

Flower complexity and fractals

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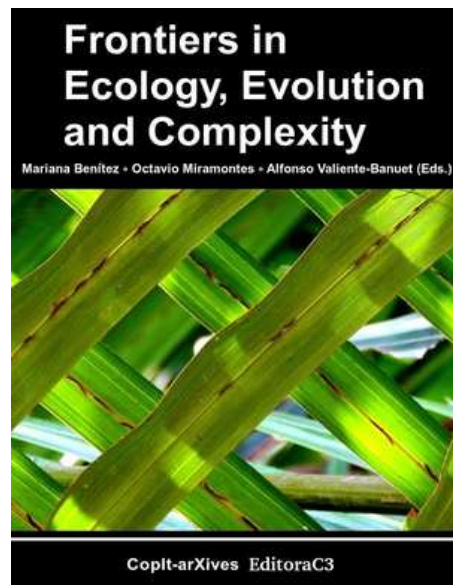
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Flower complexity and fractals

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1 Abstract

We present an approach to the study of plant-pollinator interactions based on the analysis of flower complexity, understood as the fractal dimension of corolla dissection. Corolla complexity was examined regarding its ability to predict the number of pollinator species that visit 21 flowering plant species in a Chilean ecosystem. A second order polynomial function was the best descriptor of the flower complexity-pollinator relationship. In particular, flowers with intermediate complexity were those that received the highest diversity of pollinators. Flowers with rounded and highly dissected corollas were less visited, which suggests that pollinators face a behavioral tradeoff associated to landing in broad platforms or manipulation of dissected corollas when deciding the type of flowers they visit. This result suggests that emergentist perspectives, such as the used in this study, permit to predict flower attraction, one of the most important variables in pollination ecology and evolution. More studies including Mandelbrot's perspective to flower complexity are needed to complement reductionist approaches and have a more inclusive understanding of plant-pollinator interactions.

2 Resumen

Presentamos una aproximación al estudio de interacciones planta-polinizador que se basa en el análisis de complejidad floral, entendida como la dimensión fractal de la disección del contorno de la corola. Se examinó en qué medida la complejidad floral es útil para predecir el número de especies de polinizadores visitantes en 21 especies de plantas en un ecosistema de Chile. Una función polinomial de segundo grado fue el mejor descriptor de la relación. En particular, las flores con complejidad intermedia fueron las que recibieron una mayor diversidad de polinizadores. Las flores más redondas y con alta disección de sus corolas recibieron menos especies, lo cual sugiere que los polinizadores enfrentan un compromiso al momento de decidir cuales flores visitar. Este resultado sugiere que perspectivas emergentistas, tal como la usada en este estudio, permiten predecir la atracción

floral, una de las variables más importantes en ecología y evolución de la polinización. Más estudios que incluyan la perspectiva de Mandelbrot a la complejidad floral son necesarios para complementar aproximaciones reduccionistas y lograr un entendimiento más inclusivo de las interacciones planta–polinizador.

3 Introduction

One of the most conspicuous patterns of angiosperm diversification is the enormous diversity in size, color, visual patterns, shapes, odors, and overall design shown by flowers at present times. This observation can be traced back to the first floral biologists, at least 250 years ago [1, 2], and was part of the empirical evidences used by Darwin to support his theory of evolution by natural selection (see [3, 4]). In spite of the time elapsed from such seminal contributions, the understanding of factors involved in such morphological diversity is still an important research area, in part due to the increasing awareness that flowers constitute complex structures that result from the combined action of genetic, developmental, and environmental processes.

Flowers are attractive and tractable models on which diverse hypotheses of adaptation can be tested. They are directly related to plant fitness, provide replicated units to examine the consistency of adaptation within and among populations, and represent an appropriate model to experimentally examine the relevance of different floral parts for reproductive success. Currently, there is ample correlative and experimental evidence that pollinators play an important role in floral evolution (reviewed in [5]). Indeed, diverse flower traits such as corolla color, nectar guides, and flower size, among others, have been extensively examined as relatively independent traits that participate in pollinator attraction. Likewise, recent statistical tools based on geometric morphometrics have permitted the inclusion of corolla shape in studies of pollination ecology and evolution (e.g., [6–11]).

