

SpatialBoundaries.jl: Edge detection using spatial wombling

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Spatial wombling is an approach for detecting edges within a defined two-dimensional landscape. This is achieved by calculating the rate and direction of change through the interpolation of points. This not only gives an approximation as to the shape of the landscape but can also be used to identify candidate boundaries cells that delimit a shift from one state to another within the landscape. Here we introduce the `SpatialBoundaries.jl` package for Julia, which has been developed to implement the wombling algorithm for datasets that are spatially referenced for both uniformly or randomly sampled landscapes. From a practical perspective, the wombling functionality allow the user to answer two questions: how much and in which direction does the variable of interest change within the landscape? Whereas the boundaries functionality identifies candidate boundary cells. We conclude by providing a working example of the package using the various woody plant layers for Britain and Ireland from the EarthEnv database.

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1 Background

2 There is value in being able to identify boundaries within a landscape as it provides us with a starting
3 point from which to understand changes in species assemblages, ecological communities, or even simply
4 to delineate areas (based on a shared property) into discrete units, for example ecosystemic regions (Fortin
5 et al. 2000, Post et al. 2007). Here we present a Julia (Bezanson et al. 2017) package aimed at detecting
6 boundaries across a specified geographical area by identifying zones of rapid change using the wombling
7 edge detection algorithm. This approach was originally developed by Womble (1951) in the context of
8 understanding trait variation within a geographic area and was later modified by Barbujani et al. (1989) for
9 the purpose of understanding changes in gene frequencies, although it also has a more general ecological
10 application with regards to spatial data (Fortin and Dale 2005), serving as a complimentary approach to
11 cluster analysis (Fortin and Drapeau 1995). Wombling has applicability to a wide range scenarios *e.g.* trait
12 measurements or genotypes (Barbujani et al. 1989), species interaction networks (Fortin et al. 2021), and
13 has explicitly been used (to list a few examples) to detect transitions within a landscape (Camarero et al.
14 2000, Philibert et al. 2008), and analyse the spread of invasive species (Fitzpatrick et al. 2010). Although
15 the origins of wombling may be rooted in anthropology and has been extensively used in ecology the
16 potential applicability also extends to other systems such as high-energy experiments in physics (Matchev
17 et al. 2020), or to understand the genetic-linguistic patterns of European populations (Sokal et al. 1990).

18 Broadly speaking spatial wombling is an edge-detection algorithm which traverses a geographic area (for
19 the purpose of this discussion let's imagine a spatially referenced dataset pertaining to species richness for
20 each location) and defines this area in terms of the rate (m) and corresponding direction of change (θ)
21 through interpolating between nearest neighbours. Although the wombling algorithm (as implemented
22 here) is designed to work with two-dimensional *i.e.* planar data (as delimited by x and y — which would
23 be the co-ordinates of where species richness was sampled), it is beneficial to view this plane as a
24 three-dimensional object (or series of curves), as shown in fig. 1, panel A. Here the 'amplitude' of the
25 curvature of the plane is determined by the value of z (species richness) and the rate and direction of
26 change is calculated by using the first-order partial derivative (∂) of the surface (curve) as described by
27 $f(x, y)$. This then gives us an indication of how steep the gradient/curve (m) is between neighbouring
28 cells as well as the direction (from the 'low' to the 'high' point; θ) of the slope (panel B, fig. 1). Large values
29 of m are associated with zones of rapid change in the landscape and are indicative of a shift from one

30 'state' to another *i.e.* a potential ecological boundary within the landscape (Fortin and Dale 2005), dashed
31 line in panel C, 1. One benefit of the wombling approach is that interpolation is not necessarily restricted
32 to a rectangular (2×2) window (that would entail a landscape where points are regularly arranged in
33 space) and can easily be re-written so as to accomodate points that are not regularly arranged across space
34 (as per Fortin 1994), thereby giving the user more flexibility with regards to how the sampling points are
35 arranged (*i.e.* sampled) across the landscape.

36 [Figure 1 about here.]

