THE SHAPE OF ECOLOGICAL COMMUNITIES: FROM POLLINATORS TO PURPLE MARTINS

by

Melinda Kleczynski

PREVIEW

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FROM POLLINATORS TO PURPLE MARTINS

PREVIEW

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ABSTRACT

Ecological systems are increasingly at risk. At the same time, we have more data describing these systems than ever before. Mathematicians can respond by making insights from these datasets accessible to researchers, citizen scientists, and others. We show how mathematical analysis of the shape of an ecological community generates both actionable information and new questions. This work focuses on the analysis of interactions in plant-pollinator communities and explores the detection of aggregations of swallows using weather surveillance radar.

Animal pollinators are crucial for biodiversity and agriculture. There are many available datasets which record plant-pollinator interactions. In these interactions, the plant provides a resource to the pollinator, and the pollinator provides a resource to the plant. Resource use can be naturally represented using a topological object called a simplicial complex. We build on foundations of previous work on foraging graphs and simplicial complexes with an emphasis on topological persistence and new data. We analyze a small dataset collected at the University of Delaware and more comprehensive data from around the H.J. Andrews Experimental Forest in Oregon. We frequently encounter nontrivial topological features, and discuss the significance of these findings.

We introduce RoostRingSearch, a Python tool developed in collaboration with the University of Delaware Aeroecology Lab. RoostRingSearch uses weather surveillance radar data to search for roost ring features created by large groups of swallows leaving their communal roosting sites. Our algorithm is interpretable with few parameter choices. We discuss preliminary results using data from radar stations in Delaware and Michigan and recommend next steps for improved detection.

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Chapter 1

INTRODUCTION

Throughout this dissertation, we explore the structure of ecological communities. We begin with a topological investigation of collections of mutualistic interactions between plants and pollinators. We conclude by describing an interpretable algorithm for detecting large aggregations of birds such as purple martins on weather surveillance radar. Our work provides tools for monitoring and understanding ecological systems.

Plant-pollinator interactions are both drivers of biodiversity and essential components of human agriculture. Different pollinator species play different roles. Some have a narrow focus, visiting only a small number of plant species. Others are more flexible, utilizing a variety of plant resources. There are many biotic and environmental conditions which could determine whether a given pollinator species will visit flowers of a given plant species. It would be difficult to determine these factors for all the species in a given community, especially since many potential pollinators are not well studied. We do have access to many historical and modern datasets which document interacting pairs of plant and pollinator species. By using topology to analyze the observed set of interactions, we can understand the structure of a plant-pollinator community even when we don't have coordinate information for the species in that community. This structure could have significant practical consequences related to complementary pollination services provided by different animal species.

The coordinated motion of large groups of animals provides a concrete and geometric example of organization in natural systems. When we know the characteristic

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(a) Purple martin (*Progne subis*) (b) Tree swallow (*Tachycineta bicolor*)

Figure 1.1: Two North American swallow species which can create roost ring features on weather surveillance radar

shape of an aggregation, we can use this information to inform automated detection of these groups. Classical examples of organisms which gather in large numbers and display predictable group behavior are North American swallow species, such as purple martins and tree swallows, shown in Figure 1.1. We introduce RoostRingSearch, a Python tool for detecting the characteristic shapes generated by swallows on weather surveillance radar.

For both applications, we use our techniques to generate specific hypotheses. Our topological analysis of plant-pollinator interactions reveals a "missing" interaction whose inclusion would have a significant impact on the structure of a particular community. Using our RoostRingSearch tool, we identify recent appearances (especially in 2021 and 2022) of a potential purple martin aggregation in Michigan.

The interpretability of our techniques makes them well suited for a variety of future work. We discuss several possible projects related to topological data analysis (TDA) of plant-pollinator data. The RoostRingSearch pipeline has the capacity to be modified to analyze weather radar data collected using different protocols, such as data collected outside the United States. Our current and future work have the potential

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to provide key insights about a variety of ecological systems.

