Research Field

➢ Development of evaluation methods for impacts of chemical substances and other pollutants on ecosystems and biodiversity based on ecological modeling.

➢ Elaboration of environmental effect assessment for warming, water pollution and other human-induced factors.

➢ Trait-based analyses on the relationship between biodiversity and ecosystem functions.

➢ Simulations of extinction of populations by genetic factors such as inbreeding depression and introgressive hybridization.

➢ Theoretical studies on the evolution of social communication systems in organisms.

Research Topics

(1) Ecological risk assessment of chemicals
(2) Ecosystem effect evaluation based on species ecological traits
(3) Extinction risk of populations by genetic factors
(4) Genetic variation and evolution of organisms
(5) Theories of social evolution in organisms

(1) Ecological risk assessment of chemicals

Our lives are supported by countless chemical substances such as shampoo and kitchen detergent, liquid crystal panel material, printer ink, chemical fiber, gasoline additive etc. However, some chemical substances have harmful effects on the environment and human health, and in order to maintain sustainable development, it is necessary to properly evaluate and manage the environmental risk of such chemical substances.

Especially in Japan, pollution-related diseases caused by chemical pollution symbolized by Minamata disease occurred in various places in the 1960s, and it triggered the development of the science to evaluate the health effects of chemical substances. On the other hand, research to evaluate the impact of chemicals on biodiversity and ecosystems has been delayed. I proposed a method to estimate the ecological risk of environmental pollution with the extinction risk of species and populations as a standard and tried to incorporate ecological concept into this field (selected papers [2, 9, 10, 11]). The method of assessing ecological risk by population extinction probability is in common with the method developed as the population vulnerability analysis in conservation ecology to study the risk of biodiversity.

Furthermore, I am also working on an evaluation method that takes into account the structure of the entire ecosystem. In an actual ecosystem, species live with connections tied to each other

such as the prey-predator relationship. In order to reflect the importance of interspecific interactions in the ecological risk assessment of chemical substances, ecological risk models of three trophic levels based on algae (phytoplankton), daphnids (zooplankton) and fish were prepared. And I am trying to compare it with the existing evaluation methods（http://www.nies.go.jp/ateram/index.html）.

The greatest feature of separating organisms from inorganic matters is that they evolve responding to the environment. Even in environments contaminated with chemical substances, organisms tend to increase the probability of survival by evolving resistance against chemical substances. In other words, a group that lived long in a dirty environment gets a more pollution-resistant property than a group that inhabited in a clean environment. By using this property, we can estimate how much the environment has become contaminated with a specific chemical substance by measuring the tolerance of living organisms sampled from the environment. However, to that end, how much adaptive genetic variance is actually possessed by the population, what degree of disadvantage (fitness cost) is given to the tolerant individuals (or genotypes) under conditions without contamination need to be estimated. Collaborators and I have made *Daphnia galeata*, a common species of *Daphnia* in Japan, a model organism and found that there is a difference in tolerance to the insecticide fenvalerate among populations living in several habitats around Lake Kasumigaura. We estimated the concentration of fenvalerate that would have brought about the between-population variability in the fenvalerate tolerance (selected papers [3, 4]). This ecological risk assessment framework is called retrospective ecological risk assessment.

The compound effects of chemical pollution have long been studied as an important theme in pharmacology, environmental toxicology and ecotoxicology as well as having a history that has been discussed for a long time in environmental problems. In recent years, researches on evaluation methods have progressed over how to manage the compound effect of chemical substances internationally. As a result, it is recommended that the most common method is a model called concentration addition that does not consider the interaction between chemical substances. I have developed a model of concentration addition and devised a "generalized concentration addition model" that can be used even when there is an interaction between chemical substances (selected papers [1]).

(2) Ecosystem effect evaluation based on species ecological traits

It is feared that the ecosystem will deteriorate due to human-induced factors such as global warming and overuse of biological resources and eventually the ecosystem services ecosystem provided to human beings will decline. Ecosystems are made up of many species, and the aggregation of organisms that have core interrelationships is called biotic communities. The ecosystem response to changes in the environment is caused by exchanges of species in the community and the change in the relative number of species. For example, as environmental pollution progresses, highly tolerant species against pollution become dominant, and if such species do not have favorable properties for the functioning of the ecosystem, the ecosystem will deteriorate.

