ANNUAL MEETING

The Movement Ecology of Mutualism (CSEE/ESA 2022, OOS17)

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Session goals

The study of whole organism movement has developed modern frameworks for understanding individual and population movement across space. Recent thought has begun to push the boundaries of understanding movement beyond individuals and populations to sets of interacting species. Interspecific interactions can influence individual movement either before or after the interaction, and movement can occur individually or jointly. Mutualism is an interspecific interaction where whole organism movement plays a central, but overlooked role (Shaw et al. 2021). Although ecologists typically recognize the importance of movement in the subset of mutualisms where one partner

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receives a transportation benefit (e.g., seed dispersal, pollination, spore dispersal, endosymbiotic mutualisms), the role of movement in mutualism ecology often ends there. Furthermore, movement in mutualism entails much more than the transport of gametes or propagules, as partners attract one another, influencing movement as part of the interaction, and can also affect movement trajectories following the interaction.

At the 2022 joint annual meeting of the CSEE/ESA, we ran an Organized Oral session on the movement ecology of mutualism. The goal of the organizers (C.M. Moore and A.K. Shaw) for the session was to stimulate discussion of general principles of movement across mutualistic systems. As theorists, we were personally excited to hear about a diversity of empirical mutualistic systems, and to spark cross-system discussion of mutualism. Our objectives were to bring together ecologists that study diverse mutualistic systems and have them present on the role of movement in their systems, speculate on the importance of movement in their systems, and discuss empirical and theoretical priorities; especially for the inescapable environmental “changes that are gonna come,” the theme of the meeting. Despite the challenges of our times (the ongoing COVID-19 pandemic, airline cancellations, and family emergencies), we were able to run our session with five in-person attendees plus two virtual ones (unfortunately one of our speakers, E. Bruna, could not present).

The importance of this session was twofold. First, the fields of mutualism and movement ecology have effectively developed in isolation of one another, and this session brought together ecologists who study mutualism to openly share and discuss commonalities of their work as it pertains to movement. Second, studying how organisms respond to environmental change is arguably the most pressing issue of applied ecology. Movement is centrally important to how organisms will respond to environmental change, such as climate warming or habitat fragmentation, and understanding how mutualism and other facilitative interactions will affect movement is thus critical. We believe this session produced great interest among meeting attendees because of the ecological community’s shared interest in mutualism and movement, the synthetic nature of the topic, and the diversity of the speakers and study systems. Below, we summarize the presentations, describe the themes that emerged both during the session and during a discussion afterwards, and reflect on future directions.

Presentation summaries

Bethanne Bruninga-Socolar’s presentation, *The contribution of plant spatial arrangement to bumble bee flower constancy*, explored how pollinator constancy, plant spatial arrangement, plant abundance, and pollinator preferences for certain species of plants over others affect how bees move across the landscape and visit flowers (Bruninga-Socolar et al. 2022). Bruninga-Socolar followed bees as they moved and foraged in plots and recorded the flowers they visited. These movements were overlain on a map of the plots that incorporated plant spatial arrangement as well as plant species abundance. Overall, they found that spatial arrangement of plants has a large effect on bumble bee foraging and that the effects of simple constancy, “preferential visitation to the same species as the previous plant visited,” may be overestimated when spatial arrangement is not considered. This presentation highlighted that the spatial arrangement of potential mutualistic partners can impact the movement of the mutualist seeking them. In this study, for example, bees were more likely to visit plants close to and directly in front of them. Spatial arrangement of partners must be considered when modeling the movement of mutualists.

Eleanor Caves' presentation, *Communication with mutualistic partners: sensory systems and signal active space in cleaner shrimp-client fish interactions*, explained the role species' visual systems play in mutualistic cleaner shrimp-client fish interactions and its impacts on the movement of both participants. Both cleaner shrimp and client fish send signals to each other to participate in this cleaning mutualism, with both of their signals determined by the other partners' visual capabilities, specifically visual acuity (their ability to perceive spatial detail; Caves et al. 2018). Cleaner shrimp have low visual acuity and client fish must get close to the shrimp and change color to signal to the cleaner shrimp that they are ready to be cleaned. The client fish have higher visual acuity and cleaner shrimp signal to them by whipping their antennae back and forth, which the fish can see from 30 cm away. Ultimately, the visual acuity of both of the mutualists in this interaction shapes the signaling involved, and presumably influences the distance from which they can identify one another, and thus the movement of these mutualists. Cleaner shrimp are constrained both by their dependence on a sessile host and their low visual acuity, so cannot move far to find client fish. Client fish with their high acuity can sense and move longer distances to find cleaner shrimp.

