

Complexity, Evolution, and Persistence in Host-Parasitoid Experimental Systems With *Callosobruchus* Beetles as the Host

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I. SUMMARY

Experimental laboratory systems of bruchid beetles, *Callosobruchus* in particular, and their parasitoids have been used as models to study population dynamics of single species and host-parasitoid interactions since the early 1940s. First, this paper reviews the recent advances in ecological studies on laboratory systems of bruchid hosts and their parasitoids as represented by bottom-up and top-down controls. Factors controlling the persistence of simple host-parasitoid systems that can be modified by an evolutionary change in a host beetle are demonstrated with reference to local carrying capacity, vulnerable time window of hosts to parasitism, and functional

3. Evolutionary Change

We often assume characters that play an important role in determining persistence of host-parasitoid systems are constant over time. This assumption, however, can be violated as observed in the host *C. maculatus* during a long-term experiment of a host-parasitoid system. Larval competition of *C. maculatus* was initially the scramble type, and two to three individuals survived from a small *V. radiata* seed (Fig. 2a). When the experiment was terminated on day 800, only single adults emerged indicating the larval competition was of the contest type (Fig. 2a) (Tuda, 1998). This population of *C. maculatus* was brought into the laboratory relatively recently (two years prior to experimentation), unlike the other populations of bruchids and parasitoids in our laboratory. There was no difference in the attack rates between pre- and post-experiment of the parasitoid *H. prosopidis*, which has been maintained in the laboratory for about 20 years. The change in the population dynamics occurred approximately at 20 generations of the host (Fig. 2b), and the post-experimental host and parasitoid after 800 days of coexistence showed stable population dynamics unlike the initial oscillations when they were returned to initial densities (Fig. 2c). This confirms the change was not temporal.

With a parameterized game-theoretical model, Tuda and Iwasa (1998) showed that the evolutionary change in larval competition towards the contest type can induce a large shift in the population dynamics of host and parasitoid as observed in the experimental system. For such rapid evolutionary change to occur, 20 generations was shown to be sufficient by the model with the following assumptions: 1) a small fraction of initial population was a contest-type competitor, in which the phenotype is genetically determined; and 2) the contest competitor consumes a certain volume of bean and kills other individuals in that volume, enabling a scramble competitor to survive only when beans are large enough. It is worth noting that random parasitoid attacks did not alter the evolution towards contest type but can slow the evolution.

This explains the results of experiments on a single-species *C. maculatus* population by Toquenaga *et al.* (1994), in which competition type was estimated based on the resemblance of dynamical trajectories. Their study also indicated that the transition from scramble to contest type occurred on a time scale consistent with the prediction of the present model (i.e., 20 generations). The time scale required for such a change also corresponds to the one observed in Nicholson's laboratory blowfly population (Nicholson, 1957; Stokes *et al.*, 1988). This similarity may arise not only from the stable laboratory conditions but also from a common biological mechanism, e.g., density-dependent processes in the insects.

IV. PERSISTENCE OF COMPLEX HOST-PARASITOID ASSEMBLIES

There is controversy over the relation between complexity and stability in a biological community. Random assembly models predict that complexity (in terms of species richness) reduces local stability and connectance (May, 1972), whereas Elton (1927) suggested that complexity enhances stability. In terms of global stability and permanence, which guarantee persistent coexistence of species, stability decreases with increasing complexity, which is consistent with May's prediction (Chen and Cohen, 2001b). Recent studies indicate that adaptive evolutionary changes in component species can either increase or decrease diversity (Abrams, 2000; Kondoh, 2003). Studies using micro-organisms supported May's prediction (Hairston *et al.*, 1968; Lawler, 1993; Lawler and Morin, 1993). Accumulation of sound empirical evidence is required for assemblies of higher organisms. Here, we review recent advances in empirical tests on the complexity-stability hypothesis in the experimental assembly of bruchid hosts and their parasitoids.

Tuda (1996a) and Tuda and Kondoh (2003, unpublished data) analyzed experimental results that tested the complexity-stability hypothesis by using bruchid beetles and their parasitoid (Ohdate, 1980; Fujii, 1981, 1994). The experimental design was as follows: each of the four compartments of a petri dish was filled with 5 g of azuki beans, then bruchids, followed by parasitoids. The maximum number of the initial component species was 5, i.e., three bruchid species (*C. maculatus*, *C. chinensis* and *Z. subfasciatus*) and two parasitoid species (*A. calandreae* and *H. prosopidis*), and the minimum was 2, i.e., two bruchid species (Fujii, 1994). Initial assemblies were replicated up to three times. As each species becomes extinct, different initial assemblies can end up with the same assembly, and replicated assemblies can lose different species. Each such transient assembly is treated as an additional replicate. Bean supply was continued until the assembly reached stable states, or stable species compositions. Persistence, or time to extinction of a species, of each assembly type was recorded. The original records were transformed to mean probability of extinction per generation of a component species (Tuda and Kondoh, 2003, unpublished data). The results indicate that extinction probability increased as the number of species increased (Tuda and Kondoh, 2003, unpublished data), and persistence decreased with the increasing number of species (Tuda, 1996a). While this supports May's complexity-instability relationship found from random combination of species, there was something beyond the prediction: a clear pattern in the composition of species in the final experimental assemblies (Ohdate, 1980; Fujii, 1983, 1994). The final assemblies were composed of either single bruchid, *C. maculatus*, or single host-single parasitoid, *C. maculatus*-*A. calandreae*. This shows that the bottom-up (contest competition or resultant low local carrying capacity of *C. maculatus*) and self-regulating top-down

