and capturing the energy from the sun. We used the grain of the imagery as a surrogate
206 of these meshes to characterize the more or less open character of the landscape. Hedgerow density
207 alone is not sufficient as for similar densities the spatial distribution of hedgerows, thus the grain
208 metric, may be different.

209

210 Threshold method

211 The threshold method computes landscape metrics within buffers of different radii centered on the
212 same sampling point (Table 3). Metrics were computed in 35 nested concentric circles, at 50 m
213 increments from 50 to 1750 m (radius), following the recommendations of Jackson and Fahrig
214 (2015). Although *A. parallelepipedus* shows a preference for forest habitats, we do not know the
215 dispersal pattern of the individuals, we thus used circular vector buffers. Previous studies show that
216 the area prospected by an individual varies according to the habitat, and the dispersal power of
217 individuals was found to be low—on average 1 m per day and about 2 m per day for the most active

10

218 males (Charrier et al. 1997; Marcus et al. 2015). The estimated life span is one to two years for
219 large carabid beetles (Coulon et al. 2011). Therefore, we can consider that with 250-280 days of
220 activity per year (from April to November) and an average displacement of 1 m per day (or 2 m in
221 exceptional cases for males), a buffer of 1750 m is able to capture all the displacements of the
222 individuals, on a theoretical high range. Beyond this distance, we assumed that woody elements do
223 not influence the activity-density of *A. parallelepipedus* (Petit and Burel 1998b; Betbeder et al.
224 2015; Bertrand et al. 2016). Care must be paid to the quantity of empty pixels (i.e., with NA values,
225 pixels outside the map) in a buffer for the calculation of metrics. To calculate metrics at 1750 m
226 (the largest buffer size), the proportion of empty pixels in our study varies between 0 and 40.36%.
227 Only two sites have a proportion of empty cells greater than 30%, and 17 sites have a proportion
228 less than 10%.

229

230 Weighted-distance method

231 To compute the metrics for this method, a weight was applied to the pixels in the analyzed window
232 (i.e., a circular window representing the buffer), depending on the weighting-distance function
233 applied (Table 3). Thus, the threshold method is a special case of the weighted-distance method
234 (i.e., where the weight applied with distance was constant up to a threshold, at which point it
235 dropped to 0). As in other studies (Miguet et al. 2017), we did not know what the best function was
236 to characterize the distribution of individuals. Therefore, we chose four types of common ecological
237 functions (Table 3) to test different weights placed on landscape features, divided into two main
238 groups. We used functions that gave more weight to a local landscape effect (i.e., decreasing
239 functions, Hill et al. 1996; Stevens et al. 2010; Remon et al. 2018) than to a distant landscape effect
240 (i.e., Gaussian functions, Chandler and Hepinstall-Cymerman 2016). Decreasing functions can take
241 different forms, so we used the linear decreasing curve, assuming only a distance effect, and the
242 common decreasing curve, a variant shape giving slightly more weight to nearby landscape
243 elements. We also used two Gaussian functions that gave different weights to a landscape (i.e.,

244 according to the distance at which the species may need its non-immediate environment such as
245 meadows to complete all or part of its life cycle).

246

247 Statistical and modeling approach

248 Two steps were required to analyze the data: the metric and scale identification, and then the
249 run of the global model. We ran three independent replicates, one using metrics as variables
250 calculated with the threshold method only, one using metrics as variables calculated with the
251 weighted-distance method only, and one using metrics as variables calculated with the combination
252 of the two. All statistical analyses were performed in R version 3.6.0 (R Core Team 2017). These
253 steps are detailed below.