Unlike the successful incorporation of shape analysis to pollination ecology, however, studies that measure flowers from the perspective of complex systems are almost absent in the literature (but see [12]). This omission is consistent with the historical overemphasis given to disintegrate the floral phenotype into relatively independent functional pieces. The basic assumption of reductionism is that complex systems can be understood by characterizing the properties and behaviors of their component parts. While this strategy has been obviously successful, emergent properties, by definition, do not fit into this paradigm but may instead contribute to a more complete understanding of plant-pollinator relationships. In this chapter we attempt to show that complexity, an emergent property of organisms, may represent a useful perspective to be adopted in pollination biology.

Most studies of floral preference have recorded bee’s behavior (honeybees and bumblebees) in a range of flower traits such as flower color, shape, scent, and size under laboratory conditions (e.g., [13–15]). Under such circumstances the floral preferences seem to

depend almost entirely on the pollinator cognitive abilities and the signals on which they rely on (e.g., [11, 16, 17]). Results from such studies indicate that the degree of corolla dissection is one of the main spatial parameters used by bees to discriminate flowers.

In principle, insects prefer highly disrupted over less disrupted corollas [13, 18]. However, Lehrer et al. [19] found that bees prefer less disrupted patterns to high ones. These two opposite views are not necessarily conflicting because preferences were measured under different conditions. In the first case, bee choices were evaluated at a very close distance, but the other one analyzed preference at a larger distance [13].

These foregoing findings suggest that pollinator floral preference depends on a higher number of variables than previously thought. This conclusion is supported by the study of Dafni and Kevan [16], where a relation between corolla complexity and size was detected in 42 plant species.

In general, pollinator choice differed depending on the plant species under assessment, but a clear pattern emerged: medium and large sized pollinators were associated with large flowers with simple shapes, while small pollinators were related to small flowers with disrupted outlines. The authors proposed that the high contour density in small flowers may increase their visibility hence representing a strategy to counterweigh their small size. Despite the fact that most studies were performed in bees under laboratory conditions, there are some studies performed in other pollinator groups under natural populations. For example, Johnson and Dafni [20] examined the response of bee flies to shape, size, color, and pattern separately. They found that dissected outlines were more preferred than simple ones. Similar results have been found for hawkmoths [12, 21] but an opposing trend was detected in beetles [22]. Although in general these studies have shown that pollinators respond to corolla dissection, no attempt has been made to quantify rigorously corolla complexity which precludes useful generalizations.

In this study we will examine the extent to which corolla complexity, influences the attraction of pollinators in a plant-pollinator community. In principle, plant species differing in the dissection of their corollas (i.e., the amount of edge per unit area) may differ in the amount of pollinators they attract, creating clusters of species associations around flowers. Even though there are many ways to define complexity, for our purposes, we will follow the proposed by Mitchell [23], who defines a complex system as one that exhibits at least some properties that cannot be explained as the linear sum of properties of the component elements. To measure complexity, we will use the approach devised by the French mathematician Benoit Mandelbrot. Under Mandelbrot's perspective, fractals represent the geometric shape of an object and the fractal dimension can be calculated as the number of copies of the self-similar object at different levels of magnification.

4 Methods

This study is based on data from a more inclusive study carried out in the austral spring and summer seasons of 2007 and 2008 in an area near Los Ruiles National Reserve (35° 85' S, 72° 83' W) in the coastal range of central Chile (see description in [24, 25]). The sampling procedure consisted on recording the identity and frequency of visitation of insect visitors to flowers of every plant species during 10-min observation periods. Observations were performed by 3.8 persons/day, on average, and always on sunny days. Observations on plant species were performed according to their abundance in the site. Visitors were considered legitimate pollinators when they contacted the anthers or stigma of flowers or entered the flower tube. We collected insects in the first year of the study for subsequent taxonomic identification in the laboratory.