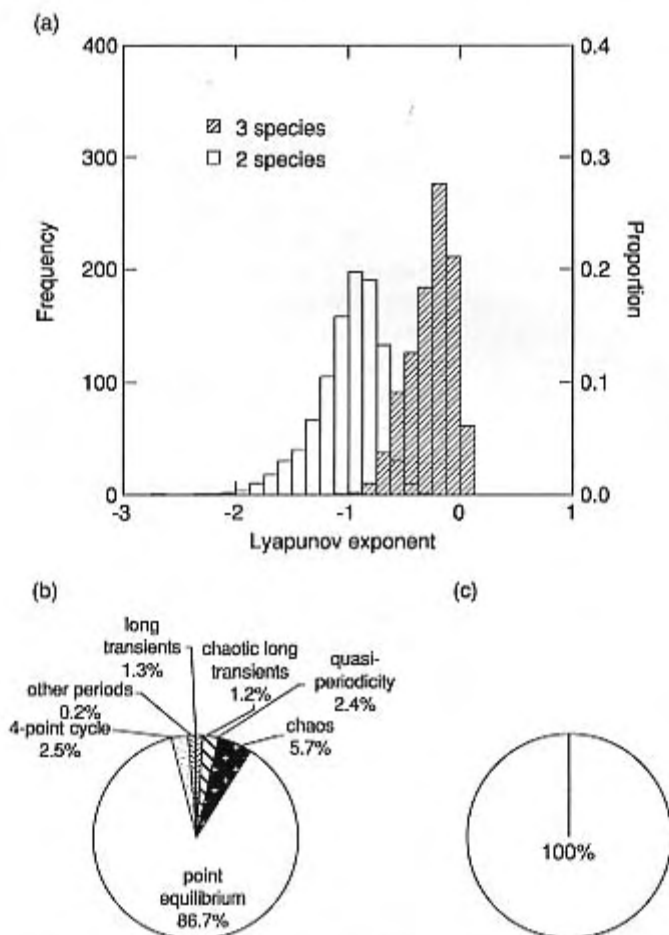


Figure 6 Estimated property of bootstrapped data sets. (a) Frequency distribution of Lyapunov exponents of deterministic three- and two-species dynamics. Population dynamic properties of attractors for (b) three-species system and (c) two-species system.

model with a generation time of *A. calandreae* of 1 time unit instead of 2 had a lower ML (-992.770), which was also declined. Our semi-mechanistic model is different from the non-parametric (or non-mechanistic) model proposed by Kristoffersen *et al.* (2001), in that multiparasitism (i.e., co-parasitism) is incorporated and mutual interference is present in *A. calandreae*. In their study, multiparasitism was assumed negligible based on experimental results by Shimada (1985). Our explicit statistical comparison of models

Bottom-up cascade control: Species of bean resources (plant) can control persistence of interactions of herbivores and parasitoids. In the simple *Callosobruchus*-parasitoid systems, the window of vulnerability was elongated by host-plant shift, which resulted in termination of the *Callosobruchus*-parasitoid interaction because of increased vulnerability of the host *Callosobruchus* to parasitism.

Evolutionary cascade effect: Evolutionary change occurred in the *Callosobruchus* beetle within a relatively short time span, as it shifted to a new bean resource that differs in size from its original bean. This change not only affected its own population dynamics but also modified host-parasitoid dynamics. An implication of the result for agricultural selection of larger and nutrient-rich crops is that pests can become more scramble-type competitors that allow more serious outbreaks of a pest population even under a control of parasitoid. It should be noted that the biology of evolution of contest/scramble competition can be more profound than shown in the present paper; the selection background of different geographical populations constrains artificial selection in the laboratory (Takano *et al.*, 2001; Kawecki and Mery, 2003; Tuda, 2005, unpublished).

In the future, how evolutionary changes modify behavior of interacting species and eventually stability/persistence of overall assembly of hosts and parasitoids will be one of the next themes to pursue. As described in the section on bottom-up control, experimental tests on the possibility of evolution 'against coexistence' are intriguing future challenges. Does evolutionary capacity of species tend to vary between trophic levels? Does it depend on the number of interacting species (generalist vs. specialist, herbivore vs. carnivore, intraguild predator vs. non-intraguild predator, and so on)? These are some of the questions that do not yet have concrete empirical answers, however, they are crucial for the prediction of possible outcomes on the whole assembly when a species either is introduced or goes extinct. Evolutionary scheme of ecological stability/persistence of biological interactions may also be extended to include a lower trophic level (i.e., producer or plant) which could be much more complex. What is known from the investigation on insect fauna associated with leguminous plants, however, suggests that it may not complicate our understandings but rather simplify them: ecological characteristics of legume species such as their distributional range (similar to island-size effect), morphology (tree or herb), and historical background (introduced, native or endemic) are found to be excellent predictors of species richness of their seed predators, including bruchid beetles, and consequently their parasitoids (Tuda *et al.*, 1998, unpublished). The process of accumulation of insect herbivores, followed by parasitoids on introduced plants or that of parasitoid on invading insect herbivores is not well understood (Tuda *et al.*, 2001); this should include learning and evolutionary processes in insects. Patterns of species richness in nature such as this