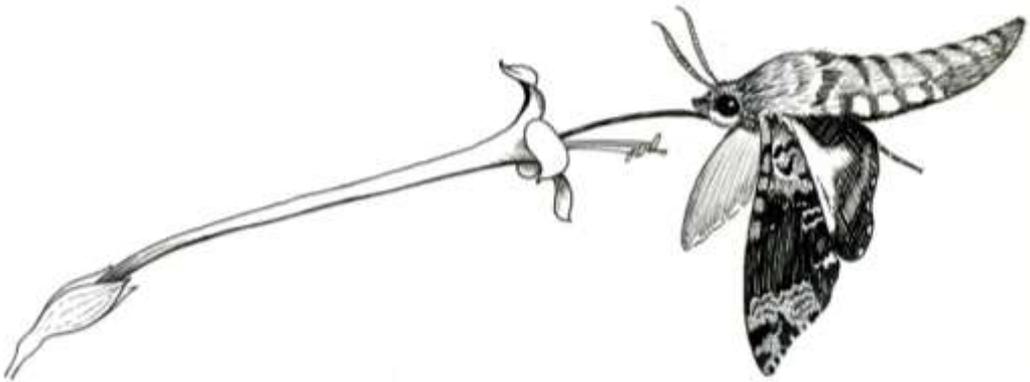


Mutualism

May 7-9, 2009, Harvard University



Coelonia fulvinotata pollinating *Combretum rotundifolium*
Drawing by Dino Martins

Conference organizers:

Naomi Pierce, Harvard University

Anne Pringle, Harvard University

Stuart Davies, Harvard University

Megan Frederickson, Harvard University

Ulf Dieckmann, International Institute for Applied Systems Analysis

Many thanks to:

The Plant Biology Initiative at Harvard, including Noel Michele Holbrook, Elena Kramer, Charles Davis, Jacques Dumais, David Haig, Andy Knoll, Sarah Mathews, Paul Moorcroft, and Don Pfister

The International Institute for Applied Systems Analysis, especially Ulf Dieckmann and Melanie Wenighofer

The European Science Foundation's TECT Programme, especially Ronald Noë, Doubravka Olsakova, and Claire Rustat-Flinton

Harvard University's Museum of Comparative Zoology, especially James Hanken

Harvard University's Center for the Environment, especially Daniel Schrag

The National Science Foundation

The OEB Administration, especially Rebecca Chetham, Margaret Caryannopoulos, Christopher Preheim, and Katie Parodi

The Irving House, especially Viviane Benchaya

Oliver Caplan, Jack Conlin, Mark Cornwall, Ron Cooper, Jeannette Fink, David Harris, Wendy Heywood, Daniel Kronauer, Jesselynn Opie, Mike Tomei, Majiec Zwieniecki, and all the members of the Pierce and Pringle Labs!



May 7

All talks in Northwest Science Building B103 (52 Oxford Street)

8:45-9:00am Welcome

(Moderator: Naomi Pierce)

9:00-9:45am **John Thompson:** “Phylogenetic and geographic divergence of coevolving interactions into small, mutualistic networks”

9:45-10:30am **Pat Willmer:** “Managing animal-plant mutualisms: volatiles and other tricks to keep ants out of flowers”

10:30-11:00am Break

(Moderator: Charles Davis)

11:00-11:45am **Florian P. Schiestl:** “Floral signals, pollinator behavior, and floral isolation in plants”

11:45am-12pm **Robert A. Raguso:** “Reconciling chemical and community ecological approaches to the study of pollination”

12:00-2:00pm Lunch

(Moderator: Anne Pringle)

2:00-2:45pm **Alan Gange:** “Interactions between insects and mycorrhizal fungi”

2:45-3:30pm **Jennifer Rudgers:** “Grass-endophyte symbiosis: community consequences and co-evolutionary dynamics”

3:30-4:00pm Break

(Moderator: Stuart Davies)

4:00-4:45pm **E. Toby Kiers:** “Sanctions, cooperation, and the evolutionary stability of plant-rhizosphere mutualisms”

4:45-5:30pm **Giles E. D. Oldroyd:** “Signaling mechanisms for plant endosymbioses”

6:30-8:30pm Reception and Dinner, Harvard Museum of Natural History, Romer Hall of Vertebrate Paleontology

May 8

Morning talks in Mallinckrodt Laboratory Pfizer Hall (12 Oxford Street)

(Moderator: Megan Frederickson)

8:30-9:15am **Judith L. Bronstein:** “Context-dependent outcomes in mutualism: ecological and evolutionary implications”

9:15-10:00am **Ronald Noë:** “Can the biological market concept serve as a general paradigm for cooperation and mutualism?”

10:00-10:30am Break

(Moderator: Jerry Green)

10:30-11:15am **Ulf Dieckmann:** “Runaway selection for cooperation and strict-and-severe punishment”

11:15am-12pm **Martin Nowak:** “Five mechanisms for the evolution of cooperation”

12:00-2:00pm Lunch (in Northwest Building)

Afternoon talks in Sherman Fairchild Biochemical Lab 102 (7 Divinity Avenue)

(Moderator: David Haig)

2:00-2:45pm **Carl Bergstrom:** “Dealing with deception”

2:45-3:30pm **Theodore Bergstrom:** “Games, golden rules and evolution”

3:30-4:00pm Break

(Moderator: Noel Michele Holbrook)

4:00-4:45pm **Claire de Mazancourt:** “Evolution of a trading mutualism from a competitive interaction”

4:45-5:30pm **Pedro Jordano:** “Complex networks of interactions and their consequences in diversified plant-animal mutualisms”

May 9

All talks in Northwest Science Building B103 (52 Oxford Street)

(Moderator: Douglas Yu)