37 **Rate of change**

38 The rate of change (m) can be used to find the zones of rapid change within the geographical area —
39 which, in turn, can be used to identify potential candidate boundaries. The rate of change is calculated as
40 follows:

$$m = \sqrt{\frac{\partial f(x, y)^2}{\partial x} + \frac{\partial f(x, y)^2}{\partial y}} \quad (1)$$

41 Where $f(x, y)$ can be expanded as:

$$f(x, y) = z_1(1 - x)(1 - y) + z_2x(1 - y) + z_3xy + z_4(1 - x)y$$

42 For convenience the values of the centroid of the 'search window' *i.e.* x and y can be standardised to 0.5
43 when working with points regularly arranged in space. Additionally, as we are interpolating between
44 points, it should also be noted that the original $n * r$ geographical area will now be an $(n - 1)(r - 1)$ sized
45 grid (*i.e.* one less row and one less column of values for the wombled landscape as illustrated in panel C of
46 fig. 1).

47 When we are working with points that are irregularly arranged within the geographical area it is possible
48 to use triangulation wombling (Fortin 1994, Fortin and Dale 2005, Fortin et al. 2021). Here the approach
49 to wombling has been modified by Fortin (1992) so as to interpolate the plane between the three nearest
50 neighbours (as opposed to the usual 2×2 grid). Nearest neighbours are found by using the Delaunay
51 triangulation algorithm (Delaunay 1934) after which the rate of change is still calculated in the same

52 manner as in eq. 1, however as we are now only working with a three-point ‘window’ $f(x, y)$ will be
 53 defined as:

$$f(x, y) = ax + by + c$$

54 where

$$\begin{bmatrix} a & b & c \end{bmatrix} = \begin{bmatrix} x_1 & y_1 & 1 \\ x_2 & y_2 & 1 \\ x_3 & y_3 & 1 \end{bmatrix}^{-1} \cdot \begin{bmatrix} z_1 & z_2 & z_3 \end{bmatrix}$$

55 and the x and y co-ordinates of the centroid of the triangle formed by the three points are calculated as
 56 follows:

$$\left(\frac{x_1 + x_2 + x_3}{3}, \left(\frac{y_1 + y_2 + y_3}{3} \right) \right)$$

57 **Direction of change**

58 It is also possible to calculate a corresponding direction (θ) for each rate of change (noting that the same
 59 equation can be used for both lattice and triangulation wombling). This is calculated as:

$$\theta = \arctan \left(\frac{\partial f(x, y)}{\partial y} / \frac{\partial f(x, y)}{\partial x} \right) + \Delta$$

$$\text{where } \Delta = \begin{cases} 0^\circ & \text{if } \frac{\partial f(x, y)}{\partial x} \geq 0 \\ 180^\circ & \text{if } \frac{\partial f(x, y)}{\partial x} < 0 \end{cases}$$

60 This gives the direction of change which, as the name implies, indicates the direction the rate of change is
 61 ‘travelling’. The direction of change should be interpreted as wind direction *i.e.* where the change is
 62 coming from and not where it is moving towards. As is the nature of maths when the rate of change is
 63 zero it is still possible to calculate a *real* direction for the non-change — which will be 180° . This means it
 64 is possible to think of and use the direction of change independently of calculating boundaries *per se* and

65 can be used to inform how the landscape is behaving/changing in a more ‘continuous’ way as opposed to
66 discrete zones/boundaries. For example if changes in species richness are more gradual (rate of change is
67 near constant) but the the direction of change is consistently East to West (*i.e.* 90°) we can still infer that
68 species richness is more or less uniformly increasing in a South-North direction (this is somewhat
69 exemplified in the direction of change landscape of panel B in fig. 1 where the dominant direction of
70 change is East-West).