Annika Nelson's presentation, *Fruit secondary metabolites decrease the quantity and quality of seed dispersal by ants*, examined the role of fruit secondary metabolites in determining both the quality and quantity of seed dispersal provided by ants for the seeds of *Piper reticulatum* (Piperaceae). Nelson isolated amides from *Piper* fruits, applied them to seeds, provided those seeds to ants, and looked at dispersal quantity (ant recruitment and fruit removal) and quality (distance fruits were moved, proportion of fruits cleaned, and re-dispersal). Overall, Nelson found that amide presence reduces both the quantity and quality of ant seed dispersal, demonstrating the ability of secondary metabolites and other chemical signals to impact mutualist recruitment and movement. Nelson found that amide presence did not impact the distance seeds were moved by ants, but did impact whether they were moved at all, with amides reducing the probability that an ant would pick up and move a seed, as well as where seeds were eventually deposited (e.g., within versus outside the ant nest). Plant secondary metabolites are widespread, with diverse impacts on both individual plants as well as on interspecific interactions (Nelson and Whitehead 2021). Thus, the presence of chemicals not directly related to a dispersal mutualism that can nonetheless mediate the outcome of that mutualism is an interesting avenue for future research, especially regarding movement and mutualisms. These secondary chemicals could potentially mediate whether mutualist partners meet and travel together, and their absence in models involving the co-movement of mutualists could lead to erroneous results.

Kasey Kiesewetter's presentation, *Fragmentation-driven effects on beneficial microbiomes drive changes in native plant performance*, focused on how habitat fragmentation and urbanization impact soil microbial communities and how this affects the plants they associate with (Kiesewetter and Afkhami 2021). They collected soil samples from undisturbed and urban locations with varying levels of fragmentation in Florida's Pine Rockland ecosystem. These samples were then sequenced to determine the microbial diversity and composition. Native plants from this ecosystem were also inoculated with microbial communities from undisturbed and urban habitats to determine the effects of these microbial communities on individual plant performance as well as plant community productivity. Overall, urbanization and fragmentation significantly shaped microbial communities and subsequently changed plant performance and resource allocation. Kiesewetter concluded the presentation with several questions on how soil microbiomes disperse across a landscape and how that may affect the plants with which they form mutualistic symbioses. Surprisingly, there is a dearth of research on how soil microbes disperse and move to new mutualistic partners, and understanding this aspect of movement of obviously vital mutualists is a new frontier in the study of mutualisms and movement.

Elizabeth Pringle's presentation, *Capitalizing on movement for optimal defense in protection mutualisms*, investigated how plants manipulate the movement of mutualistic ant defenders by provisioning rewards on or near the plant's most valuable and vulnerable tissues (new leaves or reproductive parts). Compared to chemical or physical defenses in leaves, like tannins or lignin that once added to a leaf cannot be recovered, ants, by virtue of their ability to move, are reclaimable defenses. Pringle presented case studies of plants that produced rewards, like domatia or extrafloral nectaries, near valuable tissues to attract ant defenders (Pringle 2014), and also discussed cases in which plants can alternatively repel ants, which may disrupt pollination, near flowers (Willmer and Stone 1997). Pringle concluded by stating that the ability of plants to manipulate the movement of ants and reclaim them could have possibly led to the monodominance of ant-defended plant species in certain environments. Considering the movement of mutualists and how it can be manipulated by another mutualist is a fascinating new vein in the study of mutualisms. Determining whether having this moving defense led to a form of competitive advantage for some species will certainly garner interesting results.

Emergent themes

Three recurring themes we observed among presenters were that of scale, ecological context, and sensory ecology and constraint. Movement and the spatial, temporal, or level of organizational scale were interpreted differently by each of the presenters, and scales tended to differ between pairs of mutualists in each investigation. In Table 1, we classify relative temporal scales as *behavioral/physiological* for short-term effects of the interaction, *developmental/ontogenetic* for effects of the interaction over the organism's life, and *generational* for effects of the interaction between generations, including where this leads to changes in the populations/evolution. We further classify spatial scales as *active space* for the space in which mutualists are directly interacting (Gerhardt 2009, Caves et al. 2018), *patches* for the space that individual organisms traverse, and *landscapes* for the space in which populations and communities exist or potentially exist. Temporal scales of the talks spanned from behavioral/physiological (Caves) through generational (Kiesewetter, Pringle). One talk (Pringle) even stretched ecological timescales a bit further and considered evolutionary change across generations. Spatial scales spanned within individuals in active space (trees by mutualist ants, Pringle), through patches among individual mutualists (bee foraging, Bruninga-Socolar), and ultimately at landscape scales (Kiesewetter). Organizational scales spanned within individuals (defense allocation to seeds, Nelson), through individuals, and communities. Most autecological movement was ranging (short-distance movement) or dispersal, but no talk focused on nomadism or migration. In Table 1, we also classified the interaction form(s) that mutualism and movement focused on in the talk, which includes *partnering for movement* when the mutualistic interaction shapes how individuals move, *movement for partnering* when individual movement shapes their ability to locate partners, and *co-movement* when movement and mutualism are too intertwined to consider separately (Shaw et al. 2021). In this synecological context of movement and mutualism, most of the talks focused explicitly or implicitly on partnering with implications for movement, there was some discussion of movement with implications for partnering, and there was the least focus on co-movement of both mutualistic partners. We speculate that there was little focus on co-movement

Table 1. Scale and types movement across talks. Each row represents one of two sides of a mutualism; the spatial, temporal, and organizational scales at which it is interacting with the other mutualist; and the types of broad movement and movement relevant for mutualism (*sensu* Shaw et al. 2021).