- 9:00-9:15am **Jérôme Orivel:** “Ecology and maintenance of a novel tripartite mutualistic association”
- 9:15-9:30am **Mario X. Ruiz-González:** “Three eukaryotic kingdoms of life interacting in a novel and highly specialized mutualism”
- 9:30-9:45am **Elizabeth G. Pringle:** “Indirect effects of hemipterans on ant-defended plants”
- 9:45-10:00am **Dino Martins:** “Agriculture in an ant-plant?”
- 10:00-10:15am **Megan Frederickson:** “Partner-fidelity feedback in ant-plant mutualisms”
- 10:15-11:00am Break

(Moderator: Daniel Rubenstein)

- 11:00-11:15am **Ádám Kun:** “Cooperation, mutualism and space: differences and similarities”
- 11:15-11:30am **Gergely Boza:** “The evolution and stability of conditional mutualistic interactions: model and reality”
- 11:30-11:45am **Andras Szilagyi:** “Evolution of castration and the coexistence of ant-plant mutualists in a spatially explicit model”
- 12:00-2:00pm Lunch

(Moderator: Chris Baker)

- 2:00-2:15pm **Drew Fudenberg:** “The evolution of mutation rates”
- 2:15-2:30pm **Glen Weyl:** “The labor economics of mutualism”
- 2:30-2:45pm **David Rand:** “Winners don’t punish”
- 2:45-3:00pm **Marco Archetti:** “Mutualism as a contract: asymmetric information from economics to evolutionary biology”
- 3:00-3:15pm **Charles Nathanson:** “A formula for the evolution of cooperation in structured populations under weak selection”

(Moderator: David Hughes)

- 4:00-4:15pm **Santiago Ramírez:** “Diversification and specialization in the euglossine-orchid mutualism”
- 4:15-4:30pm **Joerg Barke:** “Antibiotic resistance problem in the leafcutter ant *Acromyrmex octospinosus*”
- 4:30-4:45pm **Luis Carvalho:** “Biogeographical variation of mycorrhizal effectiveness in an invasive *Acacia* species”
- 4:45-5:00pm **Naomi Pierce:** “Endosymbiotic bacteria facilitated the evolution of herbivory in ants”

May 7, 9:00-9:45am, Northwest Science Building B103

Phylogenetic and geographic divergence of coevolving interactions into small, mutualistic networks

John Thompson

Ecology & Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA

As plants and animals coevolve with each other, the ecological and evolutionary outcomes of their interactions may diversify as populations coadapt in different ways in different ecosystems. Mutualisms may evolve multiple times, resulting in coevolving lineages that include a complex mix of mutualists, commensals, and antagonists. Over time the geographic ranges of ancestral and derived species may secondarily overlap, such that pairwise interactions become trios, quartets, or quintets of locally interacting species. The geographic mosaic of coevolution between plants and prodoxid moths provides evidence for the repeated evolution of mutualism and the formation of small multispecific networks. These interactions include the obligate interactions between yuccas and yucca moths, the geographically variable mutualisms between saxifrages and *Greya* moths, and the antagonistic interactions between yet other plant taxa and other prodoxids. Recent ecological and molecular analyses are showing that these interactions are even more geographically structured and ecologically and evolutionarily dynamic than we previously suspected.

May 7, 9:45-10:30am, Northwest Science Building B103

Managing animal-plant mutualisms: volatiles and other tricks to keep ants out of flowers

Pat Willmer

School of Biology, University of St. Andrews, Fife, Scotland, UK

Ants show complex interactions with plants, both facultative and mutualistic; but they are rarely pollinators, and their visits to flowers (usually seeking nectar) may often be detrimental to plant fitness, damaging the flower and its attractiveness to other visitors, reducing pollen viability, or directly deterring incoming legitimate pollinators. Plants therefore have various strategies to control ant distributions, and restrict them to foliage rather than flowers. These may involve physical barriers on or around flowers, or ‘bribes’ sited on the foliage (usually extrafloral nectaries). Alternatively there may be volatile organic compounds (VOCs) acting as signals to control ant behavior, attracting them to leaves and/or deterring them from functional flowers. We originally demonstrated volatile floral repellence in myrmecophytic acacias, and can now show that the VOCs are derived from pollen and specifically and transiently deter ants during dehiscence. The effects are stronger in ant-guarded species and more effective on resident ants, both in African and Neotropical species. In acacias, repellence involves at least some volatiles that are known components of ant alarm pheromones, but are not repellent to bees and other beneficial flower visitors, so that the plants can effectively ‘manage’ their mutualists in space and time. Other examples of ant repellence in tropical and temperate flowers will be outlined; in particular, we have shown an apparent trade-off in ant-management strategies, between the use of defensive floral volatiles and the alternatives of physical barriers or distracting extrafloral nectary bribes.

May 7, 11:00-11:45am, Northwest Science Building B103

Floral signals, pollinator behavior, and floral isolation in plants

Florian P. Schiestl

Institute of Systematic Botany, University of Zürich, Zürich, Switzerland

Pollinator behavior strongly impacts on the strengths and mode of pollinator mediated reproductive isolation in plants. The diversity of pollination systems in plants incorporates a variety of different types of behavior by pollinators. An important distinction is whether pollinators' visits to flowers are motivated by mating or foraging behavior. Mating behavior is characterized by innate preferences for mating signals, mediated by neuronally hard wired behavioral responses. Sexually deceptive orchids imitate mating signals, typically volatile chemicals, and thus exploit male insects that pollinate flowers through attempted copulations. These plants are primarily isolated prezygotically through ethological pollinator isolation by producing species-specific mating signals. In the Australian genus *Chiloglottis*, single volatile compounds and dual blends thereof mediate species-specific pollinator attraction. In the European genus *Ophrys*, blends of multiple compounds in specific proportions are key for pollinator isolation. In pollination systems with food searching behavior, learning of floral signals is pronounced, as pollinators establish floral constancy in the case of rewarding flowers but quickly avoid non-rewarding deceptive flowers. Food deceptive flowers are characterized by high pollinator sharing, and reproductive isolation is primarily postzygotic. Floral constancy in rewarding flowers can be an important component of reproductive isolation. Even minor modifications in floral signals, such as quantitative differences in a single odor compound can mediate assortative pollinator visitation and thus contribute to reproductive isolation.