A method that analyzes and predicts changes in communities focusing on biological properties (ecological traits) of species constituting such ecosystems is called the trait-based approach. I estimated the process that the trait of a community responded by changing the composition of the species due to the environmental change, which is the basis of the trait-based approach. And I applied this method to the plankton community data observed in Lake Kasumigaura and other lakes (selected papers [5, 7]). In the model assuming a resource-competing community, in which the constituent species are competing for resources, the rate at which the community responds to the environmental change does not depend on the number of species, but is almost proportional to the squared range of trait in the community (selected papers [7]). This indicates that not only species diversity but also species trait variability in the community is important in order to keep stability and sustainability of ecosystems to environmental changes.

(3) Extinction risk of populations by genetic factors

Extinction by inbreeding depression

It is empirically well known that children who are genetically defective are born from marriage among close relatives. This phenomenon is called inbreeding depression in genetics, and can be seen in any organism, not limited to humans. It is believed that the main cause for the occurrence of inbreeding depression is that a homozygote, that is, a recessive deleterious gene that develops harmful effects when genes (alleles) from both parents are the same, is born more frequently from breeding of related individuals. In conservation biology that protects endangered species, activities for protection must always be planned with the effect of inbreeding depression in mind. When the number of individuals becomes extremely small, the surviving individuals become only relatives, and the inbreeding will also occur, causing extinction of populations and species. In particular, considering the process of extinction in which the number of individuals declines, there is a danger that a sudden progress of a decline in the number of individuals may

be triggered by spiraling interaction with a decrease in reproductive ability due to inbreeding depression, which is called as "extinction vortex".

In this study, I studied whether such extinction vortex can be caused by the interaction between genetic factors and decreasing numbers of individuals by using an integrated model of population model and population genetics model (selected papers [13, 14]). As a result, even when setting the number of genes and the rate at which the deleterious mutations occur to realistic values, the extinction vortex due to inbreeding depression can theoretically occur. But for that result two conditions are required. One of them is that before inbreeding occurs the number of individuals must decrease at a certain rate due to some external factors (a factor different from genetic factors such as overhunting and habitat reduction) at least for a short period of time, because the extinction vortex does not occur spontaneously by inbreeding. Once the decline in the number of individuals triggers the extinction vortex by inbreeding, the population will suddenly become extinct regardless of whether or not the number of individuals decreases due to the external factors in this process. Secondly, sufficient number of individuals must be maintained for a long period (at least for several hundred generations) before the number of individuals begins to decrease due to external factors. It may seem surprising that species with a large number of individuals are likely to suffer extinction caused by inbreeding depression if they encounter population crashes by external factors. On the other hand, as for species with few individuals or species that have drastically decreased in population sizes several times in the past, almost no recessive deleterious genes have been maintained because they were removed from the population in the process of population declines. In other words, it is suggested that if a species with a large number of individuals in the past dramatically decreases in a short period of time due to some causes, it may trigger the process of extinction vortex and greatly increase the extinction risk of the species. Indeed, it may be that case such as wild pigeons and codfish in the North Atlantic Ocean, which once held huge number of individuals but rapidly had become extinct by overhunting. Conversely, it is thought that for large carnivorous animals such as lions and cheetahs, which originally had few individuals and drastically reduced the number of individuals during the last glacial period, the inbreeding depression caused by recessive deleterious genes may not work fortunately (However, the decrease in immune capacity and adaptation potential due to depletion of genetic diversity are serious problems).

Genetic risk of populations by introgressive hybridization

The invasion of alien species is known to have various adverse effects on ecosystems. One of them is the problem of genetic contamination due to introgressive hybridization. This means that the alien species hybridize with the native species and the genetic property of the native species is compromised by the entry of alien species genes into the population of native species.

This phenomenon also occurs by transgenic organisms entering the field and crossing with wild species.

