

Review

Multispecies Swarms of Social Microorganisms as Moving Ecosystems

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Microorganisms use collective migration to cross barriers and reach new habitats, and the ability to form motile swarms offers a competitive advantage. Traditionally, dispersal by microbial swarm propagation has been studied in monoculture. Microorganisms can facilitate other species' dispersal by forming multispecies swarms, with mutual benefits. One party (the transporter) moves a sessile partner (the cargo). This results in asymmetric associations ranging from temporary marriages of convenience to long-term fellow travellers. In the context of the 'microbial market', the parties offer very different services in exchange. We discuss bacteria transporting bacteria, eukaryotic microorganisms moving bacteria, and bacteria facilitating the spread of eukaryotes – and ask what the benefits are, the methods of study, and the consequences of multispecies, swarming logistics networks.

Spread of Microbes in the Environment

Instances of both competition and cooperation between microorganisms are found in most environments from the rhizosphere to the human body. Microbiologists are mapping the interactions between microbes within the same habitats; for example, in a single soil granule using genomics and imaging [1] or between related species in marine habitats using metagenomics [2]. Evolutionary biologists are developing new ways of calculating cost–benefit relationships (microbial markets) that allow quantification of the relationships between microorganisms – who does what and who benefits [3]. These recent advances give new approaches to long-standing questions, such as what constitutes a microbial community and to what extent cooperation occurs within and between species.

Natural environments are interconnected to varying degrees, and most species occupy multiple but geographically distinct niches, existing as a metacommunity [4]. There are routes between different environments, and microorganisms use these to spread. The barriers are often natural (e.g., air gaps in the soil), and different microorganisms have diverse capabilities to cross these obstacles [4,5]. In order to spread, microbes seek to disperse at an optimal rate – maximal dispersal is not necessarily the best as it can dilute the impact or survival potential of the invader, whilst minimal dispersal has an obvious limitation of range [6].

In a broad ecological and evolutionary sense, we can also ask to what extent does the spread of microorganisms matter. Given potential exponential growth and highly favourable conditions, in theory a single microbe could achieve dominance in a particular location in a very short time. So, if 'everything is everywhere but the environment selects' then dispersal may be less important than factors that affect competition during growth [7]. However, studies on microbial speciation

Trends

Increasingly, microorganisms are studied in relation to other microorganisms.

Many microorganisms can collectively migrate over surfaces to new ecological niches as a swarm.

In recent years, some swarms have been shown to transport other microorganisms as cargo. This leads to interesting, asymmetric relationships whilst 'on the move' – which can be considered a mobile ecosystem.

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⁵*In memoriam*. This article is dedicated to one of the authors, Professor Eshel Ben-Jacob (1952 to 2015), who sadly died during the preparation of the manuscript.

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suggest that physical and geographical barriers can be important, in both extreme and temperate habitats [8–10]. It follows that there are multiple strategies that microbes use to cross these obstacles, including adaptation to transport by water currents or the wind. Another such method is to be carried by a larger organism. For example, freshwater zooplankton can transport bacteria across density gradients in lakes which are otherwise impenetrable to bacteria [11].

The role of microbial motility is surprisingly poorly understood in the context of dispersal. Some microorganisms move rapidly in liquid or over surfaces; the latter is commonly a collective phenomenon and uses a variety of molecular motors with the common factor that they require significant genetic investment, typically over 50 genes [12,13]. The motors can drive the rotation of flagella (swarming) or a series of diverse, non-flagellate force-generating systems resulting in movement [13]. Both terms, gliding and swarming, can be confusing. Gliding can occur by multiple, unrelated mechanisms (Box 1). However, some of the mechanisms of bacterial motility may turn out to have more in common than has previously been suspected. Flavobacterial gliding, despite being dependent on a very different set of proteins to those that turn bacterial flagella [14], has recently also been shown to also involve a rotary motor [15]. The term ‘swarming’ can also be used in different ways; here we refer to swarming as being specific to collective bacterial movement over a surface only when driven by flagella [12]. We will use the concept of a swarm, more loosely, to describe decision making and mass migration of agents, which does not have a clear leader, and intend this term to also cover robots and other nonliving swarms (Box 1). The microorganisms providing the force for motion are defined as the transporter, and the more sessile, hitchhiking organism is the cargo [16].

Despite diversity of mechanisms, and whether swarms are composed of microorganisms, multicellular organisms, or even cybernetic agents, swarms have certain commonalities, including trigger events to start/stop (organisms do not swarm all the time), and collective action (possibly cooperative, with no leader, and exhibiting capabilities beyond the individual). Mathematical modelling can examine swarming across multiple, diverse systems and look at different scales of organization. Imaging provides experimental validation for modelling and independently generates new insights. We describe the powerful combination of imaging and modelling (Box 2) as related to transporter–cargo interactions later in this article.

Box 1. General Aspects of Microbial Motility

Many microorganisms are self-propelling, either swimming in liquids or moving over surfaces [12,13].

Motility on surfaces is often via specialized mechanisms (e.g., gliding or surface-adapted swarming cells). Surface motility is frequently collective; for example, in bacterial swarming, whilst each individual bacterium has functional flagella, groups of bacteria are required for movement to occur. Individual bacteria move within swarms, for example in ordered streams [16] or as a complex random motion pattern [65]. Gliding occurs by multiple mechanisms and, unlike flagella motility, occurs only on surfaces [12].

Whilst the velocities of swarms can exceed 1 cm/h in many cases, relatively little information is available on how motility impacts long-range dispersal in the environment. Most studies concentrate on local motile behaviour (cm to μm scale range) [12,13,66,67].

Life on this scale is different to our own experience. Liquids are highly viscous relative to bacterial mass (low Reynolds number), and individual bacteria are prone to Brownian motion. Surfaces also exert strong effects on microorganisms with factors such as surface tension and the availability of water as critical physical parameters [68].

Microorganisms actively alter their local environment during motility through the secretion of compounds (such as surfactants or lubricants) [12,68,69]. Microorganisms also affect their immediate environment [70] through motility itself, for example, a high density of actively rotating flagella can decrease the viscosity of their environment, even converting the properties of water to a superfluid [71]. The force generated by single [72,73] or multiple [16] microorganisms is sufficient to move objects, often considerably larger than an individual bacterium. For many forms of surface motility the roles of decision making and active motility are unclear.

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