May 7, 11:45am-12:30pm, Northwest Science Building B103

Reconciling chemical and community ecological approaches to the study of pollination

Robert A. Raguso

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY

Although research on plant volatiles and pollination ecology has grown explosively over the past 15 years, there remains little dialogue between these fields. The specialization–generalization debate in pollination has cast doubt on the importance of sensory biology in mediating pollination at the community scale. However, chemical ‘filters’ of volatile or nectar-borne repellents may be as likely to explain the “forbidden” interactions in plant–pollinator networks as differences in morphology, phenology or microhabitat. In addition, the omission of volatiles from path analyses measuring the impacts of herbivores and pollinators on plant fitness may be one reason for large unexplained variance terms in such models. Floral scent functions in concert with visual and gustatory cues by attracting pollinators from a distance, increasing approaches and landings, and mediating outcrossing rates through changes in visitation frequency and duration. The available data reveal that chemical aspects of floral phenotypes are important across the specialization–generalization spectrum, and should be widely applicable to mainstream pollination ecology. I will explore ways to better integrate floral chemistry and pollinator behavior into pollination ecology, presenting vignettes from ongoing studies of edaphic races of western North American *Oenothera*, guilds of red flowered plants with fermented odors in eastern North American forests, and a clade of boreal mosses for whom fly-dispersal of spores is mediated by dramatic visual and olfactory signals produced by sporophytes.

May 7, 2:00-2:45pm, Northwest Science Building B103

Interactions between insects and mycorrhizal fungi

Alan Gange

*School of Biological Sciences, Royal Holloway, University of London,
Egham, Surrey, UK*

Arbuscular mycorrhizal fungi are ubiquitous in nature and associate with the roots of about 75% of all vascular plants. The mycorrhiza donates mineral nutrients to the plant in return for a supply of organic carbon. Both of these features mean that a mycorrhizal plant may represent a very different food source for an insect herbivore, compared with a non-mycorrhizal individual. Furthermore, as both insects and mycorrhizas extract carbon from their host, the potential exists for competition between them, thus the presence of one may compromise the performance of the other. Our knowledge of how mycorrhizas can affect phytophagous insects is restricted to relatively few species of fungi and insects, but I will give an outline of the interactions that have been found and will attempt to produce a synthesis of these patterns. I will address the mechanisms by which these interactions occur and will place the work in a multitrophic context by considering higher trophic levels as well. Finally, I will consider what avenues of research should be pursued, to further our understanding of these complex interactions. I will propose that future experiments should contain greater degrees of realism, by being more complex, and involving other organisms too.

May 7, 2:45-3:30pm, Northwest Science Building B103

Grass-endophyte symbiosis: community consequences and co-evolutionary dynamics

Jennifer Rudgers

*Department of Ecology and Evolutionary Biology, Rice University,
Houston, TX*

Plants harbor a diverse assemblage of microbial symbionts, including bacteria and fungi in leaves and roots. The ecological consequences of many of these microbes remain unknown, particularly in natural ecosystems. In grasses, fungal endophytes have been well studied in a few grass host species due to their economic and environmental impacts in forage and turf production. These endophytes can protect hosts from damage by vertebrate and invertebrate herbivores, improve tolerance to drought, and enhance nutrient uptake. Despite their small contribution to community biomass, endophytes can also have wide-ranging effects on community structure and ecosystem function, by reducing plant diversity, suppressing arthropod abundance, altering rates of decomposition, and slowing the process of succession. In addition to their impacts on community dynamics, grass-endophyte symbioses provide tractable models for investigating the evolution of symbiosis and the context-dependency of mutualism. Phylogenetic analyses show broad co-cladogenesis between grasses and endophytes and suggest a long co-evolutionary history. Costs and benefits of symbiosis can depend on both intrinsic characteristics (including the mode of endophyte transmission, rate of transmission, and partner density) and factors extrinsic to the symbiosis, such as the abundance and composition of herbivores as well as abiotic conditions (drought, resource availability). Elucidating the relative importance of these intrinsic and extrinsic factors can inform our understanding of the dynamics of mutualisms and reveal how symbionts become fixed, or lost, from host populations through time.

May 8, 8:30-9:15am, Mallinckrodt Laboratory Pfizer Hall

Context-dependent outcomes in mutualism: ecological and evolutionary implications

Judith L. Bronstein

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ

One of the few features that virtually all mutualisms share, regardless of their natural history details, is that their outcomes are context-dependent (conditional). That is, under different ecological conditions both the benefits and costs of mutualisms, and indeed whether net effects are mutualistic at all, are highly variable in both space and time. Detailed examples of context-dependency are documented with increasing regularity. Yet, we have almost no conceptual or theoretical context in which to consider the implications of context-dependency; examples have largely been dealt with on a case-by-case basis. I will describe two ongoing studies from my lab to illustrate how the presence of third species can affect not only the ecological but the evolutionary dynamics of mutualism. I will then attempt to grope towards a conceptual foundation that might allow us to move forward in the future towards a unifying set of principles and testable hypotheses.