However, since species is a group of individual organisms that cannot be crossed with other species in the first place, it would be no problem for foreign species to come. Also, even if different species mistakenly mate with each other, they will not be able to have a normal offspring for the next generation, and the exogenous genes should be excluded from the population of native species (this is called postmating reproductive isolation). However, in rare cases, such outbreeding can form relatively normal hybrids, and the hybrid individuals will also cross the native species, so that genes of alien species gradually enter the population of native species.

So, what kinds of organisms are likely to cause such introgressive hybridization? I investigated the conditions for that with computer simulations (selected papers [6, 8]) based on the Dobzhansky-Muller model, which is considered to be one of the major mechanisms of isolation mechanism (assuming two or more loci governing the isolation mechanism, and harmful effects when their loci are both heterozygous. When such genes accumulate in many loci, crossing between two different lineages becomes impossible). As a result, when the number of genes is sufficient, the recombination rate between them is important, and it was found that the larger the value, the more likely it is that introgressive hybridization occurs. This indicates that the susceptibility to introgressive hybridization depends on the arrangement on the genome of isolation genes and that the reproductive isolation tends to collapse if the isolation genes are located on different chromosomes.

(4) Genetic variation and evolution of organisms

In order for organisms to adapt and evolve for coping with changes in the environment, genetic variability (or variation) must be kept adequately among individuals. This is repeatedly emphasized in Charles Darwin's Origin of Species, which laid the foundation of modern evolutionary theory. However, among the evolutionary ecologists, until the 1980's, it was thought that there was not enough genetic variability in many of the adaptive traits of wild lives so that evolutionary changes could be made instantaneously. I conducted genetic analysis on the adaptive characters (or traits) of organisms that are important in evolutionary ecology by the statistical analysis of traits called evolutionary quantitative genetics, and showed that organisms maintained rich genetic variabilities in the populations (selected papers [4, 12, 15, 18, 19]).

Among adaptive traits of living organisms, characters related to survival and reproduction (such as litter size and number of egg production, age of the first reproduction, viability) are called as life history traits, are considered to be the most important trait of adaptation, because they determine individual fitness (the quantity of genes inherited to the next generation) and are

always exposed to natural selection. On the other hand, life history patterns are known to be significant variable across species. So, how is the life history trait formed by evolution by natural selection? The most influential idea is that genetic or evolutionary trade-offs between traits exist, that is, there is a conflict of fitness benefit, and the evolution selects the best combination of traits among all possibilities under constraint by the trade-offs (the trait combination that maximizes fitness). For example, if there is a trade-off as a genetic constraint between the number of laying eggs and the size of eggs, the number of laying eggs and between fecundity and egg size or between fecundity and lifespan, species adapting to the environment where larger numbers of eggs (large fecundity) are advantageous must reduce the egg size or lifespan. In order to verify this hypothesis (antagonistic pleiotropy hypothesis), quantitative genetic analysis was performed using small white butterfly (*Pieris rapae*) and azuki bean weevil (*Callosobruchus chinensis*), and it was reported that such a genetic trade-off existed between the number of eggs laid and the lifespan and between numbers of eggs laid in early and late life stages (selected papers [18, 19]).

(5) Theories of social evolution in organisms

Some organisms especially animals live with conspecific individuals and cooperate with each other. And some organisms communicate with each other using signals. The evolution of social behaviors of such organisms should have something in common with the process of acquisition of human nature by evolution.

The evolution of altruistic cooperative behavior seen in eusocial insects like bees and ants was a major evolutionary problem that plagued Charles Darwin, but in 1964, W. D. Hamilton proposed a kin selection theory. Since then, altruistic behavior has come to be understood as an action to indirectly increase the genetic fitness (inclusive fitness) by raising the fitness of relatives.

On the other hand, many organisms have various ornamental traits to acquire mating partners (bird's body color and twittering, etc.) and traits that become weapons to intimidate competitors and behaviors that show surrender and obedience to opponents. Evolutionary origin of these traits has been explained by sexual selection and social selection caused by interaction among individuals. Sexual selection is a concept proposed in 1871 by Darwin, but as for social selection it has not been recognized for a long time until 1983, when sociobiologist West-Eberhard introduced the concept of social competition as a general framework of social evolution. I pointed out that social selection should be studied in a unified way, but it did not draw attention. I formulated social selection by evolutionary theory and studied the conditions under which the evolution of animal communication systems is driven by social selection by quantitative genetic

model (selected papers [16, 20]).

