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Floral mimicry, coevolution of hosts and pathogens, and stress tolerance vs. resistance to pathogens

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The evolution of floral mimicry

I became interested in the evolution of floral mimicry as a result of discovering flower-mimic fungi which, like flowers, rely on insect visitation for outcrossing (Roy 1993; Roy 1994b; Roy, in press). Fungal exploitation of pollination systems has the potential to affect floral evolution, pollination ecology, and the evolution of plant life history traits, as well as disease transmission dynamics and fungal evolution (Roy 1994a).

IS FRAGRANCE IMPORTANT IN THE EVOLUTION OF FLORAL MIMICRY?

In a simple world, one could imagine that floral mimicry should be favored whenever a species receives more visitation as a result of similarity to another species. However, there is a problem in pollination systems. More visits do not always translate into higher fitness due to improper pollen transfer. Pollen that is transferred between species is, at best, simply lost, or at worst, the wrong pollen on a stigma can lead to reduced seed set, either by clogging the stigmatic surface or by allelopathy (Rathcke 1983). Thus, for a floral mimicry system to evolve, the gains in visitation must outweigh the fitness losses from improper pollen transfer.

I have proposed (Roy & Raguso, in review) that one way flower mimics could increase the probability that their pollen gets to the proper species is through the use of unique

fragrances. Species that are visually similar may form a common visual advertisement to attract pollinators, but after the patch has been found, visitors may cue in on particular species by additional non-visual factors such as fragrance.

Improper transfer also affects fungal floral mimics. I have shown that spores transferred from these mimics to flowers reduce seed set, even when the plant they are carried to is not a host, and I have shown that pollen is transferred from flowers to the fungus (Roy, in press). Pseudoflowers have a strong, sweet, flower-like fragrance. However, the chemical profiles of pseudoflowers are distinct from the profiles of the flowers they co-occur with (Raguso & Roy, in review). Thus, if insects are sensitive to the particular scent compounds involved, then they should be able to distinguish pseudoflowers from true flowers. Floral mimics could increase the fidelity of insects through distinctive fragrances. I am using combinations of synthetic fragrances, flowers and pseudoflowers to test this idea under field conditions.

IS FRAGRANCE AN ISOLATING MECHANISM LEADING TO SPECIATION?

Different species of flower-mimic crucifer rusts are morphologically indistinguishable, but have divergent ITS sequences and different floral odors (Roy, unpublished data). Changes in floral odors are a plausible mech-

anism for imposing reproductive isolation in these fungi, provided insects respond sharply to the distinctive fragrances. I would like to test whether visitors distinguish among species based on fragrance, and by using synthetic mixtures I would like to determine how much of a shift in fragrance is necessary to promote reproductive isolation.

Evolution and coevolution of hosts and pathogens

Pathogens and parasites contribute to biodiversity in at least two ways. First, the specialized and isolating nature of the parasitic lifestyle leads to speciation; consequently parasites and pathogens comprise approximately half of all organisms (Price 1980). Second, because parasites and pathogens reduce host fitness, they may influence host genetic diversity (Jaenike 1978; Barrett 1988), or even cause speciation (Thompson 1994). Although pathogens and parasites can influence biodiversity, the evolutionary processes leading to diversification are poorly understood.

I am using rust fungi and their hosts to study coevolution and co-speciation. Rust fungi are an ideal model system because the genetic linkage between host and pathogen is unusually tight; resistance genes in the plant are often matched by specific virulence genes in the fungus (Thompson & Burdon 1992).