254

255 *Step 1. Metric and scale identification*

256 The first step is to identify (but not yet select) at which scales the explanatory variables
257 (metrics) can be related to the activity-density of *A. parallelepipedus*. Since the distribution of data,
258 as well as the shape of the relation between a predictor and its dependent variables can be unknown,
259 a non-parametric modelling approach using a Multivariate Adaptive Regression Spline (MARS)
260 was used (Friedman 1991). MARS models allow the non-linearity of a relation to be captured in a
261 simple form by partitioning the space of a variable into several knots, and assigning a linear model
262 in this space (Friedman 1991). For each metric, we fit a MARS model between the activity-density
263 of *A. parallelepipedus* (i.e., 30 sampling points; Fig. 2, Step 1.1) and the metrics at each scale for
264 each method (i.e., threshold method only, the weighted-distance method only, and the combination
265 of the two). MARS models were fit using the R package ‘earth’ (Milborrow 2011). For each MARS
266 model, R^2 was calculated (Step 1.1). Then, using GAMs (General Additive Models), we fitted the
267 relation between R^2 obtained from MARS and scales (Fig. 2, Step 1.2). Finally, we identified the

268 best scales (i.e., all scales with peak values, not only the highest peak, represented by red stars in
269 Fig. 2, Step 1.3).

270

271 *Step 2. Global model*

272 To select the variables computed at multiple scales explaining the activity-density of *A.*
273 *parallelepipedus*, since there could be many uninformative combinations of metrics at different
274 scales, we used LASSO optimization algorithm (Least absolute shrinkage and selection operator)
275 for variable selection and regularization (Tibshirani 1996). There are many advantages in using
276 LASSO method. First, it can provide a very good prediction accuracy, because shrinking and
277 removing the coefficients can reduce variance without a substantial increase of the bias. This is
278 especially useful when you have a small number of observations and a large number of features.
279 LASSO shrinks uninformative coefficient estimates to zero, which improves both model prediction
280 and interpretability. Moreover, LASSO is suited to perform variables selection on collinear
281 variables.

282 To fit the global model, metrics at their best scales were used as predictors of the density-
283 activity of *A. parallelepipedus*. To test our hypotheses, we built three models: (1) one with the
284 metrics obtained from the threshold method only, (2) one with the metrics obtained from the
285 weighted-distance method only, and (3) one with the metrics from both the threshold method and
286 weighted-distance method. LASSO models were fit using the R package ‘glmnet’ (Friedman et al.
287 2011). The R^2 obtained by LASSO selection procedure for each of the three sets of variables (i.e.,
288 those identified using the threshold method, the weighted-distance method, and the combination of
289 the two) were bootstrapped 1000 times to obtain a mean value and a standard deviation. Residuals
290 of the different models were checked to make sure that there was not evidence of residual spatial
291 autocorrelation. The results are represented using partial dependence plots (Friedman 1991). These
292 plots show how the selected predictors in the selected model influenced the dependent variable

293 (Greenwell 2017) and whether the relations between the dependent variables and selected predictors
294 were linear, monotonic, or more complex.

295

296 **Results**

297

298 *Step 1*

299 Considering the seven defined class metrics, a total of 24 metrics were calculated because
300 the NV metric is subdivided into 11 (one for each land use type), and the NC metric is subdivided
301 into eight (eight different interfaces with woods are referenced in our landscape). Considering the
302 35 spatial scales, 840 variables for each method were thus calculated. In total, 4200 metrics were
303 computed in Step 1: 840 for the threshold method and 3,360 for the weighted-distance method (i.e.,
304 840 for each of the functions referenced in Table 3). For the threshold method, out of 840 possible
305 variables, 76 were selected. For each of the 24 metrics, the average number of scales selected was
306 3.17 ± 1.04 . For the weighted-distance method, out of 840 possible variables for each function,
307 respectively 55, 61, 49 and 58 variables were selected for the Decreasing Curve, Decreasing Linear,
308 Gaussian and Adjusted Gaussian functions. The average number of scales selected was respectively
309 2.14 ± 0.98 , 2.39 ± 1.21 , 2.01 ± 0.91 and 2.26 ± 1.23 for the Decreasing Curve, Decreasing Linear,
310 Gaussian and Adjusted Gaussian functions.

