

Contribution ID: 301

Type: Oral Presentation

## Separation of trait-mediated and biomass-mediated indirect effects in a system of a plant and two herbivores

*Monday, 9 July 2018 10:30 (30 minutes)*

Two consumer species that share a single resource species can indirectly interact each other, even without direct interactions. A typical indirect interaction is exploitative resource competition that results from a depression of resource biomass by consumption, which can be referred to as “biomass-mediated indirect effect”. Another type of indirect interaction is called “trait-mediated indirect effect”, which is caused by changes in traits of resource species. For example, an attack from one herbivore species can either reduce biomass or induce defensive traits of the host plant individual, which may in turn suppress performance of another herbivore species on the same host. It is notable that two types of indirect effects are difficult to detect separately in nature because it is necessary to measure both reduction in biomass and changes in traits of plants and observe respective effects on herbivore performance. In order to understand the separate and joint influences of two indirect effects, we analyzed a population dynamic model of one-plant two-herbivores system, including an inducible non-specific defense of plant individuals. Our analysis revealed (1) the inducible non-specific defense can promote coexistence of three species, (2) the coexistence of three species requires reduction of population densities of both herbivores, (3) in such a case, one herbivore is controlled by biomass-mediated negative indirect effect, whereas the other herbivore is controlled by trait-mediated negative indirect effect. This indicates that both types of indirect effects need to co-occur for the coexistence of consumer species, suggesting that trait-mediate indirect effect may be as common as biomass-mediated indirect effect.

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**Session Classification:** Population dynamics models with broader ecological, evolutionary, and social feedbacks

**Track Classification:** Minisymposium: Population dynamics models with broader ecological, evolutionary, and social feedbacks