Talk	Mutualist	Spatial scale	Temporal scale	Scale of organization	Movement	Mutualism movement (addressed in talk)
Bruninga-Socolar et al.	Bee	Patch	Behavioral/ physiological	Individual	Ranging	Movement for partnering, partnering for movement,
	Plant	Active space	Generational	Community	Dispersal	N/A
Caves	Cleaning shrimp	Active space	Behavioral/ physiological	Individual	Ranging	N/A
	Fish	Active space	Behavioral/ physiological	Individual	Ranging	Partnering for movement
Nelson et al.	Ants	Patch	Behavioral/ physiological	Population	Ranging	Movement for partnering, partnering for movement, co-movement
	Plants (seeds)	Landscape	Generational	Population	Dispersal	Partnering for movement, co-movement
Kiesewetter and Afkhami	Microbes (bacteria + fungi)	Landscape	Generational	Community	Dispersal	Partnering for movement
	Plants	Active space	Developmental/ ontogenetic	Individual	N/A	N/A
Pringle	Ants	Active space	Developmental/ ontogenetic	Population	Ranging	Movement for partnering, partnering for movement
	Plants	Active space	Behavioral/ physiological	Individual	Dispersal	Partnering for movement

not because it is uncommon but because few ecologists are studying co-movement, which makes it a fairly open area for investigation. The different scales and different types of movement proved to be a focus of the speakers since many mutualist pairs minimally have very different life histories (e.g., generation/development times, body size).

The ecological context of the interactions also proved to be a recurring theme of the talks. Mutualism is often viewed through a context-dependent lens, with the context often categorized as a result of abiotic or biotic factors (third-party species), or spatial or temporal scales (Chamberlain et al. 2014). Many of the speakers presented the context-dependency of their work or system. As examples, foraging behavior (Bruninga-Socolar) depended on the context of the floral spatial arrangement, community composition (Kiesewetter) depended on the context of historical contingency and dispersal, and ant-mediated dispersal (Nelson) depended on the context of the chemical defenses of the seeds.

The third theme that arose during our session and discussion was the idea of sensory ecology and constraint. The need to sense a partner unites all mutualistic systems, so many of these organisms are faced with constraint challenges in their ability to sense a partner's presence and receptiveness. For example, many plants are outside the range of bees' sensory ability to perceive them, which can constrain pollinator visits (Bruninga-Socolar). Yet, models of pollinator choice rarely account for this constraint. In the client-cleaner shrimp system, organisms develop signaling systems to facilitate sensing of partners (Caves). Many different types of signals can be used to sense partners including visual, olfactory, and tactile ones. Which signal(s) are used may vary over different environments (e.g., aquatic, terrestrial) and timescales. Different mutualistic partners of the same system may also vary in how reliant they are on different types of signals. For example, whereas some seed dispersers (e.g., diurnal birds and some mammals) rely primarily on visual cues to locate fruits, others (e.g., ant and mammals) rely more on odors and flavors to locate and decide to consume fruits (Nelson and Whitehead 2021).

Conclusions

We met most of our goals for the session. We brought together ecologists that work on a diversity of empirical mutualistic systems. The session sparked discussion during and after about comparisons and contrasts across different systems. Finally, we debated the role of movement in different empirical systems. We generated a list of future research ideas but did not order them in terms of priorities. First is a broader understanding of direction and magnitude of feedbacks; determining when movement leads to strengthening versus weakening of mutualistic relationships, as well as determining when mutualism facilitates versus inhibits movement. For example, how much do the cleaning needs of clients actually shape their movement patterns? Second is a better understanding of how these feedbacks in turn scale up to affect overall organismal performance. Third is a better understanding of how movement fits in across the breadth of possible mutualistic interactions; determining the relative importance of movement as a benefit compared to other benefits of mutualism, and understanding how different forms of mutualism interact around movement. For example, when is it best to partner with a mutualist that provides a movement benefit versus a different benefit? We hope this session, and writeup, inspire ecologists to explore the rich ways that movement and mutualism can interact in their study systems and beyond.

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Author Contributions

C.M. Moore and A.K. Shaw should be considered co-first authors.

Data Availability

No data were collected for this study.

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