71 **Candidate boundaries**

72 Detecting boundaries *i.e.* areas where the angle of the landscape transitions sharply is surprisingly simple.
73 After having calculated the rate of change (m) for the geographical area it is possible to use these values to
74 identify and assign potential boundaries (Oden et al. 1993, Fortin and Drapeau 1995, Fortin and Dale
75 2005). As large rate of change values are indicative of a steep gradient it stands to reason that these points
76 are indicative of a shift from one state to another *i.e.* indicative of a boundary. Following the approach
77 outlined in Fortin and Dale (2005) a threshold value (or percentile class) can be set and will determine
78 what proportion of cells will be retained as potential boundaries. For example if using a 0.1 threshold then
79 the highest 10% of points (which are ranked based on m) will be classified as candidate boundaries. Note
80 that points with the same rate of change will be assigned the same rank meaning that more than 10% of
81 the $(n - 1)(r - 1)$ could potentially be identified as candidate boundary cells. This approach to identifying
82 potential boundary cells is not the sole approach and there are other ways and nuances from which to
83 approach boundary estimation, such as the use of Voronoi tessellations (Oden et al. 1993, Fortin and
84 Drapeau 1995, Matchev et al. 2020).

85 **Methods and features**

86 `SpatialBoundaries` v0.0.3 implements the Wombling algorithm within the Julia ecosystem and is made
87 available under the permissive MIT license. The source code (along with more extensive documentation)
88 can be found at <https://poisotlab.github.io/SpatialBoundaries.jl/>. This is an open project and is
89 thus open to contributions. The package itself has two main functions 1) calculate the rate (m) and
90 direction (θ) of change for landscapes for points that are both regularly (*i.e.* lattice wombling) and
91 irregularly arranged cross space (triangulation wombling) arranged in space using the wombling function

92 (for which layers can also be aggregated using mean), and 2) identifying candidate boundary cells based on
93 a user defined threshold value using the boundaries function. Objects that have been passed through a
94 wombling function are of the Womble abstract type (which has the two sub-types of LatticeWomble and
95 TriangulationWomble). This package is, to the best of our knowledge, the only package to implement the
96 Wombling algorithm within Julia.

97 **Wombling**

98 The wombling function calculates and outputs both the rate (m) and direction (θ ; where the direction is
99 denoted from the 'low' to the 'high' point) of change for a given geographical area. Leveraging the
100 multiple dispatch within Julia this one function will execute either the lattice or triangulation wombling
101 algorithm depending on the structure (spatial referencing) of the input dataset, meaning that it does not
102 need to be user specified. When a *matrix* of z values is used (where the row and column id's act as the
103 co-ordinates) the lattice wombling algorithm will be executed and when three *vectors* (consisting of the
104 co-ordinates (x and y), and z values respectively) the triangulation wombling algorithm is executed. The
105 resulting output object will have two components (m and θ) and will be typed based on the wombling
106 method used. That is a uniform matrix will result in an object of the type LatticeWomble and irregularly
107 arranged points will be of the type TriangulationWomble.

108 **Overall mean wombling value**

109 The mean function calculates the Overall mean wombling value. The methodology stems from the Overall
110 Mean Lattice-Wombling Value (\bar{m}) used by Fortin (1994) in which multiple surfaces (think different z
111 variables) can be overlaid for the purpose of finding the mean rates and directions of change for a
112 composite landscape. The mean rate of change can be defined as the average of m values (for a specific
113 centroid) for the given set of surfaces and the same is done for the direction of change using the θ values.
114 Alongside the mean the standard deviation is also calculated for both the rate and direction of change.
115 Although Fortin (1994) only present this approach for lattice wombled landscapes we have extended the
116 functionality to include both lattice and triangulation wombled types. This is provided that the landscape
117 (*i.e.* co-ordinates) of the different surfaces are *exactly* the same. Note here that the original wombling type
118 is retained and the output data will remain either type LatticeWomble or TriangulationWomble.

119 **Boundaries**

120 The `boundaries` function takes the rate of change (m) of an object of either of the two `Womble` types (*i.e.*
121 `LatticeWomble` or `TriangulationWomble`), and identifies potential boundary cells based on a user
122 specified threshold (with the default being 0.1). As opposed to selecting only one threshold value we
123 recommend inputting a range of threshold values into the `boundaries` function to assess how it changes
124 the number of points retained (*i.e.* boundary cells identified). For example we might see sharp transitions
125 in the number of points that are retained as the threshold value is increased. This inflection point is
126 probably the ideal threshold value to use for boundary selection as a rapid increase in the number of
127 points retained is indicative of a large number of cells with the same rate of change.

