Tiny ecosystem engineers: **diversity and evolution of gall midges**

Dr. Netta Dorchin

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Dr. Netta Dorchin is the chief curator of entomology of the Steinhardt Museum of Natural History at Tel Aviv University. As biosystematist, her research has been focused on the diversity and evolution of gall-inducing insects.

Could you describe your academic background and tell the readers what initially sparked your interest in studying gall-inducing insects?

I completed my BSc in biology, MSc in ecology and environmental studies, and PhD in zoology, all in Tel Aviv University. I have always been drawn to organismal biology and it was clear to me that I want to study animals and plants rather than work in the fields of cellular or molecular biology. The opportunity to conduct fieldwork rather than being restricted to the laboratory has always appealed to me, and as an undergraduate I took every course I could which included field excursions. Because my father is a beetle collector and taxonomist, I became familiar with insects already as a child. The facts that most creatures on earth are insects and that so many of them are still unknown and misunderstood has made them even more interesting to me. Wanting to combine my interests in entomology and botany, I chose to work on gall-inducing insects, which exhibit the most intimate and complicated of insect-plant interactions.

Why are these organisms good models for addressing questions in evolutionary biology?

Phytophagous insects are extremely numerous and diverse, and it has been shown that the rate of speciation among such insects is higher than in sister lineages which are not phytophagous. One level of this diversity is manifested by the different degrees of specialization found among plant-feeding insects, and this diversity can serve to investigate the role of host-specialization in the formation of new species. Gall-inducing insects are usually very host specific because they live inside the plant tissues and must develop adaptations that enable them to use the plant resources and overcome its defence mechanisms. Evolutionary shifts in host preferences among such insects require the development of adaptations to the new hosts and may thus lead to the formation of new species.

Cascading speciation is a relatively new subject, and studies addressing this process are scarce. Could you tell us the importance of understanding how prevalent this phenomenon is in a variety of organisms?

To assess whether cascading speciation is an important promoter of biodiversity, it is crucial to know how prevalent it is in different taxa and ecological systems, and why it occurs in some cases but not in others. If, for example, it will be found that external parasitoids are more prone to cascading speciation than internal parasitoids, or that predators are less prone to experience this process than parasitoids, we could start to make generalizations about what life-history attributes make speciation more likely.

What main ecological features do you expect to promote gall-midge diversification?

The ability to adapt to a new host-plant or to a different plant part on the same plant species must be a major driving force toward speciation in gall midges, and in phytophagous species in general. Shifts in activity times can also lead to diversification because they create temporal barriers between populations. To allow for diversification, a gall midge species should have adapted to exploit the tissues of a specific host plant, and its phenology should be synchronized with that of the plant. But at the same time it cannot be so specific that it cannot make the shift to new plants or new activity times. In other words, it should be specific, but not too specific.

We are living in a period of great biodiversity loss. Could you tell the readers about the importance of your research in this context?

To understand ecosystems and the role of their components, we must first know what these components are. If we don't know what species exist in a certain area and what they do there, we cannot make educated decisions about conservation programs and prioritize conservation efforts. For example, if we are familiar with the diversity and life history of natural enemies that attack certain agricultural pests, we can use chemical pesticides in a way that would minimize the negative impact on these natural enemies. If we need to decide which out of several areas should be declared as a natural reserve, we need to know what organisms are found in those areas, how common or rare they are, and what function they have in the ecological system. This is the type of information that taxonomists can offer to conservation biologists, ecologists and agriculturists.

Patterns and processes of diversification in gall-inducing insects

Gall midges are specialized herbivores that comprise a diverse and ecologically important group of insects. Diversification in these organisms may occur through shifts to new host plants. Here Dr. Dorchin discusses how her research has improved the understanding of this phenomenon.

ECOLOGY AND EVOLUTION OF GALL MIDGES

Evolution is change in heritable characteristics of natural populations over time. Several evolutionary mechanisms like natural selection and random genetic change are responsible for the vast biological diversification we see in nature. An intriguing topic in evolutionary biology is how and why species diverge in time and space resulting in the formation of new species. Dr. Netta Dorchin has been dedicating her career to this topic, seeking to describe the patterns of diversification in gall midges generated by thousands and millions of years of evolution and to understand what factors have led to such diversity. But why gall midges?

Flies comprise one of the most diverse and studied groups of insects. A particular group of phytophagous flies, the cecidomyiids or gall midges, induce galls in their host-plant tissues as part of their life cycle. Plant galls are abnormal outgrowths in vegetal tissues that may serve as both habitat and food source to the insect. Despite their great diversity of over 6000 species, knowledge on the diversity and biology of cecidomyiids is still lacking, especially in the Afrotropical and the Neotropical regions. To explain the reasons for this knowledge gap, Dr. Dorchin argues: "While many fly species are pests or disease vectors and therefore receive a lot of attention, the overwhelming majority of species are tiny, inconspicuous creatures with neither positive nor negative impact on man. Gall midges are tiny, fragile flies that are also short lived, and as such, do not appeal to many taxonomists". Their ecological importance is unquestionable though. By inducing gall formation, gall midges create new micro-environmental conditions that represent potential niches which can be exploited by other organisms. For this reason, gall-inducers may be considered ecosystem engineers or niche constructors.