311

312 *Step 2*

313 The mean R^2 value (\pm standard deviation) of the three models using LASSO were 0.34 ± 0.10
314 with the metrics derived from the threshold method only, 0.49 ± 0.11 with the metrics derived from
315 the weighted-distance method only and 0.71 ± 0.07 with the metrics derived from the weighted-
316 distance method and threshold method. The metrics selected using LASSO procedure were mainly
317 related to (1) interface metric between wood and dirt-roads (NC 1–12) at 1200 m for the threshold
318 method only (Fig. 3A) and 1500 m for the weighted-distance method only and the combination of

319 weighted-distance and threshold method (Fig. 3B); (2) landscape density metrics (NV 16: meadow
320 density) at 550 m and 1750 m for the threshold method only (Fig. 3C) and 950 m for the weighted-
321 distance method only and for the combination of weighted-distance and threshold method (Fig. 3D);
322 (3) dirt-road density (NV 12) at 1350 m for the combination of weighted-distance and threshold
323 method only (Fig. 3E). Overall, for both the threshold method only, the weighted-distance method
324 only, and the combination of weighted-distance and threshold method, metrics were selected at
325 different scales (i.e., from an intermediate scale of 550 m to 1750 m). The interface metric, NC 1–
326 12, had the highest relative importance in models and greatly improved the explanation of *A.*
327 *parallelepipedus* density-activity when it was calculated using weighted-distance method
328 (decreasing curve, Fig 3B). Among the three selected metrics, two metrics were found in all of the
329 final models (NC 1-12 and NV 16). The main difference was the method used and the scale selected
330 (Fig. 3).

331 For each model, the selected metrics are summarized in Figure 4. For the threshold method
332 only, the partial dependence plots (Fig. 4A and B) showed dissimilarities for the density of
333 meadows (NV 16). At the local scale (550 m, Fig. 4A), the activity-density decreased and reached a
334 plateau, whereas it increased and reached a plateau at the landscape scale (1750 m, Fig. 4B). For the
335 combination of weighted-distance and threshold method, the density of meadows (NV 16; Fig. 4D)
336 showed similarities to the weighted-distance method only (i.e., after the activity-density decreased
337 and reached a plateau, Fig. 4H) but used a decreasing linear function.

338 For the combination of weighted-distance and threshold method, the dirt-road density (NV
339 12; Fig. 4E) was selected at 1350 m. The activity-density decreased and reached a plateau.
340 The partial dependence plots of the selected metrics highlight some similarities between the three
341 methods. More specifically, these plots show the influence of the interface between wooded features
342 (mainly hedgerows) and dirt-road (i.e., NC 1–12) on the activity-density of *A. parallelepipedus*. The
343 interface between wood and dirt-road shows that, after a plateau was reached, activity-density
344 increased (Fig. 4C, Fig. 4F and Fig. 4G) when using a decreasing curve function at 1500 m for the

345 combination of the weighted-distance method and the weighted-distance method only (Fig. 4F and
346 4G respectively), and 1200 m for the threshold method only (Fig. 4C) .