128 **Woody areas of the Hawaiian Islands: a wombling example**

129 Below is an example using the various functions within `SpatialBoundaries` to estimate boundaries for
130 (*i.e.* patches of) wooded areas on the Southwestern islands of the Hawaiian Islands using landcover data
131 from the EarthEnv project (Tuanmu and Jetz 2014) as well as integrating some functionality from
132 `SimpleSDMLayers` (Dansereau and Poisot 2021) for easier work with the spatial nature of the input data.
133 The `SpatialBoundaries` package works really well with `SimpleSDMLayers`, so that you can (i) apply
134 wombling and boundaries finding to a `SimpleSDMLayer` object, and (ii) convert the output of a `Womble`
135 object to a *pair* of `SimpleSDMLayer` corresponding to the rate and direction of change.

136 Because there are four different layers in the EarthEnv database that represent different types of woody
137 cover we will use the overall mean wombling value. As the data are arranged in a matrix *i.e.* a lattice this
138 example will focus on lattice wombling, however for triangulation wombling the implementation of
139 functions and workflow would look similar with the exception that the input data would be structured
140 differently (as three vectors of x, y, z) and the output data would be typed as `TriangulationWomble`
141 objects.

142 using `SpatialBoundaries`

143 using `SpeciesDistributionToolkit`

144 using `CairoMakie`

145 import `Plots`

146 Note that the warning about dependencies is a side-effect of loading some functionalities for
147 SimpleSDMLayers as part of SpatialBoundaries, and can safely be ignored.

148 First we can start by defining the extent of the Southwestern islands of Hawaii, which can be used to
149 restrict the extraction of the various landcover layers from the EarthEnv database. We do the actual
150 database querying using SimpleSDMLayers.

```
151 hawaii = (left = -160.2, right = -154.5, bottom = 18.6, top = 22.5)
152 dataprovider = RasterData(EarthEnv, LandCover)
153 landcover_classes = SimpleSDMDatasets.layers(dataprovider)
154 landcover = [SimpleSDMPredictor(dataprovider; layer=class, full=true, hawaii...) for class in landcover_
```

155 We can remove all the areas that contain 100% water from the landcover data as our question of interest is
156 restricted to the terrestrial realm. We do this by using the “Open Water” layer to mask over each of the
157 landcover layers individually:

```
158 ow_index = findfirst(isequal("Open Water"), landcover_classes)
159 not_water = landcover[ow_index] .!==(0x64)
160 lc = [mask(not_water, layer) for layer in landcover]
```

161 As layers one through four of the EarthEnv data are concerned with data on woody cover (*i.e.*
162 “Evergreen/Deciduous Needleleaf Trees”, “Evergreen Broadleaf Trees”, “Deciduous Broadleaf Trees”, and
163 “Mixed/Other Trees”) we will work with only these layers. To get a sense of the overall structure of raw
164 landcover components we can sum these four layers and plot the total woody cover for the Southwestern
165 islands (The code for the plot below will give us panel A in fig. 2).

```
166 classes_with_trees = findall(contains.(landcover_classes, "Trees"))
167 tree_lc = convert(Float32, reduce(+, lc[classes_with_trees]))
168 heatmap(tree_lc; colormap=:linear_kbgyw_5_98_c62_n256)
```

169 [Figure 2 about here.]

170 Although we have previously summed the four landcover layers for the actual wombling part we will
171 apply the wombling function to each layer before we calculate the overall mean wombling value. We can

172 broadcast wombling in an element-wise fashion to the four different woody cover layers. This will give as a
173 vector containing four `LatticeWomble` objects (since the input data was in the form of a matrix).

```
174 wombled_layers = wombling.(lc[classes_with_trees])
```

175 As we are interested in overall woody cover for Southwestern islands we can take the `wombled_layers`
176 vector and use them with the `mean` function to get the overall mean wombling value of the rate and
177 direction of change for woody cover. This will ‘flatten’ the four wombled layers into a single
178 `LatticeWomble` object.

```
179 wombled_mean = mean(wombled_layers)
```

180 From the `wombled_mean` object we can ‘extract’ the layers for both the mean rate and direction of change.
181 For ease of plotting we will also convert these layers to `SimpleSDMPredictor` type objects. It is also
182 possible to call these matrices directly from the `wombled_mean` object, which has fields for m (the
183 magnitude of change) and θ (the direction of change).

```
184 rate, direction = SimpleSDMPredictor(wombled_mean)
```

