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Published: 13 September 2022
doi: 10.3389/frym.2022.811444

WHEN ANTS DEPEND ON PLANTS AND PLANTS DEPEND ON ANTS

Finote Gijsman, Yorlenis González, Maikol Guevara and Sabrina Amador-Vargas*

Smithsonian Tropical Research Institute, Ancón, Panama

YOUNG REVIEWER:

JOSEPHINE

AGE: 10

Plants use many strategies to defend themselves against animals that eat plants, also called herbivores. One clever way that some plants, called myrmecophytes, do this is by teaming up with ants. Myrmecophytes are plants that have evolved close relationships with ants. In return for protection from herbivores, myrmecophytes provide ants with food and/or shelter. Sounds like a great deal, right? Yes, but sometimes working with ants can be tricky for a plant. Because myrmecophytes cannot choose the ant bodyguards that they get, they must balance their needs with the needs of their ant defenders. In this article, we introduce a classic example of plants that have beneficial relationships with ants, describe how ants and plants in these relationships depend on each other, and investigate how these ant-dependent plants interact with various ant species.

HOW DO PLANTS DEFEND THEMSELVES AGAINST HERBIVORES?

Plants use many strategies to defend themselves against **herbivores**. They use physical defenses like thorns, spines, and prickles to prevent herbivores from eating their leaves. They also use chemical defenses like repellents and **toxins** to make their leaves taste bad. As an added defense, some plants also recruit and attract natural enemies of herbivores as bodyguards. Ants are one such natural enemy of herbivores.

Have you ever been bitten or stung by something, only to find out that the offender was a small ant? If your answer to that question is "yes," you might know that, although they are small, ants can be mighty. That is why some plants, called **myrmecophytes** or "ant-plants," use ants as bodyguards to help protect them from herbivores. Myrmecophytes are plants that team up with ants in a relationship that is good for both of them, called a **mutualism**. In these mutualisms, plants and ants benefit from working together to help each other grow and survive: ants defend plants from herbivores and plants provide ants with food and/or shelter. It is a great deal!

HERBIVORE

An animal that feeds on plants.

TOXINS

Poisonous substances that plants, animals, and bacteria produce that can be harmful to consume.

MYRMECOPHYTES

Plants that live in mutualism with ants, also called "ant-plants," and produce specialized structures for ants to live in and feed on.

MUTUALISM

A close relationship between two or more species that is good for all involved.

ACACIA TREES, ANT-DEPENDENT PLANTS

Acacia trees are one example of plants that are myrmecophytes. Acacias are a group of trees and shrubs native to tropical and subtropical regions of the world, found in Australia, Africa, and Central and South America. While not all acacia species have established relationships with ants, many completely depend on ants to survive.

In Central America, acacia trees depend on the defense that various ant species in the **genus** *Pseudomyrmex* provide (Figure 1) [1]. To reward ants for their bodyguard services, these acacia trees produce food and shelter for ants to use. Shelter is provided by hollow spines, in which ants sleep and care for their larvae, while food is provided in two ways. First, acacia trees produce a sugary liquid called nectar that ants drink. This nectar is produced by special structures called **extrafloral nectaries**, found on the bases of acacia leaves. Second, acacia trees also produce protein-rich structures on the tips of their leaves called **Beltian bodies** (Figure 2). Ants remove these Beltian bodies, one by one, from the tips of acacia leaves and feed them to their larvae.

But, with the production of tasty treats like nectar and Beltian bodies comes the risk of attracting cheaters or lazy ant defenders. Sometimes, ant species live in acacia trees and feed on the food rewards that the trees produce, without protecting the trees from herbivores in return! Because acacia trees use their energy and resources to produce these

GENUS

A group of closely related organisms.

EXTRAFLORAL NECTARIES

Specialized glands found on plant leaves that produce nectar for ants to drink.

BELTIAN BODIES

Protein-rich organs that develop on the tips of some acacia leaves and that ants use as food for their larvae.

Figure 1

An example of a species of acacia tree that depends on the protection provided by ants to survive.

Figure 1

Figure 2

Acacia trees reward ants with food and shelter in return for protection against herbivores. Shelter is provided in the form of hollow spines in which ants live, and food is provided by extrafloral nectaries and Beltian bodies (Photograph credit: S. Amador-Vargas).

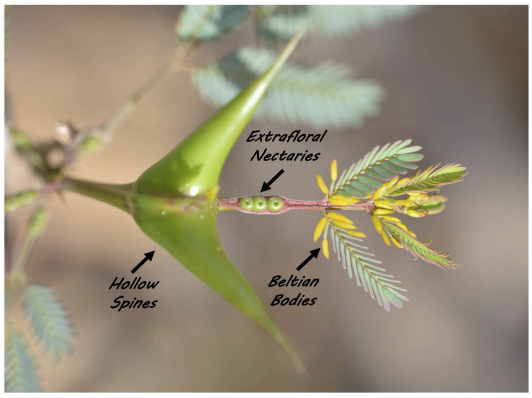

Figure 2

rewards for the ants, having ants that cheat or are lazy means that the tree is wasting its precious resources.