347

348 **Discussion**

349 We tested the power of the combination of the weighted-distance method and threshold-
350 method to obtain landscape metrics computed at multiple scales to explain a specific ecological
351 response. Compared to the threshold-based method only, as shown by Miguet et al. (2017), we
352 demonstrated that using landscape metrics computed at multiple scales (i.e., the same metric could
353 be selected at different scales) with the weighted-distance method better explained the density-
354 activity of *A. parallelepipedus*. The mean R^2 of the model explaining *A. parallelepipedus* activity-
355 density using metrics identified with metrics computed at multiple scales using threshold method
356 only was 0.34 ± 0.10 and was lower than previous studies conducted at the same study site (around
357 0.5, Betbeder et al. 2015). However, Betbeder et al. (2015) used radar SAR (Synthetic Aperture
358 Radar) image-based variables to characterize the internal structure of hedgerows. The analyses
359 performed using metrics computed at multiple scales identified through the weighted-distance
360 method yielded better results with a mean R^2 equal to 0.49 ± 0.11 . By combining metrics computed
361 at multiple scales using both the threshold method and the weighted-distance method, we greatly
362 improved the variance explained of *A. parallelepipedus* activity-density and reached 0.71 ± 0.07 . The
363 high R^2 values is attributed to the use of weighted metrics at different spatial scales, which were
364 tested individually according to the distance functions. No published study or ecological hypothesis
365 supports that each metric computed at multiple scales should have the same distance function,
366 which our results confirm (Peterson et al. 2011; Chandler and Hepinstall-Cymerman 2016; Miguet
367 et al. 2017; Remon et al. 2018). More precisely, our statistical and modelling processes only
368 retained the functions and the scales that best explained the ecological response (Step 1, Fig. 2).
369 Interestingly, two of the three selected metrics were the same. The main difference was the use of
370 metrics using weighted-distance functions and multiple scales, which greatly improved metric

371 importance. Out of the three metrics selected by the combination of the weighted-distance method
372 and threshold method, two were computed using decreasing linear and curve functions. This result
373 further emphasizes the important contribution of the metrics computed at multiple scales using
374 weighted-distance method to the more ‘classical’ threshold method. The improvement of models
375 through computing metrics using the decreasing linear and decreasing curve functions supported the
376 results of Miguet et al. (2017) who evaluated four species, including a carabid (i.e., *Pterostichus*
377 *melanarius*).

378 Interfaces including wood (NC 1–12) strongly influence the distribution of *A.*
379 *parallelepipedus* (Charrier 1997; Niemela 2001; Roume et al. 2011). The activity-density of *A.*
380 *parallelepipedus* increased with the importance of the interface between wood and dirt-road at a
381 large scale when using a decreasing curve. To the best of our knowledge, previous studies have not
382 included this specific interface with wood in their analyses, nor have they included a decreasing
383 curve to calculate this metric (Dufлот et al. 2014; Bertrand et al. 2016). This result highlighted the
384 role of dirt roads adjacent to wooded elements as potential ecological corridors in fragmented
385 landscapes (Burel 1989; Vermeulen 1993, 1994; Niemela 2001; Pichancourt et al. 2006) and could
386 suggest that dirt roads bordered by woody habitats could provide high quality corridors for *A.*
387 *parallelepipedus* (Charrier et al. 1997).

388 Metrics computed at multiple scales based on landscape element density for the combination
389 of the weighted-distance method and threshold method also showed expected results. The amount
390 of meadows (NV 16) is negatively related to *A. parallelepipedus* density-activity at < 950 m. The
391 negative relation of this landscape element might be attributed to the high specialization of *A.*
392 *parallelepipedus* for woody elements and the sensitivity of this species to fragmentation (Petit and
393 Burel 1998b). Interestingly, for metrics using threshold method alone, the density of meadows (NV
394 16) had a positive effect at broader scale (1750 m). This result suggests that meadows could act as
395 an ecological filter (e.g. against herbicides) when they are adjacent to hedgerows (Vermeulen 1993,
396 1994; Niemela 2001; Pichancourt et al. 2006), particularly in agricultural landscapes, such as our

397 study area (Fournier and Loreau 1999; Aviron et al. 2018). These results clearly support the
398 necessity of integrating multiple spatial scales for one or more variables in models to understand
399 ecological processes (Niemelä et al. 1992). In this study, spatially, we worked on raster maps where
400 the resolution is constant (5×5 m). Therefore, when the metrics were calculated in a buffer, the
401 number of pixels increased, so the spatial resolution did not change. Since our resolution was
402 constant whatever the spatial scale considered. The metrics were then comparable. However, due to
403 lack of information, we did not take into consideration the temporal dimension and the stationarity
404 of landscape metrics (Fortin et al. 2003; Rempel and Csillag 2003) that may influence the
405 conclusions of this study. More generally, our results suggested that the surrounding environment
406 were the main factors explaining *A. parallelepipedus* density-activity (5/8 metrics were selected at
407 distances ≤ 1350 m). This result is often sought in landscape ecology, because landscape
408 composition and heterogeneity represent the main drivers of species and diversity distributions
409 (Batary et al. 2011; Vasseur et al. 2013; Kennedy et al. 2013; Shackelford et al. 2013).

