

F-1.3 Effects of the disturbed species interaction on population extinction

Contact person Yoshitaka Tsubaki
Environmental Biology Division
National Institute for Environmental Studies
Environment Agency
Onogawa 16-2, Tsukuba, Ibaraki 305, Japan
Tel: +81-298-50-2482 Fax: +81-298-50-2577
E-mail: tsubaki@nies.go.jp

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Abstract Organisms in a coevolutionarily developed species interaction is prone to go extinct in case partner organisms are damaged or lost due to habitat change or invader organisms. We investigated pollination and seed set of heterostylous plants, *Primula sieboldii* E. Morren and *Persicaria japonica* (Meisn.) H. Gross in their natural habitats in fragmented landscape and demonstrated 'fruitless falls' i.e., limited fruit and seed set due to insufficient pollinator services or genet isolation, in these species.

On oceanic and continental islands in Japan, we surveyed (1) flowering phenology, (2) anthophilous insect community. On the Bonin (Ogasawara) Islands, impact of introduced honeybees upon native bee communities was studied.

Allozyme variation of European and Japanese bumblebees was investigated in order to develop a reliable genetic marker for monitoring the hybridisation between them in the field.

We analysed mathematically (1) mutualism between figs and their pollinator wasps, (2) competition between related species of lady beetles, and (3) a system of one predator and two preys, and showed the importance of species interaction on processes of extinction of wild populations.

The social structure of ants compared among three environments: natural forests, secondary forests and open lands. In natural forests monogynous ants including the majority of endemic species were dominant, while polygynous and polydomous tramp species in disturbed habitats. This pattern was consistent across the different climate regions, i.e. Java and Okinawa.

Key Words habitat fragmentation, symbiosis, invasion, hybridisation

Organisms in a coevolutionarily-developed species interaction is prone to go extinct in case partner organisms are damaged or lost due to habitat change or invader organisms. Such a interaction was studied for entomophilous flowers and pollinator bees in patchy habitats such as islands or river deltas. It has been revealed that invading bees are one of the greatest threats to survival of both the flowers and pollinators. Ant community were also investigated in relation to vegetation types on several islands. As disturbance proceeded from forest to bare land, not only the ant fauna, but the social structure of ant species also changed, suggesting that they are in close interaction with habitat structure.

1. Effects of pollinator loss and isolation on quantity and quality of seeds set in *Primula sieboldii* E. Morren populations in fragmented landscapes
Primula sieboldii is a perennial clonal herb that occurs in a range of moist habitats

throughout Japan. Although this heterostylous species was once very common, in recent years it is declining to be listed in Japanese plant red list.

Through previous studies¹⁾²⁾, serious effects of pollinator loss have been recognised for a *P. sieboldii* population of a small nature reserve (4 ha) in the floodplain of the Arakawa River in the urban area of Greater Tokyo. Entire insect fauna of the reserve appears impoverished¹⁾, but the absence of long-tongued bumble bees may be the main reason for the fruitless fall of the species, since the queens of long-tongued bumblebees, of which tongue length is nearly equal to corolla tube length of *P. sieboldii*, are known to be especially effective pollinators³⁾. The strong fertility selection for the rare homostyle morph suggests the possibility of a large loss of genetic variation within a few generations. Simulation with a genetic population model predicts either of a strong genetic bottleneck due to fertility selection or an overall recruitment failure in case of the presence of very strong inbreeding depression⁴⁾.

In the present study, seed set and various biological and other environmental factors potentially affecting reproductive success were compared among 20 *P. sieboldii* local populations in a fragmented landscape of Hidaka region, southern Hokkaido.

Although various biological agents including herbivores and pathogens affected the fertility of the plants⁵⁾⁶⁾, seed set of the populations was strongly dependent on the population size and pollinator availability which can be assessed by craw marks left on the flower petals by long-tongued bumblebee queens. Among the 20 populations investigated, negligible seeds were set in smaller populations consisting of less than four genets, while in larger populations, population mean seed set strongly depended on pollinator availability especially in the year with generally low pollinator activities.

Reduced opportunity for mating due to both pollinator loss and isolation may be the major cause of fruitless falls for small populations or isolated genets of declining populations in fragmented landscapes.

Results of our study in other deciduous forest habitat suggested that not only quantity of the seeds, but also their quality, i.e., fitness of the seeds which were barely produced on isolated mother plants of *P. sieboldii* are also significantly lower than those of the seeds from less isolated mother plants having potential mating partner(s) in their vicinity.