SO, WHAT HAPPENS IF AN ACACIA TREE GETS A LAZY ANT DEFENDER?

You might expect an acacia tree to respond to a lazy ant colony in two ways. First, the tree could produce more rewards to try to motivate the ants to protect it better from herbivores. This would be a costly response in the beginning, because the acacia tree would need to use its resources and energy to make more rewards for the ants, but it could pay off in the long term if the ants get better at scaring off herbivores. Second, the acacia tree could punish the ants by reducing the number and amount of rewards the ants receive. This would be cheap for the tree in the short term, but it could mean that the ants would have no reason to protect the tree in the future, which would not be good for the tree. So, which one is it?

To answer this question, we investigated whether acacia trees in Panama, a country in Central America, reward their ant defenders differently depending on how well the ants protect them against herbivores. To do this, we first selected acacia trees that were each occupied by one of three ant species: a strong defender, a medium defender, and a weak defender. Each of these ant species provide acacia trees with different levels of defense against herbivores and consume different rewards. The best defender is *Pseudomyrmex spinicola* (Figure 3A). *P. spinicola* protects acacia trees by delivering a painful bite and sting to herbivores and, in return, lives in the spines of acacia trees and feeds on both types of food rewards (nectar and Beltian bodies) [2, 3]. The medium-level defender is *Pseudomyrmex simulans* (Figure 3B). *P. simulans* also lives in the spines of acacia trees, feeds on both types of food rewards, and stings and bites herbivores but does not defend acacia trees from herbivores as well as *P. spinicola.* This is because their stings and bites do not hurt as much as *P. spinicola*'s. But at least *P. simulans* ants *try* to defend their acacia homes! Lastly, the weakest defender is *Crematogaster crinosa* (Figure 3C). *C. crinosa* uses shelter and consumes *only* the nectar food rewards, but this species provides little defense against herbivores [4]. Instead of stinging or biting herbivores (because they cannot), *C. crinosa* shoot drops of acid from their abdomens. This sounds like it would be very scary for herbivores but it really does not hurt the herbivores very much. For that reason, *C. crinosa* ants are considered cheaters of the ant-acacia mutualism; they take advantage of the rewards that acacia trees produce without giving them much defense in return!

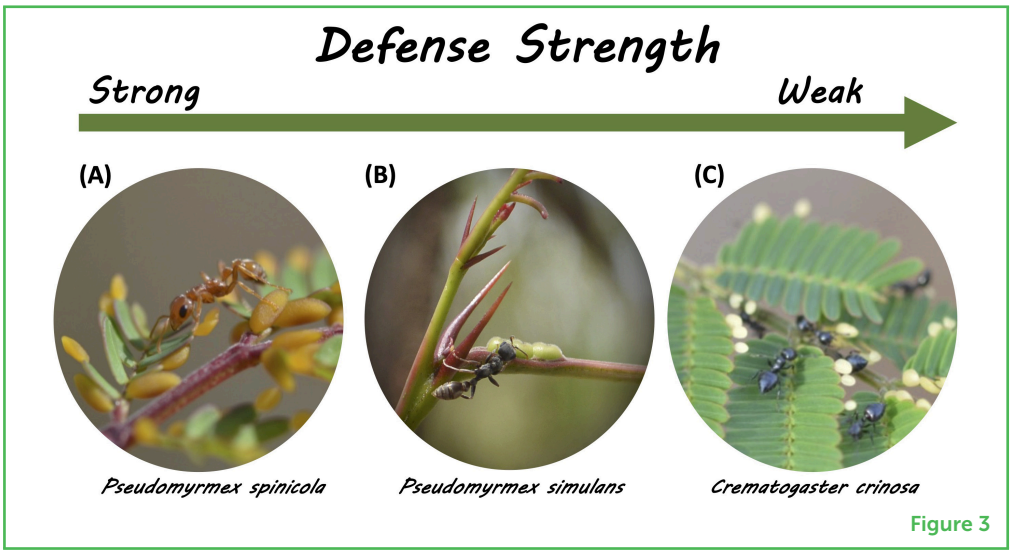

Figure 3

Some ant species protect acacia trees from herbivores better than others. **(A)** The best defender, *P. spinicola,* protects acacia trees by biting and stinging herbivores. **(B)** The medium defender, *P. simulans*, also protects acacia trees by biting and stinging herbivores, although not as well. **(C)** The weakest defender, *C. crinosa*, only sprays a mild acid that does not hurt the herbivores (Photograph credit: S. Amador-Vargas).

Next, to compare how acacia trees reward their different ant bodyguards, we counted the number of food and shelter rewards they produced when occupied by the different ant species. For food rewards, we counted the number of extrafloral nectaries and Beltian bodies that leaves had on them. For shelter rewards, we measured

the size and counted the number of spines ("ant homes") that trees produced. So, what did we find?