410 One limitation of this study was that sampling did not cover the full period of activity of *A.*
411 *parallelepipedus* (Pichancourt et al. 2006; Niemelä et al. 1992; Magura 2000), which would have
412 provided a better understanding of how this species is distributed in the landscape. Another issue
413 may lie in the automated selection process of LASSO variables, which may hide common metrics
414 used to explain ecological processes. As for example the grain metric MD (Forman and Baudry
415 1984; Vannier et al. 2011), which has been demonstrated to explain *A. parallelepipedus* density-
416 activity (Betbeder et al. 2015), but was not found in our selected metrics. Finally, our ecological
417 results are based on small sample sizes, and thus should be interpreted with caution. But
418 nevertheless, the framework and workflow can be useful across systems and taxa when sample sizes
419 are appropriate for individual studies' goals.

420 To improve the results, several solutions can be considered. For the sake of simplicity, we
421 have also considered in Step 1 the identification of scale of interest on a variable by variable basis.
422 This method ignores the potential for covariates to be synergistically effected by others. Although

423 our final results show a strong explanatory power of the models, the models could be improved in
424 this way. Regarding the weighted-distance analysis, first, it was limited when not all scales were
425 available. Specifically, when the scale was changed, the maximum distance in the metrics using
426 weighting functions also changed, but did not generate the best scale for the effect (i.e., the weight
427 given by the function). Miguet et al. (2017) overcome this problem by deducing a cumulative
428 distance function from the weighting function, which corresponded to “the proportion of the
429 landscape weight that is modelled within each distance”. This approach made it possible, for
430 example, to determine at which scale 50% of the landscape effect is contained, with the decision
431 threshold being left to the experimenter. Second, even when our results generated high R^2 values
432 and support known results based on the published literature for *A. parallelepipedus*, we used four *a*
433 *priori* weighted-distance functions (decreasing linear, decreasing curve, Gaussian, and adjusted-
434 Gaussian functions). Other ecological functions should be tested according to the species (Remon et
435 al. 2018). It would also be interesting to test these methods using variables derived from remotely
436 sensed data that reflect the internal structure of landscape elements (such as hedgerow structure and
437 crop phenology, Betbeder et al. 2015). Third, the interpretation and extrapolation of the results in
438 other studies must consider the metrics used. Indeed, metrics could be very sensitive to
439 compositional changes and when sites with different compositions are compared or lumped,
440 differences may be driven by a subtle imbalance in the composition differences (e.g., inclusion of
441 an additional minor land cover category) rather than an actual ecological difference (Fortin et al.
442 2003; Cushman et al. 2008). Moreover, using more than two categories increases the possible
443 configurations beyond a reasonable ability to enumerate all possibilities and thus making
444 comparisons among maps or sites challenging (Boots 2003; Csillag and Boots 2005; Turner 2005).
445 Caution should also be taken in the consideration of non-linear relations between metrics with
446 changes to composition and configuration (Hargis et al. 1998). Changing the extent, the grain, the
447 composition and/or the configuration may result in a change in the metric value. Thus, correlating
448 metrics with physical measurements may be biased, particularly if the underlying structures are not

449 properly controlled for. Finally, in this study, while it might be interesting to implement all
450 calculated metrics at once in a LASSO model, we did not consider this option. Indeed, we
451 calculated 24 metrics at 35 scales following different calculation modes (landscape metrics
452 computed using threshold and weighted-distance method with 4 different functions) and we
453 obtained 4200 metrics (840 per mode). Although LASSO is a robust method when presenting a
454 dataset with a small number of rows compared to a large number of variables (Tibshirani 1996), it
455 does not work with so many variables. However, as soon as the number of explanatory variables is
456 reduced, LASSO method is particularly interesting and Steps 1.2 and 1.3 can be avoided to select
457 the best scales.