1.1 Organization of the dissertation

Chapter 2 provides ecological background relating to plant-pollinator communities. These communities have already generated significant interest in the research community, with the result that some of their general properties are already known. We make use of some of these properties when designing our constructions. We discuss aspects of plant-pollinator datasets which are important when interpreting our results. We review some mathematical background related to existing analysis of plant-pollinator interactions and similar ecological systems.

Chapter 3 reviews the main mathematical background relating to this work. The chapter focuses on topics from applied topology, with a short introduction to category theory to provide some mathematical context. We review existing applications of topological data analysis to the field of ecology.

Chapter 4 formally defines the resource complex, the primary mathematical object used in this work. We introduce the foraging complex, a specific instance of a resource complex. We discuss and relate major precursors to our constructions. We illustrate these concepts using a subset of the interactions in the University of Delaware (UD) insect-flower visitation dataset.

Chapter 5 addresses the reality of working with real datasets by extending our analysis from the homology of a single simplicial complex to the persistent homology of an increasing sequence of simplicial complexes. We discuss how to define this sequence and how to estimate an upper bound for the dimension in which the dataset could possibly produce any nontrivial persistent homology. Using these constructions, we show that plant-pollinator interactions frequently produce nontrivial topological features and that the presence of these features is related to the size of the dataset.

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Chapter 6 explores how a small change in a dataset can eliminate multiple topological features. We discuss the implications of this fact for the mathematical stability of our constructions and the ecological conclusions of our analysis. We propose a preliminary monitoring recommendation based on our conclusions.

Chapter 7 summarizes the conclusions of the plant-pollinator analysis in this dissertation. We are optimistic that our foundations will create many opportunities for future work. We suggest several possible projects here.

Chapter 8 discusses our RoostRingSearch tool for detecting aggregations of North American swallow species on weather surveillance radar. We discuss a potential roost detected in Michigan. We propose next steps for improved detection, focused on utilizing the time evolution of roost rings.

Appendix A describes an insect-flower visitation dataset the author collected at the University of Delaware. Appendix B is an index of the mathematical definitions included in this work. Appendix C is an index of the theorems included in this work. Theorems 3.6.1 and 3.6.1 are classical results [32] which are included in the dissertation for convenience. We introduce theorems 4.4.1 and 4.4.2 relating the two major precursors to this work, and theorems 5.3.1 and 5.3.2 which facilitate our data analysis.

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Chapter 2

ECOLOGICAL BACKGROUND

This work develops techniques for the topological analysis of ecological communities. Plant-pollinator communities are the primary focus. This chapter provides important background information related to this application area. Section 2.1 introduces some helpful terminology. Section 2.2 motivates this research by communicating the importance of biotic pollination. Section 2.3 describes a common form of historical and current datasets documenting pollinator activity. Section 2.4 points out some ecological realities which affect mathematical representations of these systems. Section 2.5 reviews the concept of an ecological niche and its relation to plant-pollinator interactions. Section 2.6 discusses bipartite networks, a common representation of ecological interactions including plant-pollinator interactions. Section 2.7 describes some known properties of plant-pollinator networks. Section 2.8 summarizes constructions by Sugihara [87] which provide important theoretical foundations for the current work. Section 2.9 reviews some important considerations regarding the dimensionality of ecological networks. Section 2.10 covers the foraging graph introduced by Peleg, Shmida, and Ellner [72], which is an important precursor to the current work. Finally, Section 2.11 discusses the relevant topic of 1-mode networks.

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2.1 Terminology

In this section, we establish some standard terminology as described in [98]. Animal visitors to flowers facilitate the reproduction of many types of plants by transporting pollen. This process is known as biotic pollination. From now on, we simply

refer to this process as pollination. Typically a pollination interaction involves the animal providing a pollination service to the plant and the plant providing a food resource to the animal. Thus pollination is a mutualistic interaction, meaning that the interaction is beneficial to both participants. Not all flower visitation is mutualistic; illegitimate visitors are animals which visit flowers without providing any pollination service.