May 8, 9:15-10:00am, Mallinckrodt Laboratory Pfizer Hall

Can the biological market concept serve as a general paradigm for cooperation and mutualism?

Ronald Noë

Ethologie des Primates (CNRS & Université de Strasbourg), Strasbourg, France

Humans or animals trading goods and services have to take three crucial steps: (1) choose a partner, (2) determine how much needs to be invested in order to obtain the desired commodity and (3) prevent being short-changed by the chosen partner. Over the past decades cooperation research has concentrated on the question of partner control (step 3) rather than on the relative values of goods and services exchanged. The biological market paradigm on the other hand focuses on the link between steps (1) and (2) and predicts that the law of supply and demand affects the exchange rates in non-human ‘trading’ in a similar fashion as in human economic exchanges. Step 1, partner choice, is considered to be the pivotal mechanism that makes markets turn. It not only forms the link between supply and demand ratios and exchange rates, but also drives the evolution of certain traits that are preferred by the choosing agents in much the same way partner choice drives the evolution of secondary sexual characters under sexual selection. Several empirical examples of both phenomena, supply-demand dynamics and market selection, have been published till date in systems ranging from nutrient exchange mutualisms between plants and bacteria or fungi, protection mutualisms between ants and other insects or plants, cleaning interactions in fish, helper systems in mongoose, grooming exchanges in primates, mating markets in birds and humans and so forth. This wide variety of different markets has much in common, but there are of course many differences too, especially in the mechanisms involved. A notable dichotomy exists between systems in which cognitive mechanisms play a role, such as the primate grooming markets, and systems in which strategies are largely hard-wired, such as the nutrient exchange mutualisms. Not only are the mechanisms very different, but the scientific cultures of those working with these systems are too. I think that it is worth the effort trying to keep the research as well as the literature connected. I will use examples of intra-specific cooperation in primates and other vertebrates to point out common denominators with examples taken from the inter-specific mutualism literature.

May 8, 10:30-11:15am, Mallinckrodt Laboratory Pfizer Hall

Runaway selection for cooperation and strict-and-severe punishment

Ulf Dieckmann

Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria

Co-author: Mayuko Nakamaru¹

1. Department of Value and Decision Science, Tokyo Institute of Technology, Tokyo, Japan

Punishing defectors is an important means of stabilizing cooperation. When levels of cooperation and punishment are continuous, individuals must employ suitable social standards for defining defectors and for determining punishment levels. Here we investigate the evolution of a social reaction norm, or psychological response function, for determining the punishment level meted out by individuals in dependence on the cooperation level exhibited by their neighbors in a lattice-structured population. We find that (1) cooperation and punishment can undergo runaway selection, with evolution towards enhanced cooperation and an ever more demanding punishment reaction norm mutually reinforcing each other; (2) this mechanism works best when punishment is strict, so that ambiguities in defining defectors are small; (3) when the strictness of punishment can adapt jointly with the threshold and severity of punishment, evolution favors the strict-and-severe punishment of individuals who offer slightly less than average cooperation levels; (4) strict-and-severe punishment naturally evolves and leads to much enhanced cooperation when cooperation without punishment would be weak and neither cooperation nor punishment are too costly; and (5) such evolutionary dynamics enable the bootstrapping of cooperation and punishment, through which defectors who never punish gradually and steadily evolve into cooperators who punish those they define as defectors.

May 8, 11:15am-12:00pm, Mallinckrodt Laboratory Pfizer Hall

Five mechanisms for the evolution of cooperation

Martin Nowak

Program for Evolutionary Dynamics, Harvard University, Cambridge, MA

Cooperation is needed for evolution to construct new levels of organization. Genomes, cells, multicellular organisms, social insects, and human society are all based on cooperation. Cooperation means that selfish replicators forgo some of their reproductive potential to help one another. But natural selection implies competition and therefore opposes cooperation unless a specific mechanism is at work. I will discuss five mechanisms for the evolution of cooperation: kin selection, direct reciprocity, indirect reciprocity, network reciprocity, and group selection. For each mechanism, a simple rule is derived that specifies whether natural selection can lead to cooperation.

May 8, 2:00-2:45pm, Sherman Fairchild Biochemical Lab 102

Dealing with deception

Carl Bergstrom

Department of Biology, University of Washington, Seattle, WA

Social function and organization are predicated on effective coordination and cooperation; these in turn require honest communication among the participants in a social group. But in order to facilitate any sort of social structure and interaction, there has to be some way to deal with the threat of deception. We see this not only at the level of complex animal societies such as baboon troops or cooperatively nesting birds or social insects, but also in the complex social organization within the body of any single multicellular organism. The problem of avoiding deception to allow social organization can be broken down into at least two categories: 1) the legitimate members of the social institution have some overlap in interests, but they also have individual incentives for deception, and 2) non-members of the social organization attempt to parasitize and exploit the system by subversion and other forms of trickery. We see the former category in the evolution of mate-choice signals; we see the latter in the evolution of immune strategies to deal with pathogens. I will discuss the problem of deception in biological systems, and outline some of the strategies that organisms use to deal with it.

May 8, 2:45-3:30pm, Sherman Fairchild Biochemical Lab 102

Games, golden rules and evolution

Theodore Bergstrom

*Department of Economics, University of California, Santa Barbara,
Santa Barbara, CA*

Two alternative “golden rules” appear in the writings of many philosophers and religious teachers. One of these rules exhorts people to “Love thy neighbor as thyself.” The other prescribes “Do unto others as you would have them do unto you.” Though these rules seem similar, it is not difficult to construct game situations in which they recommend different courses of action. William Hamilton’s theory of kin-selection theory suggests that humans and other animals would evolve a willingness to make personal sacrifice for the benefit of their close relatives. Hamilton’s theory can be paraphrased as animals evolve to love their siblings *half as well* as them selves. Hamilton’s *inclusive fitness* rule is supported by a plausible genetic model for sexual diploids if the game played between relatives is of a rather special form. For general symmetric games, Hamilton’s inclusive fitness rule should be replaced by the *semi-Kantian* maxim “treat your sibling as if the probability that your sibling will mimic you is one-half.” In asymmetric games, it can be shown that depending on the linkage structure of genes that control contingent strategies, evolutionary dynamics may support either inclusive fitness or the semi-Kantian behavior between siblings.