185 Lastly we can identify candidate boundaries using the `boundaries`. Here we will use a thresholding value
186 (t) of 0.1 and save these candidate boundary cells as `b`. Note that we are now working with a
187 `SimpleSDMResponse` object and this is simply for ease of plotting.

```
188 b = similar(rate)
```

```
189 b.grid[boundaries(wombled_mean, 0.1; ignorezero = true)] .= 1.0
```

190 In addition to being used to help find candidate boundary cells we can also use this object (`b`) as masking
191 layer when visualising wombling outputs. In this case we can view the rate layer in a similar fashion to
192 the original landcover layer but by masking it with `b` we only plot the candidate boundaries (B in fig. 2) *i.e.*
193 the cells with the top 10% of highest rate of change values. For visualisation we will overlay the identified
194 boundaries (in green) over the rate of change (in levels of grey)

```
195 heatmap(rate, colormap=[:grey95, :grey5])
196 heatmap!(b, colormap=[:transparent, :green])
197 current_figure()
```

198 For this example we will plot the direction of change as radial plots (third and fourth panels in fig. 2) to get
199 an idea of the prominent direction of change. Here we will plot *all* the direction values from `direction` for
200 which the rate of change is greater than zero (so as to avoid denoting directions for a slope that does not
201 exist) as well as the `direction` values from only candidate cells using the same masking principle as what
202 we did for the rate of change. It is of course also possible to forgo the radial plots and plot the direction of
203 change in the same manner as the rate of change should one wish.

204 Before we plot let us create our two ‘masked layers’. For all direction values for which there is a
205 corresponding rate of change greater than zero we can use `rate` as a masking layer but first replace all zero
206 values with ‘nothing’. For the candidate boundary cells we can simply mask `direction` with `b` as we did
207 for the rate of change.

```
208 direction_all = mask(replace(rate, 0 => nothing), direction)
209
210 direction_candidate = mask(b, direction)
```

211 Because `stephist()` requires a vector of radians for plotting we must first collect the cells and convert them
212 from degrees to radians. Then we can start by plotting the direction of change of *all* cells (`C` in fig. 2).

```
213 Plots.stephist(
214     deg2rad.(values(direction_all));
215     proj=:polar,
216     lab="",
217     c=:teal,
218     nbins = 36,
219     yshowaxis=false,
220     normalize = false,
221     dpi=600)
```

222 Followed by plotting the direction of change only for cells that are considered as candidate boundary cells
223 (D in fig. 2).

```
224 Plots.steplist(  
225     deg2rad.(values(direction_candidate));  
226     proj=:polar,  
227     lab="",  
228     c=:red,  
229     nbins = 36,  
230     yshowaxis=false,  
231     normalize = false,  
232     dpi=600)
```

233 **Summary**

234 Edge and boundary detection (as well as their delineation) is an important and valuable concept in spatial
235 ecology (Cadenasso et al. 2003) of which wombling serves as an approach that is flexible in its execution
236 (owing to the non-lattice or triangulation capacity of the function) (Fortin 1994, Fortin and Dale 2005) as
237 well as it's capacity to detect more nuanced landscape changes as opposed to being limited to more abrupt
238 discontinuities such as cliffs/ridges by reducing noise in the landscape (Matchev et al. 2020). Wombling
239 sets us up to answer two questions about the geographic area of interest: at what rate and in which
240 direction does the variable of interest change? This of course has value when it comes to evaluating the
241 variation (or uniformity for that matter) of a suite of ecological variables as well as how they may vary with
242 relation to each other.

243 `SpatialBoundaries.jl` provides the toolset with which to implement both lattice and triangulation
244 wombling using the `wombling` function - multiple dispatch means that the structure of the input dataset
245 will determine exactly which algorithm is implemented. This will simultaneously calculate both the rate
246 and direction of change and if desired multiple sets of different layers of the same geographic area but
247 defined by different z-variables/surfaces can be aggregated and averaged to calculate the overall mean
248 wombling value. Both `wombling` and `mean` will return objects of the type `Womble` of either the sub-type

249 LatticeWomble or TriangulationWomble depending on which method was used. An object of any
250 sub-type Womble can be input into the boundaries function so as to identify cells that can be considered as
251 candidate boundaries based on a user specified threshold.