Mutualists range from specialists to generalists. A specialist may refer to a mutualist whose morphology or behavior limits the interactions it may participate in. Additionally, the term specialist may denote a mutualist with a small number of partners. On the other hand, a generalist is a mutualist which does not have qualities excluding certain interactions, or a mutualist with a large number of partners.

2.2 The significance of biotic pollination

Mutualistic pollination is the process we wish to study. We will discuss reasons why available datasets are approximations of pollination interactions. For now, we simply note that datasets may contain illegitimate visitors and the interactions observed could in fact provide little to no benefit for one or both of the participants.

Many species engage in pollination interactions. Bees, which frequently come to mind when one thinks of pollination, are a diverse group likely containing more than 18,000 species (with more waiting to be discovered) [65]. Many types of insects are potential pollinators; our introductory dataset includes bees, wasps, flies, beetles, butterflies, and moths [58]. Hundreds of bird and mammal species act as pollinators; hummingbirds and bats are significant examples [75]. Despite the ubiquity and importance of plant-pollinator interactions, we still do not fully know which species participate in them. For example, a 2023 article [27] identified the first candidate for a pollinating frog species (*Xenohyla truncata*).

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Rodger et al. estimate that globally, about half of all species of flowering plants depend on the services of animal pollinators for 80% or more of their seed development [78]. The dependence of some plants on animal pollination means that pollinator losses place additional species at risk. There are already indications of decreases in pollinator biodiversity. For instance, worldwide records suggest pervasive drops in bee diversity [99]. There are many potential causes of bee declines; a frequently cited contributing factor is the loss of suitable habitat [13]. An additional concern is invasive species; invasive generalists may interact with many native species and destroy preexisting relationships among native mutualists [1].

2.3 Plant-pollinator interaction data

One way to describe a plant-pollinator community is by listing the interactions which are observed, where each interaction occurs between a type of plant and a type of pollinator. It is common for each mutualist type to correspond to a species. This form of record keeping has a long history. For example, two extensive datasets published in the 1920s include this type of information [21, 77]. Modern monitoring of plant-pollinator communities continues to include interaction data. This includes the two datasets analyzed in this dissertation. In Chapters 4 and 5, we use a small insect-flower visitation dataset the author collected at the University of Delaware to introduce our techniques. Appendix A contains a detailed description of this dataset. In Chapters 5 and 6, we analyze a long-term dataset including observed pairs of flower and visitor taxa. This dataset was collected in 2011-2021 around the H.J. Andrews Experimental Forest in Oregon, specifically in meadows in the western Cascades [85].

2.4 Ecological factors affecting mathematical representations

There are many ecological realities which can affect our mathematical representations of plant-pollinator communities. Some considerations are common to almost

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every analysis method, such as data completeness (Section 2.4.1), external influences on the observed interactions (Section 2.4.2), and variability in community composition (Section 2.4.3). There are also attributes of some plant-pollinator communities which have particular significance for topological representations. Within-group interactions can occur, and these are not accounted for by our methods even though they have an effect on the between-group interactions we do track (Section 2.4.4). There can be considerable variability in the foraging behavior of individuals within a species (Section 2.4.5) which we will see has the potential to generate nontrivial topological features.

2.4.1 Data completeness

For various reasons, plant-pollinator studies may restrict data collection to particular taxa. For example, [56] focuses on hoverflies; this provides valuable data, but plants have other visitors that are artificially excluded from the dataset. Omissions of species or interactions can also be unintentional, occurring due to limitations of the data collection process. For example, [56] showed an increasing trend relating the number of individuals observed for each hoverfly species and the number of plant types visited by that hoverfly species, suggesting that interactions involving uncommon species can be undersampled. It is common in studies of bees for many species to be represented by only 1-2 specimens [97].

Observational studies can be incomplete if data collection only takes place during the day, because some plants are visited by animals both during the day and at night [60]. It is also important to consider that animals may utilize flowers in large areas, potentially larger than the location of a study. As an extreme example, migratory pollinator species such as hummingbirds may require floral resources in multiple countries [83].