The study was performed in a typical habitat of the species in central Honshu, i.e., a forest dominated by *Quercus mongolica* spp. *crispula* (Blume) Menitsky (35°57'N, 138°28'E, 1350m a.s.l.), and seed set, germinability of the seeds and survival and growth of the germinated seedlings were examined for many mother plants growing along a stream. Seed set as well as germination of the seeds and early survival of the germinated seedlings were significantly lower and variable among isolated mother plants having no opposite morph flower in the neighbourhood within 5m than the mothers having potential mating partners in their neighbourhoods. However, there was no significant difference in survival and relative growth rate of the established seedlings between the mother groups differing in the degree of isolation. Moreover, the level of allozyme heterozygosity of the progenies surviving to this stage did not significantly differ between the isolated and less isolated mothers.

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2. Pollination failure in common heterostylous species *Persicaria japonica* (Meisn.) H. Gross due to isolation

Seed set failure due to pollination limitation was also demonstrated for isolated genets and smaller populations of *Persicaria japonica* (Meisn.) H. Gross, which is a heterostylous perennial herb common to various moist or wet habitats throughout Japan. The species has dish-shaped corolla, and is supposed to be a generalist concerning pollinator insects, since many insects including syrphids, flies, bees, and butterflies can pollinate the flower^{7,8)}. The species is common in moist tall grasslands dominated by *Phragmites australis* W. Clayton in floodplains and lakeshores of lowland Japan. However, recently these habitats of the species has been subjected to extensive fragmentation due to reclamation and other construction works. Moist tall grasslands on the shore of Lake Kasumigaura, the second largest lake in Japan, are not exceptional, and at present there remains a highly fragmented landscape of the grasslands with small and/or low-density populations of *P. japonica*.

In the remaining patches of fragmented grasslands on the lakeshore, we compared seed set among 25 local populations of *Persicaria japonica* growing in remnant grassland patches of various sizes scattered along 25 km shoreline of the lake. The populations greatly differed in the area of inhabiting grassland patches (120-18000m²), genet number (1-53), and morph bias. Pollinator insects were generally abundant, and pollinator insects such as *Eristalomyia tenax* Linne, *Campsomeris annulata* Fabricius and *Lucilia illustris* Meiga frequently visited even isolated populations or genets. However, seed set greatly varied among the local populations but rather consistent within the populations between the study years. Mean seed set of the local population was correlated with genet or index for morph bias. Most small populations found in small grassland fragment showed consistently low seed set in both years. Artificial pollination with mixed pollen from three opposite morph genets significantly increased the seed set of 3 small populations each consisting of a single genet. Therefore, it is suggested that compatible pollen supply due to solitude is largely responsible for the reproduction failure of the isolated genets.

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2. Impacts of an introduced honey bee on endemic bee communities in Bonin Islands

The Bonin (Ogasawara) Islands are oceanic islands located in the Northwest Pacific, and have ten native (nine endemic) bee species, all of which are non-social. The European honeybee (*Apis mellifera*), which was introduced to the islands for apiculture in the 1880s, became naturalized in a few islands shortly after introduction. In order to detect the impact of the honeybees upon the native bee diversity, we analysed pollen harvest by honeybees and surveyed the relative abundance of honeybees and native bees on flowers on several islands. Both hive and feral honeybee colonies were active throughout the year, and harvested pollen of both native and alien flowers and from both entomophilous and anemophilous flowers. Honeybees strongly depended on the alien plants especially during winter to spring when native melittophilous flowers were rare. From June to November, honeybees exhaustively utilized native flowers, which had originally been utilised and pollinated by native bees. On Chichi and Haha Islands, where human disturbance upon forests has been severe, honeybees dominated both native and alien flowers, and native bees were rare or extinct even in well-conserved forests. In contrast on Ani Island and Haha's satellite islands, where primary forests were well conserved and honeybees were still uncommon or absent, native bees remained dominant. These results suggest that competition for nectar and pollen of the native flowers between honeybees and native bees favours honeybees on the disturbed islands, which are thoroughly invaded by alien nectariferous, sometimes aggressive, weedy plants.

Flowering phenology and pollination symbiosis were also studied on the other southern islands in Japan. On another oceanic islands, the Daito Islands, only four bee species were found. The continental islands such as Amami, Okinawa and Sakishima islands, had characteristic bee fauna, which surprisingly differed from that of the Bonin Islands. Even on these islands, impact of hived honeybee colonies upon natural bee community was thought to be grave.