Human communication is mainly carried out by languages and may seem fundamentally different from animal communication. Indeed, the human language is highly regularized by syntactic rules that are shared by groups of individuals as culture, and its evolution may not be feasible until there is strong cooperative motivation between interacting individuals as Tomassero an evolutionary linguist pointed out. From the viewpoint of evolutionary theory, we should integrate the evolutionary models of communication by social selection into the evolutionary process of altruism and cooperation by kin selection and group selection. The progress of future research is expected.

Selected Papers

[1] Tanaka, Y. and Tada, M. 2016. Generalized concentration addition approach for predicting mixture toxicity. Environmental Toxicology and Chemistry 36(1): 265-275. [pdf]

[2] Mano, H. and Tanaka, Y. 2015. Mechanisms of compensatory dynamics in zooplankton and maintenance of food chain efficiency under toxicant stress. Ecotoxicology 25(2): 399-411.

[3] Tanaka, Y. and Tatsuta, H. 2013. Retrospective estimation of population-level effect of pollutants based on local adaptation and fitness cost of tolerance. Ecotoxicology 22: 795-802. [pdf]

[4] Tanaka, Y., Mano, H. and Tatsuta, H. 2012. A toxicant threshold model and the genetic variance of tolerance to pollutants. Environmental Toxicology and Chemistry 31: 813-818. [pdf]

[5] Tanaka, Y. 2012. Trait response in communities to environmental change: Effect of interspecific competition and trait covariance structure. Theoretical Ecology 5: 83-98. [pdf]

[6] Tanaka, Y. 2010. Recombination and epistasis facilitate introgressive hybridization across reproductively isolated populations: a gamete-based simulation. Evolutionary Ecology Research 12: 523-544. [pdf]

[7] Tanaka, Y. and Yoshino, M. 2009. Predicting the phenotypic response of resource-competing communities to environmental change. Journal of theoretical Biology 257: 627-641.

[8] Tanaka, Y. 2007. Introgressive hybridization as breakdown of postzygotic isolation: A theoretical perspective. Ecological Research 22: 929-939.

[9] Tanaka, Y. 2003. Ecological risk assessment of pollutant chemicals: extinction risk based on population-level effects. Chemosphere 53: 421-425. [pdf]

[10] Tanaka, Y. and Nakanishi, J. 2001. Model selection and parameterization of the concentration-response functions for population-level effects. Environmental Toxicology and Chemistry 20: 1857-1865. [pdf]

[11] Tanaka, Y. and Nakanishi, J. 2000. Mean extinction time of populations under toxicant stress

and ecological risk assessment. Environmental Toxicology and Chemistry 19: 2856-2862. [pdf]

[12] Tanaka, Y. 2000. A realized heritability of behavioral responsiveness to oviposition deterring pheromone in azuki bean weevil. Entomologia Experimentalis et Applicata 96: 239-243.

[13] Tanaka, Y. 2000. Extinction of populations by inbreeding depression under stochastic environments. Population Ecology 42: 55-62.

[14] Tanaka, Y. 1998. Theoretical aspects of extinction by inbreeding depression. Researches on Population Ecology 40: 279-286.

[15] Tanaka, Y. 1996. The genetic variance maintained by pleiotropic mutation. Theoretical Population Biology 49: 211-231.

[16] Tanaka, Y. 1996. Social selection and the evolution of animal signals. Evolution 50: 512-523.

[17] Tanaka, Y. 1996. A quantitative genetic model of group selection. American Naturalist 148: 660-683.

[18] Tanaka, Y. 1993. A genetic mechanism for the evolution of senescence in *Callosobruchus chinensis* (the azuki bean weevil). Heredity 70: 318-321.

[19] Heritability estimates of life history traits in small white butterfly *Pieris rapae crucivora*. Researches on Population Ecology 33: 323-329.

[20] Tanaka, Y. 1991. The evolution of social communication systems in a subdivided population. Journal of Theoretical Biology 149: 145-163.