Plant species satisfying the two following criteria were included in analysis: i) to be an herbaceous plant, and ii) to exhibit a planar corolla (i.e., with petals open in about 180° in anthesis). After applying these selection criteria to the species present at Los Ruiles National Reserve, we recovered 21 plant species, most of them (17 species) belonging to different plant genera. Corollas were then photographed from a perpendicular perspective to mimic the view of a pollinator approaching to the plane of the corolla. Pictures were transformed to black and white so that flowers and outlines were clearly distinguished from white backgrounds. We quantified corolla complexity as the fractal dimension of the corolla outline in Benoit 1.2.

The concept of fractal dimension D [26] can be used as a simple descriptor of complexity for any object. By using calculation methods for identification of self-similar patterns in 2D graphic objects, this method provides a useful approach to detect scale-invariant properties where traditional statistical approaches fail. We estimated the fractal dimension of the corolla outline through the mass dimension procedure. Briefly, this method consists in finding the mass radius (mr), that is, the number of points within a circle of radius r in the outline of interest and to estimate the changing mr data across circles of increasing radius from the center of the figure. If the figure of interest has fractal structure, plotting the logarithm of m versus the logarithm of r will result in a straight line with slope D_m , where D is the fractal dimension. In this way, low D -values will be observed in flowers with simple (non-dissected) corollas because the number of white points will not increase from the centre to the periphery of flowers. On the contrary, the number of white points interspersed in the corolla outline will increase from the centre to the periphery of flowers with complex (dissected) corollas. To reduce the measurement error attributable to variation in the initial values of parameter estimations (i.e., those coordinates corresponding to the center of corollas), we recorded 10 measures of fractal dimension corresponding to circles with radio 1.1 to 2.0 and calculated an average D -value per plant species. All analyses were performed in *Benoit 1.2* and *R* version 3.0.1 (The R Foundation for Statistical Computing 2013).

5 Results

Fractal dimension D -values ranged from 1.22 to 2.0 with a mean (SD) of 1.58 (0.29) in the plant community. The data come from a lognormal distribution (Kolmogorov's D test, $D = 0.137$, $P = 0.150$). As no abrupt decrease of D -values was evident (Figure 1a), the fractal dimension was homogeneously distributed in the plant community. GLM models were adjusted for each parameter (linear and quadratic) using Poisson-distributed errors and log link using D as predictor variable, and maximum likelihood as estimation method. While the linear model did not predict the number of pollinator species on flowers [estimate (SD) = -0.108 (0.227), $P = 0.633$, $AIC = 347.6$], the quadratic model predicted successfully the variation in the number of pollinator species [D estimate (SD) = 0.048 (0.262), $P = 0.854$; D_2 estimate = -532 (1.102), $P < 0.001$, $AIC = 325.82$]. This result implies that interspecific variation in corolla complexity, estimated through the fractal dimension, accounts at least in part for differences in the number of pollinator species attracted to flowers. The negative coefficient of the quadratic term indicates a concave function, with a maximum degree-value around $D = 1.6$ (Figure 1b), that is, in the medium region of the fractal dimension scale.

This result indicates that flowers with intermediate complexity tend to receive the highest number of pollinator species, and plants with minimal and maximal complexity received a lower number of them. As most plant species belong to different genera (with the exception of two pairs of species, *Anagallis* (Primulaceae) and *Hypericum* (Clusiaceae), phylogenetic effects may have a minor importance in the resulting pattern. But why should pollinators be less attracted to flowers with high or low corolla complexity? One potential line of reasoning relates to pollinator specialization and attraction. The low number of pollinator species observed in the left side of Figure 1b may be a direct consequence of the low attraction provoked by simple and non-dissected corollas. On the other hand, it is likely that highly dissected and complex corollas tend to be visited by specialized pollinators with phenotypes that permit them to manipulate adequately the flower in order to obtain rewards (see [27]).

