Short Note

Namibian fairy circles and epithelial cells share emergent geometric order

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1. Introduction

Let us begin with a clear statement of intent: We do not wish to assert that the fairy circles of the Namib desert and epithelial or skin cells are similar “kinds of entities”. Our main result is the observation of a similarity in pattern, and describing how and why we made this observation is the focus of our report. We understand that raw observations are not always worthy of scientific attention, but we argue that our observation is valuable due to the continuing importance of pattern and scale to ecology (Chave, 2013; Levin, 1992). Furthermore, we firmly believe in the use of analogy as one of the many approaches open to theorists in their efforts to reach understanding. The observation of hexagonal lattices in both bees’ compound eyes and the honeycombs they construct is an expression of the deeper theoretical fact that packing problems are ubiquitous in nature, and tend to generate similar patterns, even at different scales. This extends, for example, to dusty plasmas (Thomas et al., 1994), where hexagonal crystals form without any obvious boundaries, providing an abstract image of pattern formation between seemingly small and isolated but interacting objects.

Fairy circles are quasi-circular barren patches distributed in the sparse grassland of the Namib Desert. They have been an object of study for decades, called “kaal kolle” (meaning “barren patches”) in the earliest publication known to us (Theron, 1979), and continue to be the object of much investigation and speculation, particularly regarding their likely cause (Albrecht et al., 2001; Becker and Getzin, 2000; Cramer and Barger, 2013; Fernandez-Oto et al., 2014; Getzin et al., 2014; Juergens, 2013, 2015; Naude et al., 2011; Picker et al., 2012; Tlidi et al., 2008; Tsinkel, 2012; van Rooyen et al., 2004). Inspired by the observation that fairy circles have a life cycle and life span (Albrecht et al., 2001; Juergens, 2013; Tsinkel, 2012) and evidence pointing to biological entities competing for space-related resources as the causal agents (Cramer and Barger, 2013; Juergens, 2013; Picker et al., 2012), we speculated that fairy circles may permit the same type of analysis already developed for the architecture of epithelia in animals and plants (Gibson et al., 2006; Gibson and Gibson, 2009; Guillot and Lecuit, 2013; Korn and Spalding, 1973; Nagpal et al., 2008; Patel et al., 2009). Animal and plant territories can be studied in many ways, including mechanistic (Potts and Lewis, 2014) or geometric points of view (Adams, 1998, 2001; Barlow, 1974; von Hardenberg et al., 2010). If one chooses to take a geometric point of view, it is natural to suppose that territory boundaries might be amenable to types of analysis originally developed for cell walls (Axelrod, 2006; Gibson et al., 2006). From this point of view, the centres of fairy circles can be seen as the centres of approximately
polygonal zones of influence, dominance or control, i.e. territories (Adams, 1998; Barlow, 1974) (see Fig. 1b), where we are using the word “territory” in an extremely broad sense. The dynamics of territory shape are consistent with such a point of view, as the example of fire ant territory boundaries moving in response to the removal of neighbouring colonies shows (Adams, 1998). With this approach we examine the distribution of numbers of neighbouring territories, or cell topology (Gibson and Gibson, 2009).

Although polygonal patterns are frequently observed in nature (Barlow, 1974; Buckley and Buckley, 1977; Gray et al., 1976; Kessler and Werner, 2003; Pieri, 1981a,b; Quilliet et al., 2008; Thomas et al., 1994; Thompson, 1942), metazoan epithelial architecture has appeared to be distinctive (Gibson and Gibson, 2009). See Fig. 2 for an example of zebrafish lens epithelial cells, reproduced with permission of the authors and publisher, from Mochizuki et al. (2014). Gibson et al. (2006) proposed a mathematical model predicting that, in the absence of cell sorting or migration, stochastic cell division processes should converge to a generic distribution of polygonal cell shapes dominated by hexagons (Gibson et al., 2006; Gibson and Gibson, 2009; Naggal et al., 2008; Patel, 2008; Patel et al., 2009), regardless of initial state. Experimental data suggested this cell shape distribution is common to the epithelial tissue of many metazoans (Axelrod, 2006; Patel et al., 2009). The aim of our investigation was to determine whether this distribution would also be observed in fairy circle territories that can be inferred using satellite image data.