458

459 **Conclusions**

460 This study demonstrated the utility of combining metrics computed at multiple scales using
461 threshold and weighted-distance method at several scales to calculate variables and explain
462 ecological responses of species, such as activity-density. This study highlights with an *in situ*
463 experiment the promising advances offered by metrics computed at multiple scales using weighted-
464 distance method in combination with more traditional metrics computed at multiple scales using
465 threshold method. Compared metrics computed at multiple scales using threshold method or
466 weighted-distance method separately, the combination of these two methods significantly improved
467 explained variance of the activity-density of *A. parallelepipedus*. Combining metrics computed at
468 multiple scales using the two methods to calculate the explanatory variables results in a coefficient
469 of determination of the final model of 0.71. This result confirms our hypothesis and the ecological
470 interest of using metrics computed at multiple scales using weighted-distance method to improve
471 the predictive power of explanatory landscape variables in models. Because we tested this approach
472 on a well-known species, its utility for other species must also be explored, such as more generalist
473 species like *Pterostichus melanarius* (Fournier and Loreau 2002; Retho et al. 2008), as well as with
474 other weighted-distance functions and other taxa. Indeed, several functions frequently derived from

475 species dispersal kernels explain the effects of landscape as a function of distance, such as the
476 negative exponential function (e.g., butterflies, Baguette 2003; Remon et al. 2018) and power law
477 (e.g., carabids or birds, Miguet et al. 2017; butterflies, Baguette 2003; Fric and Konvicka 2007).
478
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695 Figure captions

696

697 Fig. 1 (A) Location of Brittany in France. (B) Location of Zone Atelier Armorique (ZAAR) in Britany
698 (48° 30' N, 1° 34' W). (C) Sampling point locations. The borders of the study area are shown in dark
699 grey in (B); black icons represent the 30 points where carabid beetles were sampled.

700

701 Fig. 2. Statistical and modeling scheme for the step 1 “metric and scale identification” (MARS:
702 Multivariate Adaptive Regression Spline, TM: threshold method, DWM: weighted-distance method,
703 GAM: General Additive Model). For each metric, the model with the highest R-squared (R^2)
704 represented the best scale.

705

706 Fig. 3. Graphs showing the R^2 values depending on the scale (Fig. 2, Step 1.2) of the five selected
707 metrics. Metric terms: NV i = density of landscape element i , NC i - j = Interfaces i - j , 1 = Wood, 12 =
708 Dirt-roads, 16 = Meadows.

709

710 Fig. 4. Partial dependence plots between the activity-density of *Abax parallelepipedus* and the
711 selected metrics using the threshold method (A–C), the combination of weighted-distance and
712 threshold methods (D–F) and the weighted-distance method (G–H). Metric terms: NV i = density of
713 landscape elements i , NC i - j = Interfaces i - j , 1 = Wood, 12 = Dirt-roads, 16 = Meadows.

714

715 Online Resource 1: Raster maps of the land use categories and the wooded features.

716

717

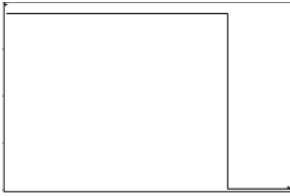
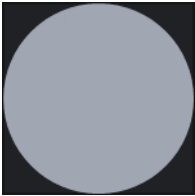
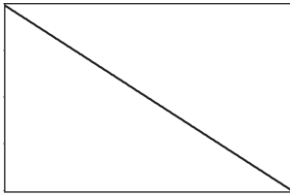