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255 **References**

- 256 Barbujani, G., N. L. Oden, and R. R. Sokal. 1989. [Detecting Regions of Abrupt Change in Maps of](#)
257 [Biological Variables](#). *Systematic Zoology* 38:376–389.
- 258 Bezanson, J., A. Edelman, S. Karpinski, and V. B. Shah. 2017. [Julia: A Fresh Approach to Numerical](#)
259 [Computing](#). *SIAM Review* 59:65–98.
- 260 Cadenasso, M. L., S. T. A. Pickett, K. C. Weathers, and C. G. Jones. 2003. [A Framework for a Theory of](#)
261 [Ecological Boundaries](#). *BioScience* 53:750–758.
- 262 Camarero, J. J., E. Gutiérrez, and M.-J. Fortin. 2000. [Boundary Detection in Altitudinal Treeline Ecotones](#)
263 [in the Spanish Central Pyrenees](#). *Arctic, Antarctic, and Alpine Research* 32:117–126.
- 264 Dansereau, G., and T. Poisot. 2021. [SimpleSDMLayers.jl and GBIF.jl: A Framework for Species](#)
265 [Distribution Modeling in Julia](#). *Journal of Open Source Software* 6:2872.
- 266 Delaunay, B. 1934. Sur la sphere vide. *Bulletin de l'Académie des Sciences de l'URSS. Classe des sciences*
267 *mathématiques* 6:793–800.
- 268 Fitzpatrick, M. C., E. L. Preisser, A. Porter, J. Elkinton, L. A. Waller, B. P. Carlin, and A. M. Ellison. 2010.
269 [Ecological boundary detection using Bayesian areal wombling](#). *Ecology* 91:3448–3455.
- 270 Fortin, M.-J. 1992. Detection of ecotones: Definition and scaling factors. PhD thesis, State University of
271 New York at Stony Brook, United States – New York.
- 272 Fortin, M.-J. 1994. [Edge Detection Algorithms for Two-Dimensional Ecological Data](#). *Ecology* 75:956–965.
- 273 Fortin, M.-J., and M. R. T. Dale. 2005. *Spatial analysis: A guide for ecologists*. Cambridge University Press,
274 Cambridge, N.Y.

- 275 Fortin, M.-J., M. R. T. Dale, and C. Brimacombe. 2021. [Network ecology in dynamic landscapes](#).
276 *Proceedings of the Royal Society B: Biological Sciences* 288:rspb.2020.1889, 20201889.
- 277 Fortin, M.-J., and P. Drapeau. 1995. [Delineation of Ecological Boundaries: Comparison of Approaches and](#)
278 [Significance Tests](#). *Oikos* 72:323–332.
- 279 Fortin, M.-J., R. J. Olsen, S. Ferson, L. Iverson, C. Hunsaker, G. Edwards, D. Levine, K. Butera, and V.
280 Klemas. 2000. Issues related to the detection of boundaries. *Landscape Ecology* 15:453–466.
- 281 Matchev, K. T., A. Roman, and P. Shyamsundar. 2020. [Finding wombling boundaries in LHC data with](#)
282 [Voronoi and Delaunay tessellations](#). *Journal of High Energy Physics* 2020:137.
- 283 Oden, N. L., R. R. Sokal, M.-J. Fortin, and H. Goebel. 1993. [Categorical Wombling: Detecting Regions of](#)
284 [Significant Change in Spatially Located Categorical Variables](#). *Geographical Analysis* 25:315–336.
- 285 Philibert, M. D., M.-J. Fortin, and F. Csillag. 2008. [Spatial structure effects on the detection of patches](#)
286 [boundaries using local operators](#). *Environmental and Ecological Statistics* 15:447–467.
- 287 Post, D. M., M. W. Doyle, J. L. Sabo, and J. C. Finlay. 2007. [The problem of boundaries in defining](#)
288 [ecosystems: A potential landmine for uniting geomorphology and ecology](#). *Geomorphology*
289 89:111–126.
- 290 Sokal, R. R., N. L. Oden, P. Legendre, M.-J. Fortin, J. Kim, B. A. Thomson, A. Vaudor, R. M. Harding, and
291 G. Barbujani. 1990. [Genetics and Language in European Populations](#). *The American Naturalist*
292 135:157–175.
- 293 Tuanmu, M.-N., and W. Jetz. 2014. [A global 1-km consensus land-cover product for biodiversity and](#)
294 [ecosystem modelling](#). *Global Ecology and Biogeography* 23:1031–1045.
- 295 Womble, W. H. 1951. [Differential Systematics](#). *Science* 114:315–322.