3. Allozyme variation of European and Japanese bumblebees

A bumble bee species, *Bombus terrestris*, has been introduced into Japan from Europe for pollination of tomato plants since 1991. Many ecologists have warned about biological invasion of the species. In 1996, a natural nest of the species was found in Hokkaido, indicating that it became naturalised. *B. terrestris* is such a competitive species that it would make strong ecological impact on Japanese native species through competition for food and nest site. Furthermore, *B. terrestris* has some potential for bringing genetic pollution into the populations of native species. Laboratory experiments showed that *B. terrestris* and a Japanese native species, *B. hypocrita sapporoensis*, could copulate and make hybrids. Because the hybrids are morphologically similar to the native species, useful genetic markers will be needed for monitoring of the hybridisation between the two species and consequential genetic pollution in the native species in the field. In this study, we investigated allozyme variations in various colonies of the two species, in order to develop a reliable genetic marker for differentiating them. Until now, we detected genetic differentiations in PGM allozyme between the species, which is considered to be effective marker for monitoring the hybridisation.

On the other hand, the Japanese makers have started trying the commercialisation of the native species according to some ecologists' proposal. However, I think that a new genetic problem will occur through the commercialisation. That is the genetic disturbance

caused by reckless hunting of natural queen bees for breeding and transportation of artificial colony to many places in Japan. It is necessary to investigate the pattern of geographic variation and the degree of genetic variance in the populations of the native species before we use them as pollinators. We investigated microsatellite DNA variations among the native populations of bumblebees in Japan in order to clarify the geographic variations of them. We detected large variation on microsatellite loci within and among populations, and there seemed to be some geographic pattern in genetic constitutions among the populations.

4. A stochastic model analysis of a figs and pollinator wasps mutualistic system

The relationship between figs and their pollinator wasps is one of the most well known examples of the species-specific obligate mutualism. In this paper we make a stochastic model of this mutualistic system, referring to data on a dioecious fig (*Ficus schwarzii*) in Borneo, and examine the conditions for the persistence of a wasp population for a given period. (1) When the average duration of the flowering interval of fig trees is short, even a small fig population can sustain a wasp population successfully. A population whose average period of flowering cycle halves can sustain a wasp population with the number of trees less than half of the original population. (2) The wasp survival rate (WSR) is higher when (a) the variation of the interval periods of fig flowering is smaller, (b) the fig population size is larger, and (c) figs can prolong their receptivity to wait for wasp if no wasps are available. (3) WSR is predictable from the average proportion of the fig's receptive phases, in which wasps are available, to their total receptive phases. (4) The persistence period of a wasp population increases exponentially with the number of fig trees. Based on the above results we propose a new hypothesis on the evolution of dioecy from monoecy in *Ficus*.

Related species of lady beetles in Japan make hybrid zones in several areas. It is expected that a common species eradicate a rare species through sperm competition in an isolated habitat of the hybrid zone. I made a mathematical model, including sperm displacement rates between different species, to predict the time before the eradication.

Enrichment is an increasingly serious trend in natural ecosystems. A theoretical model of predator-prey system with a natural assumption of satiation in predation predicts that enrichment causes the populations to fluctuate to stochastic extinction. Yet, this "paradox of enrichment" has not been demonstrated clearly in experimental and natural communities. Here we present a theoretical model that describes a novel mechanism for resolving the paradox in the case of a predator with optimal selective feeding. Specifically, a less profitable but edible (thus, "unpalatable") prey species sharply reduces the amplitude of the population oscillation and firmly prevents the minimum abundance of species from falling below certain values. The presence of such an unpalatable prey thus guarantees the robustness of the system against enrichment.

6. Ant social structure as an indicator of habitat disturbances

We tests the hypothesis that not only the species composition but the social stricture of the ants (the number of queen per colony, the number of nests per colony and the colony size) could be a good indicator of the degree of condition of natural habitat conservation. We also investigated the ecological causes for the correlation of environmental parameters and the ant social structure.

The time unit sampling for 30 minutes, within which all ant nests found on the near the surface grounds were collected, was repeatedly performed in Java and Okinawa. Collected ants were identified and their social structures were recorded. Environments

were classified into tree types depending on the degree of artificial disturbance: natural forests, secondary forests and open lands. Species composition of ants and their social structure were compared among different habitats. Some ants were used genetic analyses and behavioural observations.

Throughout tropical Java and subtropical Okinawa islands, there existed a consistent tendency that in natural forests monogyny (single queen per colony) and monodomy (single nest per colony) with relatively small colony size was the common social structure, while in more disturbed habitats (open lands and secondary forests) polygynous (multiple queen per colony), polydomous (multiple nests per colony) ants with large colonies became more dominants. Endemic and/or narrow ranged distributed species were mostly included in the firmer category, while dominants ants in disturbed habitats consisted of non-endemic tramp species. The observed correlation supported Tsuji & Tsuji's life history model¹⁾, but for more rigorous tests phylogenetic information is needed.

To conserve local ant faunas conservation of natural forests seems most important. In tropics ant taxonomy is often incomplete, but to assess the degree of neutrality and the conservation ecological value of study sites, the frequency of polygynous ants and the presence of tramp species can be a good indicator of the history of environmental disturbances that the site has experienced.

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