2. Material and methods

Three large satellite images of uninterrupted and clearly distinguishable fairy circles in the Namib and Nature Reserve (Wolfswamps hotspot, as in Fig. 1B of Juergens, 2013) were obtained using Google Earth Pro (Google Inc., Mountain View, CA, USA) version 7.1.1.1580 (beta), provided by DigitalGlobe (2013). The northwestern corners of these images are 24.971639° S 15.942003° E, 24.934428° S 15.925844° E and 25.119744° S 15.913392° E. The respective eye altitudes and image dates are 1.15 km, 1.01 km and 842 m, and 16/5/2012, 16/5/2012 and 8/1/2012.

Automatic feature recognition from satellite images is known to suffer from various artefacts of the processing methods used, and fairy circles can indeed be difficult to identify (Cramer and Barger, 2013). For this reason, two methods were adopted to automatically recognize fairy circles. One was to convert to a grey scale and then threshold. The other was to define an appropriate colour range, by examining the differences between colour values within and outside of fairy circles, and then threshold. The selected points constitute clusters, each one ideally representing a single fairy circle. Cluster analysis was performed using the nonparametric mean shift algorithm (Fukunaga and Hostetler, 1975), providing us with cluster (i.e. fairy circle) centres. Algorithm parameters were adjusted for each image individually, to minimize the number of misidentifications (by visual examination).

Given fairy circle centres, we next computed the territory associated with each centre by computing the Voronoi diagram or Dirichlet tesselation of these points. Edge effects, due to the images being rectangular selections from more extended fairy circle fields, were dealt with using guard area correction, with an external buffer zone of rectangular strips, one on each of the four edges of each image. The vertical/horizontal buffer zones each had a width/height of 5% of the image being processed. The number of fairy circles classified as interior were 4182, 2427 and 2122 for the three images, respectively, when fairy circles were defined using a grey scale, and 4117, 2465 and 2067 when using colour-based recognition.

The comparison of polygon class distributions for fairy circles and epithelia was performed using Pearson’s Chi-squared test with given probability, as implemented in the statistical software R (The R Foundation for Statistical Computing) version 2.15.2. Here, the alternative hypothesis is that the two distributions are different. The distributions of epithelial cell shape vary slightly among different species, but they are similar to those predicted by the Markov Model based on observed general proliferation rules of epithelial cells (Gibson et al., 2006). We used the result predicted
by the model as the given probability in Pearson’s Chi-squared test. For this comparison, we lumped the rare cases of rectangles (2%) with pentagons, and the rare cases of decagons (0.05%) with enneagons (9-sided polygons), since these were likely to be artefacts. No data points were excluded. Our treatment of these polygon classes is in accord with the published work on epithelial cells, where only tiny percentages of triangles and decagons were observed in experiment. In both our analysis and that of epithelia (Gibson et al., 2006), the emphasis is placed upon polygons with 5–9 sides. We also tested the fairy circles’ randomness by the nearest-distance method of Clark and Evans (Clark and Evans, 1954). We used the R package “spatstat” (Baddeley and Turner, 2005), removing edge effects by Donnelly’s Method (Donnelly, 1978).

3. Results

We found that the polygon class distributions of fairy circle territories and epithelial cells are indistinguishable (p-values are all much larger than 0.05), as illustrated in Fig. 1. Hexagons predominate, and the mean of the number of polygon edges is in fact 6.0 in all cases. The estimated numbers of fairy circles vary only slightly between the colour and grey scale recognition methods (less than 2.6% difference).