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2.4.2 External influences

The foraging strategies employed by pollinators can vary based on external influences. For example, there is evidence that generalization increases in colder climates [20]. Anthropogenic factors can have unexpected influences on plant-pollinator communities. For example, artificial light at night can actually alter the flower visitation which occurs during the day [40].

2.4.3 Community variation

Plant-pollinator communities evolve over time; it is possible that features of the community can persist even as individual species or interactions vary [68]. For example, the species composition of bee populations can change significantly over space and time [97]. Aggregating data collected over an extended period of time can obscure the temporal dynamics of the community [63].

2.4.4 Within-group interactions

Records and analysis of plant-pollinator communities do not typically account for within-group interactions. By within-group interactions, we mean interactions between two plants or interactions between two pollinators. These types of interactions can occur, and they can affect the plant-pollinator interactions we observe. For example, the work in [80] documents bees attacking hummingbirds, which causes some deterrence of the hummingbirds from the flowers occupied by bees.

2.4.5 Taxa heterogeneity

Many studies group all individuals of a species or higher taxon together. This makes sense if all individuals in a taxonomic group behave similarly with respect to their foraging preferences. However, this is not necessarily the case. Research has shown, for example, that bees of the same species but of different sexes can be about

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as different as bees of different species [79]. Social role can also be an important factor; for instance, bumble bee queens can have noticeably different flower visiting behavior than their workers [36]. Due to identification difficulties, it may be necessary to group some animal pollinators together; see, for example, [38].

Variation can also occur within a single type of plant. For example, flowers in different locations on cotton plants attract different types of animal visitors [26]. Plant-pollinator interactions are sometimes determined by identifying the types of pollen on an animal's body; some pollen grains are difficult to distinguish, so in the dataset these plants must be grouped together [50].

2.5 The ecological niche

In order to interpret the topological constructions in this work, it will be helpful to invoke the classical ecological concept of the niche, introduced by Hutchinson [47, 48]. Let X be a space whose axes correspond to factors describing potential habitats. The niche of an individual or group of individuals is the set of points in X corresponding to livable habitat. This region is frequently referred to as a hypervolume in ecological literature [47, 48].

A plant and pollinator can only interact if there is some set of environmental conditions which is suitable for both of them; in other words, their abiotic niches must intersect [3]. Even if a plant and a pollinator can live in the same environment, they do not necessarily interact. There are plant traits and pollinator traits which help determine whether interactions occur. For example, flower height influences the animals which will visit a flower; this occurs even in habitat types such as grasslands, where the range of heights is relatively small [57]. Related species may exhibit variable sensitivities to the same partner trait. A study investigating pipevine swallowtails (*Battus philenor*) and skippers (Hesperiidae family) found that swallowtails are adaptable in

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their flower color preferences, while skippers seek out light blue flowers [12].

There is evidence that the pollination effectiveness of a collection of bee species is driven more by the niche coverage it provides than its membership count [37]. This has important practical implications. Some researchers advocate for functional complementarity as an important objective for pollinator conservation [26].

2.6 Bipartite networks

A topic of considerable interest in the current work is how to usefully represent plant-pollinator communities. Early work analyzing the structure of mutualisms found success by extending representations utilized for food webs [53]. Bipartite networks are a useful option for representing many types of biological systems; this includes mutualisms such as plant-pollinator interactions [71].

Although we focus on plant-pollinator interactions, the techniques we develop apply to any system which can be represented as a bipartite network. This creates many additional application areas, such as analyzing mutualistic cleaning interactions in reef environments [41]. Observed disparities in the number of cleaner species and number of client species [41] would have interesting implications for the algorithms we introduce.

In a bipartite network, there are two types of vertices. A common pipeline when analyzing plant-pollinator data is to use different plant species for the first set of vertices and different pollinator species for the second set of vertices [33]. In place of species, a higher taxonomic level such as genus may be used [58]. It is also possible to associate each vertex with a single individual rather than a group of individuals [33]. For example, one study used individual thistle plants as one set of vertices and individual honeybees as another set of vertices [33].

Mathematically, the best grouping is not necessarily a taxonomic classification

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