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Short Note

Namibian fairy circles and epithelial cells share emergent geometric order

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ABSTRACT

Fairy circles are enigmatic features of the Namib desert landscape. They are large, almost perfectly circular patches of barren soil in sparse grassland. Although a matter of continuing debate, we make no attempt to explain their origin. The focus of our approach is a statistical analysis of the spatial patterns. These are easily accessible via aerial and satellite imagery. Observations over extended periods of time have revealed that they have a life-cycle of birth, growth and death. It has also been known for some time that the fairy circles are not randomly distributed. Our novel finding is that the connectivity patterns of fairy circles and metazoan epithelial cells are statistically indistinguishable, while remaining clearly distinct from other commonly observed polygonal patternings. This result identifies an analogy between the microscopic world of epithelial cells and the macroscopic realm of the Namib, suggesting that approaches developed specifically for the analysis of microscopic structures may extend into ecologically relevant, macroscopic dimensions.

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; Tschinkel, 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; Tschinkel, 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

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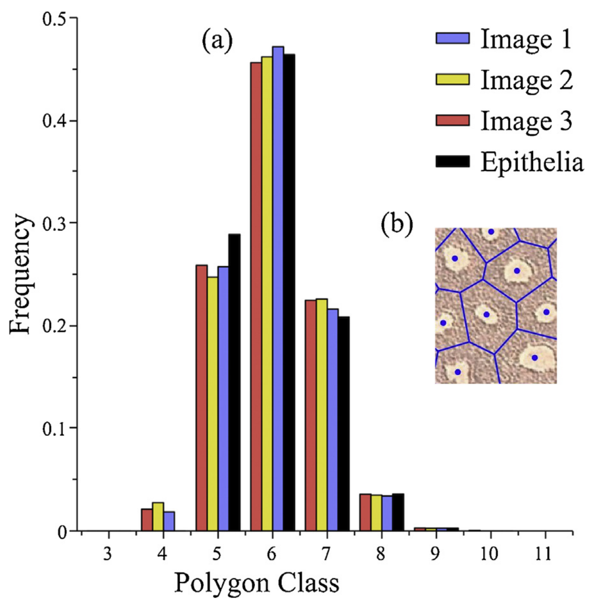

Fig. 1. (a) The polygon class distributions (connectivity patterns) of fairy circle "territories" and epithelial cells are statistically indistinguishable. The comparison is between three satellite images (Google, DigitalGlobe) of Namibian fairy circles and a typical distribution for epithelial tissue. (b) Identified fairy circle centres and their associated hypothetical territory boundaries in blue. At the centre of the image is a fairy circle with a six-sided polygonal territory (i.e. a hexagon–polygon class 6).

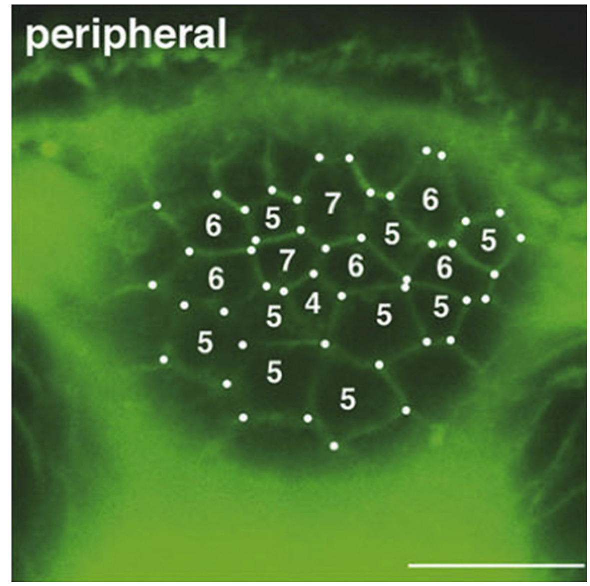

Fig. 2. Lens epithelial cells in the peripheral region of 49 h post fertilization zebrafish lenses. Cell membranes are labelled green. Numbers indicate the respective polygon classes. Reproduced with permission from Mochizuki et al. (2014).

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; Nagpal 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 NamibR and Nature Reserve (Wolwedans 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