

Contribution ID: 274

Type: **Oral Presentation**

## **Adaptive defense of a shared pest can enhance efficiency of biological control by two natural enemies**

*Monday, 9 July 2018 11:00 (30 minutes)*

It has long been debated whether introduction of two (or more) natural enemies results in more efficient pest control than that of either one enemy. Intra-guild predation (IGP) among two natural enemies sharing a single pest has been recognized as an important factor to reduce efficiency of pest control. While the classical theoretical model of IGP showed that introduction of two natural enemies is less efficient for pest control, empirical works have showed positive, negative, and neutral results. However, the classical IGP model did not consider any behavioural plasticity of the pest and natural enemies.

In this study, we extended the classical IGP model by considering adaptive defense by the pest and switching predation by the omnivorous natural enemy (omnivore) and examined separate and joint effects of them on efficiency of pest control. We assumed that the pest can adaptively allocate efforts toward two kinds of defense respectively against the two natural enemies to increase its own fitness, with cost of reduction in its own reproduction. Switching predation by the omnivore is expressed as the Holling's type III functional response to the pest and another natural enemy (intermediate predator). Equilibrium pest density is used as an index of efficiency of biological pest control.

If the pest employed the adaptive defense, introduction of two natural enemies performed more efficient pest control than that of either one enemy, unless the IGP was too intensive. This is because the pest allocated more defensive effort against the more threatening enemy, and thus it was difficult for the pest to simultaneously prevent predation from the two enemies. On the other hand, switching predation could not improve biological control by two natural enemies. However, the type III functional response tempted the pest to abandon defensive effort against the omnivore, because the predation pressure was negligible at low pest density and saturated at high density. Since the intermediate predator was suppressed by the undefended omnivore, defensive effort against the intermediate predator also diminished. Thus, switching predation could offset the effects of defense and the prey density could be lowered by two natural enemies even under severe IGP. Consequently, types and combination of behavioural plasticity might cause qualitatively different outcomes of biological control introducing two natural enemies.

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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