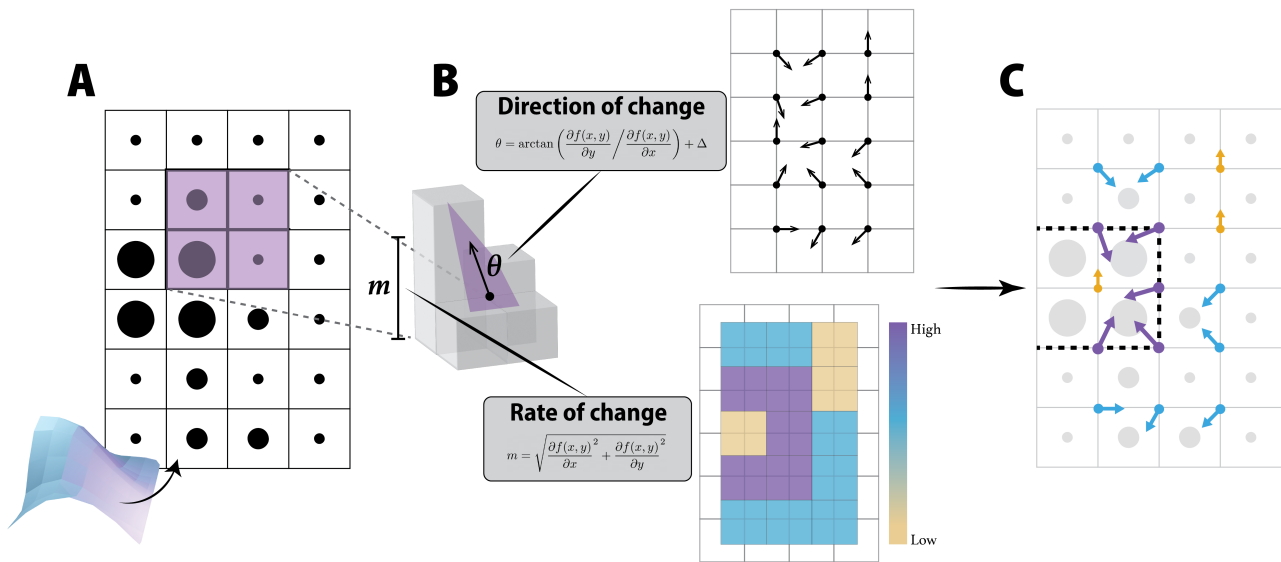


Figure 1: A visual conceptualisation of how the wombling algorithm interpolates points across a geographical area (in this case the points are regularly arranged in space) for a variable of interest (z) to calculate the rate (m) as well as the direction (θ) of change. Here the sampled landscape is shown in panel A with the size of the points correlating to the magnitude of the variable of interest (z). Panel B shows the two components of the landscape once wombled, which are then combined and superimposed across the original landscape in panel C, with the dashed line indicating a candidate boundary. Here the colours as well as the size of the arrows indicate the rate of change and the direction should be interpreted as moving from the 'low' to the 'high' point. Note that the dimensions of the wombled landscapes (B) will be smaller than the original landscape (A) due to the interpolation process *i.e.* where we originally had an $n \times r$ grid we now have an $(n - 1)(r - 1)$ sized grid.