PATTERNS OF CO-EVOLUTION AND CO-SPECIATION IN THE RUST FUNGI AND THEIR HOSTS

As part of my attempt to understand the coevolution of a host/pathogen system, I am preparing a molecular phylogeny (by sequencing the internal transcribed spacer region) of the crucifer rusts (*Puccinia* spp.) and their hosts (members of eight genera of Brassicaceae). Because rust fungi are genetically tightly linked to their hosts, it is commonly

assumed that radiation to new hosts should occur incrementally, through shifts to closely related hosts. This assumption is rarely examined, and may not always be true. For example, the crucifer rusts occur on only eight of the 380 genera of the Brassicaceae, and these genera are not closely related to one another, at least in terms of morphologically based taxonomy. However, I have found that these eight genera tend to co-occur in the same habitats, suggesting that the rusts have radiated to genera that are geographically available, but not necessarily closely related.

HOW DO LIFE-HISTORY TRAITS AFFECT HOST FITNESS IN RESPONSE TO INFECTION BY RUST FUNGI?

I have found that infection by crucifer rusts usually kills monocarpic species of *Arabis*, whereas polycarpic *Arabis* species often outlive infection. This could reflect the hosts' different life history traits, but it is also possible that the different hosts are actually infected by different rust species. Although the rusts infecting these *Arabis* spp. are classified as a single species, there may be important – though morphologically cryptic – differences between them. Phylogenetic reconstruction will permit me to begin to determine whether differences in life history traits, or different rust species, are responsible for the observed differences in host survival.

HOW MUCH ARE THE SYMPTOMS OF INFECTION CONSTRAINED BY THE HOST'S PHYLOGENETIC HISTORY?

For example, I have found that the appearance and fragrance of rust induced pseudoflowers varies depending on the species of host infected. This pattern suggested two hypotheses (1) what the rust fungi can induce in their hosts may be constrained by host morphology or chemistry, and/or (2) cryptic speciation may have occurred in the rusts and

this is the reason why the shapes and odors induced in different host species vary. Preliminary data support the notion of cryptic speciation in the fungus since there are large sequence differences between morphologically identical rust species when they are collected from different host species.

The relationship between physiological stress tolerance and resistance or tolerance to infection by pathogens

Plants face both abiotic stresses (such as lack of water or nutrients) and biotic stresses (such as pathogens or herbivores) in their environments. Tolerance to these different kinds of stress varies, both among individuals and among species. The C-S-R model proposes that plants have evolved three major life history strategies (competitive, ruderal, and stress tolerant) for different kinds of environments (Grime 1977). Biologists generally agree that ruderal traits ("r-selected") tend to arise in disturbed habitats, and that competitive traits ("K-selected") evolve in stable habitats, but they disagree over whether a distinctive stress tolerant strategy exists. Maureen Stanton and I have a three-year NSF grant to test whether a generalized stress-tolerant strategy exists, and to test whether there are genetic trade-offs between stress-tolerant, ruderal, and competitive traits. Two of the major questions I am addressing are as following.

DOES GENERALIZED STRESS TOLERANCE OCCUR?

Because different stresses affect plants in fundamentally different ways, adaptation to stress in general seems unlikely. To test whether generalized adaptation to stress can occur, populations of *Brassica rapa* are being selected in several controlled environments, each characterized by a distinctive environ-

mental stress. After selecting lines that are particularly tolerant of their "home" stress, they will be grown under each of the other stress environments, thus gauging whether adaptation to one kind of stress confers tolerance to other kinds of stress as well. In this way, we are empirically testing whether generalized stress tolerance can arise by natural selection.

ARE THERE GENETIC TRADE-OFFS BETWEEN PATHOGEN OR HERBIVORE RESISTANCE AND STRESS TOLERANCE?

In the C-S-R model all factors (both abiotic and biotic) that destroy living plant tissue are classified as agents of disturbance, whereas factors that reduce the production of existing tissues are classified as stresses. For a distinct "stress-tolerant" strategy to persist, there must be fitness trade-offs between stress tolerance and alternative selective pressures. If the C-S-R model is correct, adaptation to abiotic stress may increase vulnerability to natural enemies. I am studying this relationship experimentally, by determining whether plant lineages selected for tolerance to abiotic stress also have altered susceptibility to attack by herbivores and pathogens.

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