A second line of reasoning relates to the tradeoffs faced by pollinators when visiting and manipulating flowers. As flower shape is a character that provides attraction to pollinators and at the same time participates in the mechanical fit with pollinators [10, 11], there is a potential conflict for plants between attracting pollinators and providing an adequate phenotype that adjust the flower-pollinator interface. Evidence from pollinator preference provides support to such dichotomy. Many laboratory and field studies have demonstrated that pollinators tend to prefer flower models with narrow petals and dissected corollas (e.g., [8, 13, 14, 18, 20]). Flowers with dissected outlines are probably more detectable to moving insects because they create a greater on-off stimulus in the compound eye [28, 29], and provide a reliable informative cue about the quantity and quality of pollen and nectar reward. However, recent field evidence indicates that contrary to expectations, some pollinators tend to prefer flowers with rounded and simple corollas over

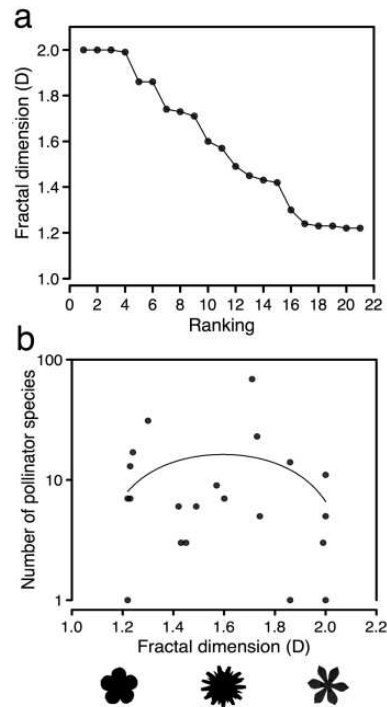


Figure 1: a) Distribution of D fractal values ranked from high to low values. Log-transformed values come from a normal distribution (Shapiro-Wilk W test, $W = 0.943$, $P = 0.277$). b) Relationship between the corolla fractal dimension and the number of pollinator species visiting flowers. The polynomial equation is $\text{Pollinators} = -133 + 188D - 59D^2$. The silhouettes depicted from left to right along the X-axis correspond to *Anagallis arvensis* (Primulaceae), *Chamaelemun mixtum* (Asteraceae), and *Sisyrinchium graminifolium* (Iridaceae).

complex outlines, apparently because rounded corollas provide suitable landing surfaces and higher handling effectiveness in reward retrieval [11, 27, 30]. Under such circumstances, pollinators may face an obvious conflict in their foraging decisions, that can be solved, at least in part, by preferring intermediate floral phenotypes that provide the best of two options.

6 Concluding remarks

Recent interest in the conceptualization of biological systems from a complexity perspective has stimulated the emergence of new programs in ecological and evolutionary research such as ecological networks, phenotypic integration, phenotypic plasticity, and genetic of developmental processes, among others. These perspectives have revealed new

patterns of organization that often escape to the eye of mechanistic approaches. In this chapter we have shown that pollinator attraction, a critical element in pollination ecology, can be further understood under the perspective of complex systems and flower fractality. Even though flower complexity is frequently invoked as an organismic property detectable by pollinators, attempts to measure complexity are almost lacking in the literature, in part, because complexity means different things for different people. In this chapter, we argue that it is time for pollination ecologists to search for common definitions and move beyond the reductionist focus to examine how much we might be missing by not treating flower complexity on its own right. We think complexity is one of the major remaining frontiers in plant-animal interactions. This chapter has provided a simple example of the way an emergentist approach may suggest new avenues of research and complement previous findings in pollination ecology.

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