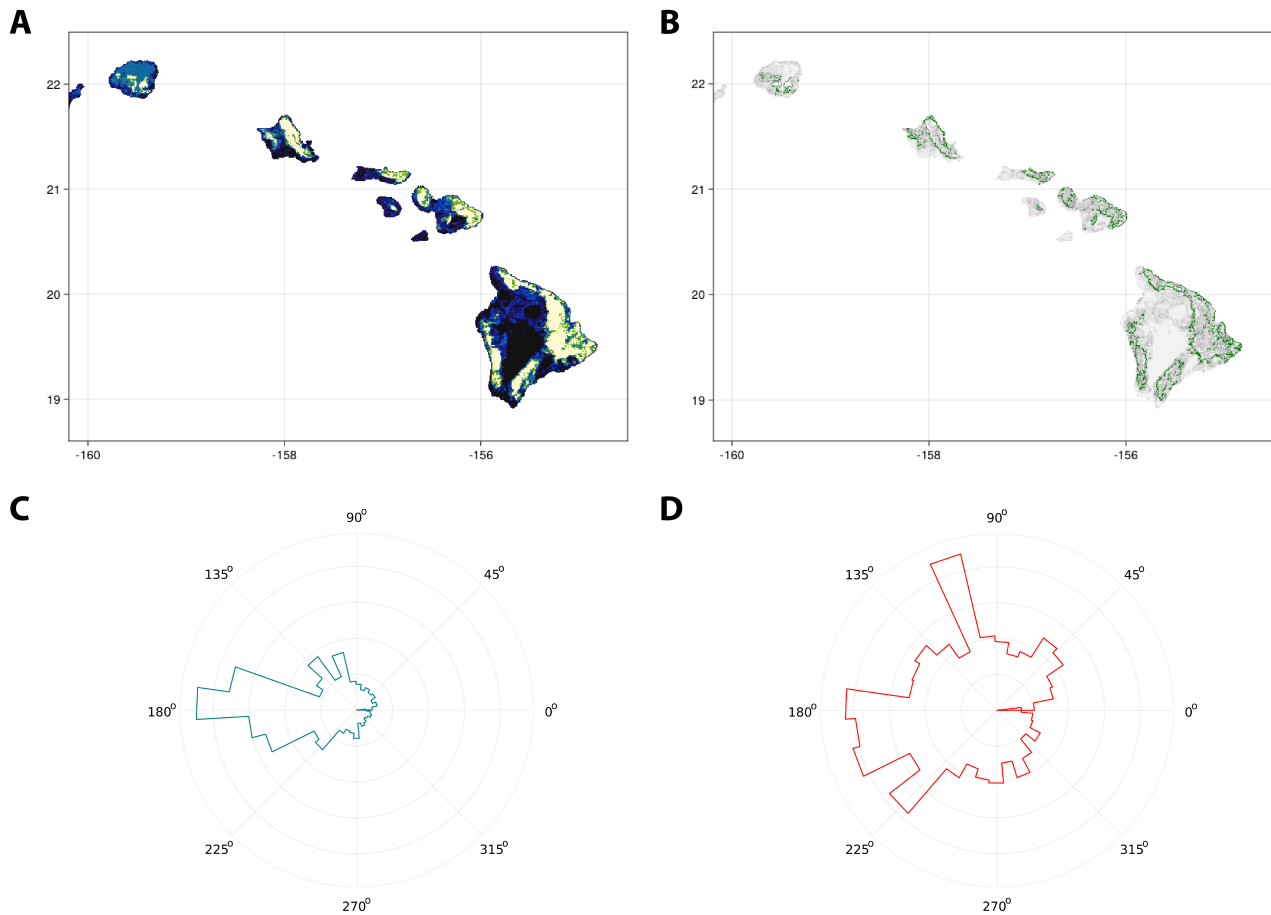


Figure 2: **A** Woody plant coverage for Southwestern islands of the Hawaiian Islands based on the sum of the cover for layers 1-4 from the EarthEnv project. **B** the overall mean rate of change (*i.e.* the composite of the wombled layers for layers 1-4) but only for the cells identified as candidate boundary cells when using a 10% threshold, with identified boundaries (shown in green) over the rate of change (shown in levels of grey). The final two panels show the direction of change for all cells (**C**) and only for cells considered to be candidate boundary cells (**D**).