May 8, 4:00-4:45pm, Sherman Fairchild Biochemical Lab 102

Evolution of a trading mutualism from a competitive interaction

Claire de Mazancourt

Redpath Museum, McGill University, Montreal, Canada

Using a theoretical model, I will show how a trading relationship might arise from resource competition for two resources. I will show that individual-level and population-level consequences of trading are decoupled, so that under many conditions, individuals gain an individualistic benefit from trading at the expense of their population size. I will discuss the implications in terms of our understanding of mutualism.

May 8, 4:45-5:30pm, Sherman Fairchild Biochemical Lab 102

Complex networks of interactions and their consequences in diversified plant-animal mutualisms

Pedro Jordano

Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Sevilla, Spain

The mutualistic interactions between plants and the animals that pollinate them or disperse their fruits have molded the organization of Earth's biodiversity. Pollen and seed movement are the primary outcomes these interactions, yet we know very little of how these highly complex webs of mutualistic interactions coevolve and what are the consequences of these diversified mutualisms. Recently, it has been shown that these interactions can form complex networks involving dozens and even hundreds of species. These coevolutionary networks are highly heterogeneous, nested, and asymmetric. I explore how the past evolutionary history conveyed in the phylogenies of plants and animals can explain these network patterns and the robustness of the network to species extinctions. Because phylogenetically similar species tend to play similar roles in the network, extinction events trigger non-random coextinction cascades. This implies that taxonomic diversity is lost faster than expected if there was no relationship between phylogeny and network structure. Zooming in the interaction pattern itself, I use two examples of plant-frugivore interactions to show how the overall interaction pattern depicted in the network is more influenced by the plant phylogeny, suggesting that the plant assemblage drives the interaction. Plant-frugivore coevolution is suggested to be a process of resource tracking by frugivores so that each plant species 'filters out' subsets of frugivore species given species-specific traits that constrain their interaction through trait matching and trait convergence. The overall network of interaction thus has a distinct signal marked by the plants phylogenetic history. These results illustrate how the simultaneous consideration of phylogenetic information and network structure can aid in the conservation of biodiversity. Finally, I explore two further examples of considering networks of plant-animal mutualisms: mating networks in plant populations mediated by insect pollinators, and connectivity networks among fragmented populations linked by long-distance dispersal events mediated by animal frugivores. Taken together, these uses of network thinking applied to plant-animal mutualisms are helping us to understand the complex patterns of interactions involved in their evolution.

May 9, 9:00-9:15am, Northwest Science Building B103

Ecology and maintenance of a novel tripartite mutualistic association

Jérôme Orivel

*Laboratoire Evolution et Diversité Biologique, UMR-CNRS 5174,
Université Paul Sabatier, Toulouse, France*

Inter-specific, mutualistic interactions involving ants are widespread in tropical ecosystems and they play a key role in shaping biodiversity. In protective mutualisms between ants and plants, the host-plants provide ants with nesting space and sometimes food rewards, in exchange for protection against enemies. Most studies on these systems have concentrated on bipartite associations and only a few systems involving obligate and highly specific mutualistic relationships among more than two species have received attention. We focused here on a novel tripartite and mutualistic association involving the ant-plant *Hirtella physophora*, its specific associated ant *Allomerus decemarticulatus* and a fungus manipulated by these ants. From the plant side, the morpho-anatomical structure of the leaf domatia differed considerably from the lamina and these specialized structures are colonized by ants very early in the plant ontogeny once the first domatia are formed. As in any protective ant-plant interaction, *A. decemarticulatus* provide anti-herbivore defenses to their host and thus favor its vegetative growth. They have however a negative effect on the reproductive success of their host, most probably in answer to the space limitation affecting colony size and reproduction. Nevertheless, the impact of such conflict of interests needs to be reinterpreted in the light of the presence of a third, specific and obligate partner – a *Trimmatostroma* fungus. The exploration of its potential roles in the interaction demonstrated that this third partner could have a crucial role in the maintenance of this association. Moreover, such results lead us to believe that the beneficial outcomes of this tripartite interaction could be more nutritional than protective.

May 9, 9:15-9:30am, Northwest Science Building B103

Three eukaryotic kingdoms of life interacting in a novel and highly specialized mutualism

Mario X. Ruiz-González

Laboratoire Evolution et Diversité Biologique, UMR-CNRS 5174, Université Paul Sabatier, Toulouse, France

Co-authors: Céline Leroy¹, Hervé Gryta², Patricia Jargeat², Alain Dejean¹, Jérôme Orivel²

1. Ecofog, Ecologie des Forêts de Guyane, UMR-CNRS 8172, Université des Antilles et de la Guyane (UAG) Campus Agronomique, Kourou, France

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Mutualistic interactions between ants and plants or fungus led to the evolution of complex symbioses and evolutionary innovations such as agriculture. However, only few systems involving mutualistic relationships among more than two species have been studied. We have focused on a system involving partners from three different eukaryotic kingdoms of life: the myrmecophytic plant *Hirtella physophora*, the ant species *Allomerus decemarticulatus* and a fungus which is manipulated by the ants. The ants build up a robust trap strengthened by the mycelium of the fungus along the stems of the host plants to capture prey. In fact, building traps on its host plants seems to be a generalized behavior across the different ant species from the genus *Allomerus*. Here we provide some insight onto this complex system. First, we explore the ants' use or exploitation of the fungus to build the trap. Second, we focus on the isolation and biology of the fungus, as well as on its molecular characterization and phylogenetic position. Third, we explore other potential roles of the fungus in its interaction with the plant. Finally, we extend our study to a second ant species, *A. octoarticulatus*, and we find that they are manipulating the same fungus present in *A. decemarticulatus* traps, suggesting an old origin for the ant-fungus association. The study of the population genetic structure of the fungi in the traps of different ant populations in French Guiana both spatially and in terms of transmission mode by the ants will provide stronger evidence for this long term association. Our results point to an extreme evolutionary output in the field of interactions among different species.