ACACIA TREES REWARD THEIR ANT BODYGUARDS DIFFERENTLY

We discovered that acacia trees treat their ant bodyguards differently depending on how well the ants protect them against herbivores. While the number and size of spines were the same for trees occupied by each of the ant species, the number of food rewards produced by trees were different! When occupied by strong defenders like *P. spinicola* or medium defenders like *P. simulans*, acacia trees produced a similar number of nectar food rewards. But when acacia trees were occupied by lazy defenders like *C. crinosa,* they added an extra nectary on the tips of their leaves!

Why might that be? Although this is still very much a mystery, we think that acacia trees might try to encourage lazy ants to patrol and defend the entire length of a leaf, by producing an additional extrafloral nectary at the leaf tip. Remember, *C. crinosa* ants only consume the nectar that acacia trees produce, so maybe the best way to motivate them to patrol the entire leaf is by producing a nectar reward that is far away from their spine homes. Many herbivores are afraid of ants, so even if these ants do not attack or hurt intruders, having a lazy ant colony like *C. crinosa* might still be better than having no ants!

WHY DOES THIS MATTER?

Ant-acacia mutualisms are an example of positive interactions that have evolved between organisms in nature. Studying how these interactions vary with different ant bodyguards can teach us a lot about relationships and finding the balance between give and take. It can also help us to understand how these types of relationships are maintained and how they affect the survival and reproduction of both participants—the ants and the plants.

Our discovery now opens a lot of new questions. For example, we would like to know how acacia trees can tell which ant species is living in their spines. Also, if trees reward a lazy ant species like *C. crinosa* with an extra nectary reward, why do the other ant species not cheat as well? Ant-acacia mutualisms present an exciting system to study questions on species interactions, and there are still so many mysteries that we need uncover. We hope that you join us in future quests to find these answers and, maybe the next time you get stung by an ant, you will remember this article and understand why some plants use ants as their bodyguards!

ORIGINAL SOURCE ARTICLE

Gijsman, F., González, Y., Guevara, M., and Amador-Vargas, S. 2021. Short-term plasticity and variation in acacia ant-rewards under different conditions of ant occupancy and herbivory. *Sci. Nat.* 108:31. doi: 10.1007/s00114-021-01738-w

FUNDING

Funding for this research was conducted with support from the Smithsonian Tropical Research Institute (STRI) Internship Program to FG and MG.

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SUBMITTED: 08 November 2021; **ACCEPTED:** 24 August 2022;
PUBLISHED ONLINE: 13 September 2022.

EDITOR: John T. Van Stan, Cleveland State University, Berkeley, United States

SCIENCE MENTOR: Manuel Esperon-Rodriguez

CITATION: Gijsman F, González Y, Guevara M and Amador-Vargas S (2022) When Ants Depend on Plants and Plants Depend on Ants. Front. Young Minds 10:811444. doi: 10.3389/frym.2022.811444

CONFLICT OF INTEREST: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

YOUNG REVIEWER

JOSEPHINE, AGE: 10

My name is Josephine, I am 10 years old and I am in 5th grade. I live with my mom and dad, my four parakeets and a husky. My favorite color is neon-orange, I figure skate, swim and play golf. I like to read and watch shows about animals, dragons and mythology. I love animals, but I do not have a favorite since all have different skills and features. I enjoyed working on the article and I hope to do another one.

AUTHORS

FINOTE GIJSMAN

Finote Gijsman is a PhD student in the Department of Ecology and Evolutionary Biology at Princeton University. Her work broadly focuses on species interactions, the roles that they play in maintaining ecosystem biodiversity, and the impacts that human disturbances have on food webs. Currently, she is studying the structure and composition of dung beetle food webs in African savannas. In her free time, Finote enjoys cooking, hiking, and watching movies with friends. *fgijsman@princeton.edu

YORLENIS GONZÁLEZ

Yorlenis González is a botanist from Panama. She is currently working in the organization, design, coordination, and execution of research projects on the behavior of Neotropical arthropods and the interaction of ants with plants. She is interested in diversity, ecological associations, and in learning new ways to communicate science, in a practical way that others can easily understand. In her free time, Yorlenis likes to listen to music, hike, and spend time with family.

MAIKOL GUEVARA

Maikol Guevara has a bachelor's degree in biology. He likes to learn about the diversity of plants in Panama and loves visiting various types of forests that have different plant species. He is also interested in how plants can affect the animals living in those forests. Besides forests, he likes studying plants in the ocean, and the tiny plant-like components of phytoplankton, because that microscopic world harbors a huge diversity of species.

SABRINA AMADOR-VARGAS

Sabrina Amador-Vargas is a biologist interested in animal behavior and ant-plant interactions. She investigates how ants make decisions and how they solve problems alone or as a group. She also wants to understand the responses of plants that associate with ants, and she is intrigued by how these very different organisms cannot live without the other. Besides ants, Sabrina enjoys birdwatching, photography, and long walks on the beach.