P-values of the Clark–Evans tests are all much smaller than 0.05 and R-values (Clark and Evans, 1954) range from 1.59 to 1.63. This is in reasonable agreement with a hand analysis of an aerial photograph involving 292 circles, which gave an R-value of 1.68 with an estimated error of 0.05 (Albrecht et al., 2001), an agreement which gives us confidence that our circle recognition methods were effective. The high R-value indicates over-dispersion of fairy circles, in agreement with the literature (Albrecht et al., 2001; Cramer and Barger, 2013).

4. Discussion

Naturally occurring cellular structures (Barlow, 1974; Buckley and Buckley, 1977; Gray et al., 1976; Kessler and Werner, 2003; Korn and Spalding, 1973; Pieri, 1981a,b; Quilliet et al., 2008; Thompson, 1942), while often being loosely described as hexagonal, are not identical. Metazoan epithelial polygonal class distributions, for which the percentage of six-walled cells is approximately 45%, as we and others (Getzin et al., 2014) have observed for fairy circles, differ from the distributions observed for some leaf surfaces, where the percentage of six-walled cells is approximately 58% (Korn and Spalding, 1973), although both types appear hexagonal and over-dispersed. Note that not all authors acknowledge over-dispersion of fairy circles, with the distribution described as random in (Fernandez–Oto et al., 2014), although we would consider failure of a model to predict over-dispersion to be a reason to reject it. However, do polygonal class distributions tell us anything about fairy circles that was not already known? To demonstrate that they do, let us take the prediction of 57% six-cornered tiles for a recent model which assumes fairy circles are a self-organized vegetation pattern (Getzin et al., 2014). Despite the fact that the model produces over-dispersed patterns which resemble those of fairy circles in many ways, this percentage difference alone rules it out for the Wolwedans fairy circles we have analyzed, as well as those from other sites analyzed in the same paper (Getzin et al., 2014) (see their Table 2), since 57% and 45% are clearly very different. Thus, comparing polygonal class distributions is a strong test. Nonetheless, we do not think it is a coincidence that fairy circles and proliferating epithelial cells share the same distribution of polygon classes. Assuming that the fairy circles are essentially in equilibrium, with births compensating deaths, we must ask what role fairy circle death could play in influencing the polygon class distribution. If we make the reasonable assumption that the death process is, statistically speaking, a time-reversed birth process, then the equilibrium distribution of the birth or proliferation process will be the same as the equilibrium distribution of the death process. Note that the death of an epithelial cell can be thought of as corresponding to the removal of a colony (Adams, 1998), both of which result in restructuring of cell or territory boundaries. Thus, it is not unexpected that a model developed for proliferating metazoan epithelial cells (Gibson et al., 2006) could also be applied to an apparently stable system with complete life cycles (Albrecht et al., 2001; Guilford and Lecuit, 2013; Juergens, 2013; Tschinkel, 2012).

The fact that the boundaries we have inferred (Fig. 1b) from fairy circle centres do not obviously correspond to any features seen in satellite imagery or on the ground is not entirely unexpected. Ant foraging territory boundaries are demonstrably real (Tschinkel et al., 1995; Wilson et al., 1971), made tangible in one study (Thomas et al., 2006) by the presence of dead workers, the victims of intercolony conflicts. Also, it is known that territories can be marked with persistent pheromones (Holldobler and Wilson, 1977). Furthermore, fairy circles form in an extreme environment in which it is reasonable to imagine that interactions between circles may play out at least to some extent under ground. We therefore argue that there is no reason to see the hypothetical territorial boundaries illustrated in blue in Fig. 1b as purely imaginary, however imprecise or provisional they may be. The metaphor of fairy circles as tips of icebergs may be useful as an oversimplified illustration of what we are suggesting here.

Our observation does not allow us to make any statements regarding the cause of fairy circles, although it does add to our understanding of their spatial patterns and must be explained by any hypothesis proposed regarding fairy circle dynamics.

We suggest that the value of our result actually lies more in the demonstration that analysis developed for the microscopic world can apply to the macroscopic world as well. We hope that our work will encourage those working at both ends of the size spectrum to continue to look for commonalities of theory.

References

Chave, J., 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecol. Lett. 16, 4–16.