May 9, 9:30-9:45am, Northwest Science Building B103

Indirect effects of hemipterans on ant-defended plants

Elizabeth G. Pringle

Department of Biology, Stanford University, Stanford, CA

Co-authors: Deborah M. Gordon¹, Rodolfo Dirzo¹

1. Department of Biology, Stanford University, Stanford, CA

Symbiotic mutualisms between ants and plants, in which plants provide ant colony space and ants defend against leaf-eating herbivores, are frequently associated with hemipteran phloem-sucking insects. Hemipterans are antagonists of the plant, but symbiotic ants tend to defend hemipterans, consuming their honeydew waste. If ants utilize honeydew as a primary food source, do hemipterans have indirect, positive effects on plants, mediated by symbiotic ants? We studied the interactions among a common Neotropical tree, *Cordia alliodora*, its symbiotic ants, *Azteca pittieri*, and several species of hemipterans at two sites in seasonally dry tropical forest in Middle America. We asked whether larger ant colonies defend tree leaves more effectively against herbivory, whether ant colony sizes appear to be food- or space-limited, and whether well fed ants are more active or aggressive defenders. We found that larger colonies of *A. pittieri* ants do defend *C. alliodora* leaves more effectively against herbivory, although the strength of this effect depends on both site and season. *A. pittieri* ant colonies may be food-limited, and better fed ants are more aggressive defenders. We conclude that hemipterans may provide important, indirect benefits to plants that rely on ant defenders.

May 9, 9:45-10:00am, Northwest Science Building B103

Agriculture in an ant-plant?

Dino Martins

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA

Symbioses take many complex and intricate forms. Among the more intriguing of these is the cultivation of fungi by ants. The ants involved digest plant matter using the fungus, accessing a rich source of energy that would otherwise be difficult to exploit. Studies of ant-agriculture to date have been limited to one Neotropical clade of ants: the Attines. We have found evidence for fungal gardening by ants in an African ant-plant mutualism between *Acacia drepanolobium* and *Tetraponera* ants. The existence of fungal agriculture in an African ant as part of a partnership in a well-established mutualism is interesting example of both convergence in fungal-gardening symbioses and an independent evolution of agriculture. These ant-plant-fungal tripartite symbioses may more common than previously thought.

May 9, 10:00-10:15am, Northwest Science Building B103

Partner-fidelity feedback in ant-plant mutualisms

Megan E. Frederickson

Society of Fellows, Harvard University, Cambridge, MA

Partner-fidelity feedback is one mechanism that can promote the evolutionary stability of mutualism. Partner-fidelity feedback occurs when the benefits provided by individual *A* to individual *B* feed back over time to individual *A*, in effect linking the fitnesses of *A* and *B*. Symbiotic interactions between ants and plants are classic examples of mutualism and good candidates for partner fidelity feedback. I will give several examples of how the benefits that an ant colony provides to its plant(s) feed back to the ant colony and *vice versa*. In such systems, natural selection favors mutualism and not cheating because an individual (or colony) that fails to cooperate reduces its own fitness. Partner-fidelity feedback is strongest when it operates across generations, as in vertically transmitted mutualisms. However, in ant-plant mutualisms, horizontal transmission gives rise to a conflict of interest between partners over reproduction. I will conclude by giving one example of how such a conflict of interest can lead to the breakdown of cooperation.

May 9, 11:00-11:15am, Northwest Science Building B103

Cooperation, mutualism and space: differences and similarities

Ádám Kun

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There is a vast theoretical literature on the factors promoting cooperation within a species. One such factor is space or population structure. Here, individuals do not interact randomly, but may restrict interactions to their neighbors in physical space or on a social network. It has been shown that in such setting cooperators can spread and persist if the temptation to defect is not too large. The reason is that spatial settings cause defectors to suffer from their own deeds, by making cooperation less attractive in their local environment, so defectors will end up mostly interacting with other defectors, which drastically reduces the advantages of defection. Here individuals interact and compete with the same set of individuals, which is true generally in intraspecific cooperation. However in interspecific cooperation, i.e. mutualism, the competition between interacting individuals is at most limited, and in some well studied cases there is no competition as the species occupy different niches (e.g. pollinating insects and plants, nutritional symbioses, ant-plant mutualisms, etc.). Thus positive fitness differences due to interaction with another species translates to spread among conspecifics. While space is suggested to be able to maintain mutualistic interactions, the underlying mechanism might be different compared to intraspecific cooperation. Could we apply our knowledge gained from modeling intraspecific cooperation to that of mutualism?