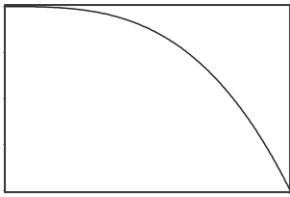
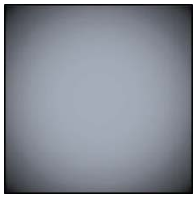
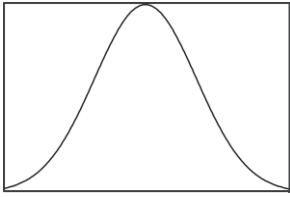
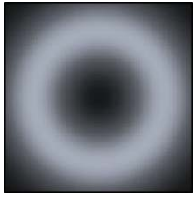
Table 1. Percentage of each land cover type in the study area for 2017.

Land cover type	Percentage (%)
Meadow (16)	30.55
Maize (7)	21.94
Cereals (8)	20.85
Wood (1)	16.64
Artificial areas (13)	5.14
Dirt-road (12)	2.03
Uncultivated (4)	1.06
Water (2)	1.01
Other crop (9)	0.63
Rails road (14)	0.08
Grass strip (17)	0.08

Table 2. Metrics computed with CHLOE software, i represents the elements of a specific land cover type, i - j the interfaces between two elements of a specific land cover type, d represents the distance chosen for the metric calculation, wd represents the weighted-distance function used, n represents the number, p represents the proportion.

Metric	Description	Formula (Threshold Method)	Formula (Weighted-distance method)
NV i	Number of pixels of class i	$n(i)$	$\sum wd(i)$
NC i - j	Number of pair values i - j	$n(i, j)$	$\sum wd(i, j)$
NC-hete	Number of pair values where $i \neq j$	$\sum n(i, j)$ with $i \neq j$	$\sum \sum wd(i, j)$ with $i \neq j$
SHDI	Shannon diversity of the land cover	$-\sum p(i) \times \ln(p(i))$	$-\sum p(i) \times \ln(p(i))$ with $p(i) = \frac{\sum wd(i)}{\sum \sum wd}$
HET	Heterogeneity metric (i.e., SHDI for pair values)	$-\sum p(i, j) \times \ln(p(i, j))$	$-\sum p(i, j) \times \ln(p(i, j))$ with $p(i, j) = \frac{\sum wd(i, j)}{\sum \sum wd}$
HET-frag	Structural heterogeneity metric (i.e., SHDI for heterogenous pair values)	$-\sum_{i \neq j} p(i, j) \times \ln(p(i, j))$	$-\sum_{i \neq j} p(i, j) \times \ln(p(i, j))$ with $i \neq j$ and $p(i, j) = \frac{\sum wd(i, j)}{\sum \sum wd}$
MD	The grain metric	$\frac{\sum \min(d, 100)}{n}$	$\frac{\sum wd \times \min(d, 100)}{\sum wd}$

Table 3. Summary of the threshold and the four weighted-distance functions used for the weighted-distance method. Terms and formulae are presented (radius: radius for a given buffer size). The center of the weight pixel window is the sampling point (the lighter the color, the more important the effect is).

Function term	Formula	Effect of a landscape metric (Y axis) according to the distance from the sampling point (X axis). Sampling point is at distance 0.	Pixel Weight (the center of window is the sampling point)
Threshold	radius		
Decreasing Linear	$-\left(\frac{\text{distance}}{\text{radius}}\right)^{3.14} + 1$		
Decreasing Curve	$\text{distance} \times \left(\frac{\text{radius}}{\text{radius} \times -\text{radius}}\right) + 1$		
Gaussian	$e^{-\left(\frac{\text{distance} - (\text{radius}/2)}{\text{radius}/4}\right)^2}$		
Adjusted-Gaussian	$e^{-\left(\frac{\text{distance} - (\text{radius}/12)}{\text{radius}/23}\right)^2}$	