DESCRIBING AND NAMING BIODIVERSITY

Biodiversity is being lost at unprecedented rates and many species will become extinct before they are described. For most groups of living organisms, researchers are still far from understanding how many species compose the ecosystems on both global and regional scales. This limitation makes taxonomy a priority field of study. In taxonomic studies, species are named and components of biodiversity are described in detail. Without a robust taxonomic knowledge, researchers cannot start addressing questions about ecological and evolutionary features of particular groups of organisms.

There is much more knowledge and progress is faster in groups which have some appeal or economic importance to humans. To improve this situation, aspiring taxonomists especially in those parts of the world for which knowledge is scarce, should be trained by specialists such that the taxonomic work produced is robust and of high quality.

Several of Dr. Dorchin's research projects have provided basic understanding about the components of biodiversity in gall midges, including description of new species, systematic revisions and faunal surveys. Such studies provided fundamental basis for further projects dealing with the ecological forces behind the diversification of gall midges.

ECOLOGICAL SPECIATION THROUGH HOST-PLANT SHIFTS

High species diversity in organisms with tight host specialization has been an intriguing question to evolutionary biologists and ecologists. In phytophagous insects, one of the main ecological events that can lead to the formation of new species is shifts to new host plants. When individuals or populations of phytophages shift to a new plant, they become subjected to different conditions. Over several generations, such new conditions may lead these organisms to change and adapt.

On one hand, shifts to new hosts can be disadvantageous to the insect due to possible physiological maladaptations to the new host. On the other hand, because natural enemies are also expected to be highly specialized, escape from these enemies may be a factor that offsets possible physiological constraints. Although evidence in favour of speciation through host shifts has increased in recent years, most studies are restricted to a single type of evidence, for example, genetic variation. "If multiple, independent types of evidence all point to the same conclusions, this makes the conclusions more robust and more likely to be correct. Combining multiple types of data in a phylogenetic reconstruction of a group can also provide insight into the evolution of certain characters in that group, such as adaptive morphological characters and host associations", explains Dr. Dorchin.

Dr. Netta Dorchin and collaborators employed a powerful approach based on multiple types of evidence to understand what factors may be involved in the diversification of *Dasineura folliculi*, a midge that induces galls in goldenrods (plants from the family Asteraceae). They tested if populations of the midge reared from two distinct species of host plants, *Solidago rugosa* and *Solidago gigantea,* were differentiated in terms of morphology, behaviour and genetics. Morphological analyses revealed that adult gall midges reared from *S. rugosa* were larger than those reared from *S. gigantea.* In terms of behaviour, the researchers showed that individuals chose to mate preferentially with individuals from the same host plant. Finally, populations of midges from *S. rugosa* were also different from populations of *S. gigantea* with respect to genetic variation. These results provide strong evidence that *D. folliculi* has differentiated into two distinct host races on its two hosts, suggesting that shifts between host plants may be important factors promoting biological diversification in gall midges.

CASCADING SPECIATION IS A PROMISING RESEARCH FIELD

Another theory that has recently been brought to the context of biological diversification in specialized herbivores is the concept of cascading speciation. It postulates that diversification of herbivorous insects through shifts in their host plants may lead to diversification in their natural enemies in response. The idea behind this theory is that these natural enemies are often as specialized as the gall-inducing species, which made the researchers believe that, when shifting their host plants, gall inducers may create new niches and thus enable diversification of their natural enemies. Gall midges represent an excellent model for studies of cascading speciation since they have intimate relations with different guilds of natural enemies: endo and ectoparasitoid wasps, herbivorous caterpillars that invade the galls and larvae of predatory organisms.

Despite its importance in the context of biological diversification, researchers are far from understanding the role of cascading speciation in promoting biological diversity. Dr. Dorchin's research has been expanding to elucidate not only the potential drivers of diversification in gall midges but also the coevolutionary processes between them and their natural enemies. What types of natural enemies of gall midges evolve in response to host shifts? How prevalent is this phenomenon in different groups of natural enemies that attack the same herbivorous species? "If this escalation of the speciation process up the trophic chain is common, it may be a major source of biodiversity, but because this concept is relatively new, the abundance of this process in nature is unknown and requires more study. Within the context of cascading speciation, I hope to improve the understanding of what life-history attributes dispose an insect to this process and why", says Dr. Dorchin. These novel contributions will be of great significance not only to specialists in gall midges, but also to the scientific community interested in cascading speciation in general.

Researcher Profile

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With years' of experience in studying phytophagous insects, Dr. Netta Dorchin is one of a handful of experts in gall-midge taxonomy and ecology. Her research is focused on the systematics, ecology, physiology, and speciation of these organisms. To address questions in these areas she uses a variety of approaches such as classical taxonomy, molecular systematics, and experimental biology.

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