May 9, 11:15-11:30am, Northwest Science Building B103

The evolution and stability of conditional mutualistic interactions: model and reality

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For many years scientists tried to understand the role of different factors that facilitate the evolution and long term stability of different types of interspecies and intraspecies cooperation. However there are still questions to be answered. One type of mutualistic interaction is where partners can make adjusted continuous investments, which can be adequately described by the Continuous Prisoner's Dilemma Game. Previous studies suggested that population structure or spatial confinement is the only factor that can maintain mutualism in such a system. A reanalysis of the system shows that while the only evolutionary fix point of the system is mutual defection we were able to find parameter regions where higher payoffs were detected even in a well mixed case. We found that there is no stable mutualism in the system, but a permanent, unstable fluctuation between different levels of mutualism and exploitation (parasitism). We conclude that factors, including space, high mutation rate, or environmental heterogeneity that promote the polymorphism of the population, increase the average payoff that can be gained in the system. Experimental observation shows that interspecies interactions can move along the mutualism-antagonism continuum, and mutualism may be inherently unstable. Our model provides a novel explanation for these observations.

May 9, 11:30-11:45am, Northwest Science Building B103

Evolution of castration and the coexistence of ant-plant mutualists in a spatially explicit model

Andras Szilagyi

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Motivated by the *Allomerus-Azteca-Cordia* ant plant system we investigated a spatially-structured model for the evolution of ant dispersal and castration behavior. One of the ant species can castrate plants and thereby increase its own fecundity, while the other ant species has superior dispersal abilities. Despite the existence of cheating behavior and interspecific competition, we demonstrated that the host plant and the two ant species can all coexist in this explicitly spatial model. We measured the evolved castration level and relative densities of ants at evolutionary equilibrium as a function of plant density, and the results are consistent with field data.

May 9, 2:00-2:15pm, Northwest Science Building B103

The evolution of mutation rates

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May 9, 2:15-2:30pm, Northwest Science Building B103

The labor economics of mutualism

Glen Weyl

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Mutualism closely resembles an employment relationship. Mutualists, like workers, provide services in exchange for compensation. We are therefore investigating how the economic theory of labor markets can be used to understand, explain and eventually quantitatively predict patterns of mutualistic interactions. In particular our research focuses on two classic topics: the interaction of supply, demand and market structure in determining wages and the optimal provision of incentives when workers cannot be perfectly monitored.

May 9, 2:30-2:45pm, Northwest Science Building B103

Winners don't punish

David Rand

Program for Evolutionary Dynamics, Harvard University, Cambridge, MA

I will present an experimental study of the role of costly punishment in the repeated Prisoner's Dilemma (the standard paradigm for repeated cooperation games). Each round subjects can either cooperate (pay a cost to help their partner), defect (steal from their partner), or punish (pay a cost to make their partner lose points). We find that those who punish defectors do worst, while those who reciprocate defection with defection do best. Punishment does not serve to end conflicts, but rather to escalate them. I will also show results from an evolutionary model which shows that natural selection disfavors punishment in such situations. Thus, I conclude that as long as there are other options for reciprocity, punishment is not beneficial, and such repeated cooperation settings do not explain the evolution of cooperation.

May 9, 2:45-3:00pm, Northwest Science Building B103

Mutualism as a contract: asymmetric information from microeconomics to evolutionary biology

Marco Archetti

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Cooperation in nature is usually explained by reciprocation, reputation effects or punishment, which require repeated interactions. Many mutualistic interactions, however, are one-shot games, in which individuals have only one chance to cooperate or defect. I use contract theory from microeconomics to show two ways in which cooperation can be maintained without iterations in different cases of symbiosis. First, how is it possible to establish an interaction only with cooperative individuals when it is not possible to distinguish them from cheaters? I show that in a bilateral relationship in which one individual contracts another to carry out an action, imposing a deliberate cost for establishing the interaction can stabilize mutualism without iterations if entering the interaction is too costly for cheaters. Like in optimal contract theory, setting the right costs and rewards of the interaction may lead the possible partners to screen themselves according to their own interest. The case of bioluminescent bacteria and squids, one of the most well known examples of symbiosis, provides a clear and elegant example of this model. Second, when an interaction is already established, how is it possible to avoid defection by the partner if monitoring and punishment are not possible? Even if an individual cannot monitor the effort offered by the partner, he can offer different rewards according to the outcome of the effort. By making the reward conditional on the outcome of the effort, an individual can give an incentive to the partner to cooperate even in the absence of iterations. The symbiosis between legumes and rhizobia provides a clear example of this system. A similar system is also likely in the symbiosis between ants and acacia and can explain why mutualism collapses when herbivory is eliminated.

May 9, 3:00-3:15pm, Northwest Science Building B103

A formula for the evolution of cooperation in structured populations under weak selection

Charles Nathanson

Harvard University, Cambridge, MA

Recent research has shown that in an evolutionary framework, cooperation is favored over defection in the prisoner's dilemma on a variety of population structures when selection pressures are weak. Examples of these structures include graphs, islands, and linear lattices. This paper unifies these results with a formula. Given a general population structure and an updating algorithm, the formula computes the minimum "benefit-to-cost ratio" needed for cooperators to outnumber defectors in population dynamics. This formula suggests "clustering" of agents of the same type as the driving force behind the success of the cooperative strategy on the structures that have been explored in the literature.

May 9, 4:00-4:15pm, Northwest Science Building B103

Diversification and specialization in the euglossine-orchid mutualism

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Males of euglossine orchid bees (Hymenoptera: Apidae) actively collect chemical fragrances from orchid flowers, store them in specialized hind leg pockets, and subsequently present them to females during courtship. Male bees act as the exclusive pollinators of ~700 orchid species by vectoring their pollinaria (small packages containing all of the flowers' pollen grains). Orchids partition bee pollinators by attaching pollinaria to different parts of their bodies, a feature that enables reproductive isolation without pollinator shifts. Although euglossine-pollinated orchids depend on male bees for pollination, populations of euglossines can thrive in the absence of their customary orchid hosts. I reconstructed the evolutionary history of this association by building a molecular phylogeny of euglossine bees and their orchid hosts (DNA was sequenced directly from pollinaria attached to male bees collected in the field). In particular, I (1) test the prediction that orchid lineages tracked the evolutionary trajectories of their pollinating bees, (2) determine whether shifts in the diversification rates—observable via molecular phylogenies—of orchids coincide with shifts in the diversification rates of bee lineages, (3) reconstruct the evolutionary transitions of pollinaria placement, and (4) describe the architecture of bee-orchid affiliation networks to explore the evolutionary patterns of host specialization. The phylogenetic and fossil-calibrated molecular clock analyses suggest that extant euglossine lineages share a single most recent common ancestor during the Oligocene-Miocene period, ~27-42 million years ago (Mya). Conversely, lineages of euglossine-pollinated orchids originated at least three times independently, but radiated synchronously with their bee pollinators during the Miocene, ~20-35 Mya. I found evidence for (i) overlapping shifts in the diversification rates of bee and orchid lineages, (ii) rapid changes in the placement of orchid pollinaria, and (iii) local (geographical) host specialization in some orchid lineages. These results support the hypothesis that euglossine bees served as a template for orchid diversification.

May 9, 4:15-4:30pm, Northwest Science Building B103

Antibiotic resistance problem in the leafcutter ant *Acromyrmex octospinosus*

Joerg Barke

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Fungus cultivation in ants evolved around 50 million years ago, leading to a present diversity of more than 210 attine ant species. The leaf-cutter ant *Acromyrmex octospinosus* feeds its cultivar (a Basidiomycete) with fresh leaf material. One common and very dangerous nest parasite is the fungus *Escovopsis* (Ascomycete). It is a contact necrotroph and feeds on the fungal cultivar. Various control mechanisms have been described, potentially preventing exploitation by *Escovopsis*. One such mechanism is related to antimycotic compounds produced by actinomycete bacteria. These bacteria occur on the ants' bodies, their infrabuccal pockets (mouthpart) and the fungal garden. *Escovopsis* is horizontally transmitted between ant colonies. The fungal cultivar is thus expected to be attacked by a variety of parasite strains, some of which might be resistant to the antifungals of the actinomycetes. Furthermore, the effectiveness of the actinomycetes might be affected by black yeast, which is another parasite of the ant mutualism. How can the ants and their mutualistic partners deal with diverse *Escovopsis* parasites, having access to merely a limited number of antibiotics? Recent evidence suggests that not one type of bacteria, namely *Pseudonocardia*, but a variety of actinomycetes, including *Pseudonocardia* and *Streptomyces*, provide antifungals against *Escovopsis*. The only antibiotic identified so far is the well-known polyene antifungal candicidin, produced by a nest associated *Streptomyces* strain. In this study, the antifungals of various *A. octospinosus*- associated actinomycetes have been investigated. Initial evidence seems to indicate that besides candicidin (an)other antifungal(s) is/are produced by the isolated bacteria.

May 9, 4:30-4:45pm, Northwest Science Building B103

Biogeographical variation of mycorrhizal effectiveness in an invasive *Acacia* species

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Mycorrhiza is a widespread symbiotic association between roots and certain soil fungi. Although generally regarded as a mutualistic association, variability in host plant growth response to different mycorrhizal fungi has been found within ecosystems ranging from positive to neutral and even to negative, and there is evidence suggesting local adaptation in some host-symbiont interactions. Therefore, geographical variation in mycorrhizal effectiveness may be expected to exist with potential ecological and coevolutionary implications. However, very little is known about biogeographical variation in mycorrhizal mutualisms. An inter-continental biogeographical approach was taken to test the influence of the origin of arbuscular mycorrhizal fungi on seedling growth of the highly invasive plant species, *Acacia longifolia*. Mycorrhizal fungal inoculum associated with *Acacia longifolia* from native sites in Australia and introduced sites in Portugal, South Africa and the US were compared to assess differences in mycorrhizal effectiveness in the growth of *Acacia longifolia* seedlings. Native (Australia) and introduced (Portugal) populations of *Acacia longifolia* were used. The results showed that symbiotic effectiveness in plant growth varied with the origin of mycorrhizal fungal inoculum (ranging from negative to positive) with *Acacia longifolia* experiencing generally higher benefits from mycorrhizal fungi of the introduced sites.

May 9, 4:45-5:00pm, Northwest Science Building B103

Endosymbiotic bacteria facilitated the evolution of herbivory in ants

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Ants are a dominant feature of terrestrial ecosystems, and yet we know relatively little about the evolution of their varied life histories. Recent measures of stable isotopes have helped to elucidate these mysteries, showing that ants range from herbivorous to predaceous, with “herbivores” feeding primarily on nitrogen-poor exudates from plants and sap-feeding insects. Bacteria have been observed in the guts of some herbivorous ant species, leading to the hypothesis that microbes play beneficial nutritional roles for their ant hosts. In a survey of 283 species from 18 of the 21 ant subfamilies, we have uncovered a wealth of specialized bacterial gut symbionts. Herbivorous ants from the tribe Cephalotini (turtle ants) commonly harbor gut symbionts from ant-specific clades within the orders *Burkholderiales*, *Pseudomonadales*, *Rhizobiales*, *Verrucomicrobiales*, and *Xanthomonadales*. Related microbes from the *Rhizobiales* are also distributed beyond the Cephalotini, showing a significant pattern of association with unrelated, herbivorous ants. We infer that *Rhizobiales* symbionts have independently evolved associations with herbivorous ants on at least five occasions, and a comparative analysis provides robust support for correlated evolution between *Rhizobiales* association and herbivory in ants. We therefore propose that symbiotic bacteria have facilitated the convergent evolution of herbivory across this ecologically dominant insect family.