

Some aspects of ecological modeling developments in China

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Abstract

The achievements of the applications of ecological modeling to population dynamics, evolutionary and behaviour ecology, global climate change, ecotoxicology, conservation of biodiversity, sustainable use of biological resources and ecological engineering, and space analysis of ecological data are reviewed. After undergoing three evolution stages in China, some new methods and ideas for ecological modeling have been proposed. It will be a trend that quantitative in combination with qualitative methods are used in future. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The development of ecological modeling has undergone three evolution stages in China. The first one was in 1960s. In 1962, the first ecological modeling research group of China was set up in the Institute of Zoology, Chinese Academy of Sciences. Ma et al. (1965) published the pioneer paper in this field, which dealt with insect population dynamics by stochastic process and compute simulation. These models had made good prediction for long term changes of locust population. The many works for ecological modeling focused on statistical ecology before 1970, for example, studies on the patterns of distribution and sampling techniques of field insect population.

The second period is from 1970 to 1990, scientific progress and social development caused two factors to promote the development of ecological modeling and ecosystem analysis: that is, one was the rapid advancement of modern computer technology, and the other was the increasing concern about ecological crises. Scientists began to deal with underlying large-scale, complex ecosystems for the purpose of management of environment, exploitation of natural resources, utilization of energy and so forth. System analysis and computer simulation are major tools for treating such large systems. The typical research work included dynamic model for cotton aphid's population, by experimental component approach, the dynamic model of cotton boll worm, which is based on time-varying distributed delay process and the dynamic model of oriental migratory locust in Hongze lake area, which is based on the generalized Lotka-Volterra–Verhulst's interaction equations.

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Since 1990, the applications of ecological modeling have expanded in the area of environmental conservation and economic development in China. Several main fields of research are ecotoxicology, conservation biology, and the sustainable use of biological resources and ecological planning. The dynamic model of toxicants in the food chain described toxicant's transfer and accumulation in aquatic ecosystem. The model for multi-objective optimal sustainable use of biological resources was developed on the basis of the theory of optimal control, which considered the effects on environmental and social benefits caused by harvesting. The models for conservation biology were developed, too, such as the model of population viability analysis (PVA). Global climate change is another inspiring area for ecological modeling.

Ecological modeling is a relatively new and exciting subdiscipline of ecology in China. After decades of development now ecological models are widely acceptable in China. In this paper, we would like to review some aspects of recent development.

2. Population dynamics

Chinese ecological scientists have taken a great interest in the modeling for population dynamics since 1960s. Li (1993) reviewed and compared several single models of insect species, which could be used as a part of a large ecosystem model for further research. The first one was SSP process that showed how to use simple differential equation to simulate the dynamics of a single insect population. The second one was account process that was based on a life table approach and contained all the parameters of natural population growth. The third one was distributed time variable maturation process with predation losses (DTVMPL). The fourth model was an age specified model that simulated population growth in insects grouped both by stages and age classes. The fifth one was of poisson process in which individual development behavior followed a poisson process.

The model for the dynamics of the cotton aphids' population was built based upon physiological time scale, by experimental component approach (Li and Xie, 1991). The parameters of the survival rates at different instars, the ratio of winged aphids and the density dependent reproductive rates at different ages were incorporated in the computer models. The models had been checked with field data to prove their validation. And according to the basic form of time-varying distributed delay process, a simulation model for cotton bollworm was established (Zhai and Li, 1991). Continuous temperatures varying functions of development duration of seven development stages (egg, 1–6 larvae) were formed from their development duration under five temperature gradients.

Age-structure, stage-structure and genetic structure effects are likely to be ecologically important when we are studying a single population or a small number of populations over a time scale comparable with the lifetime of an individual member of the population(s). Liu and his colleagues (Liu and Chen, 1988; Liu and Cohen, 1989; Liu and Zhou, 1989; Liu and Wang, 1991; Huang and Liu, 1998) have studied such kinds of structural population dynamics. The discrete, stochastic and nonlinear dynamics are also discussed in their work (Liu and Liu, 1994a,b; Liu and Gong, 1995; Jin and Liu 1999).

The research work on the metapopulation model is a brisk area, too. The two kinds of determinate models for the metapopulation of single species, general and structure models were studied, analyzing the condition of persistence of species in overall region (Zhou and Zhu, 1994). The research on two species showed the condition of coexists in the situation of competition, predator-prey or mutualism. In recent years, theorists have been exploring how an explicit consideration of space affects the dynamic interactions between hosts and parasitoids. One of the best examples of a classical metapopulation is provided by the work of Hanski and his colleagues on *Melitaea cinxia*, the Glanrille fritillary butterfly in Finland. Previous studies had shown that extinction rates were correlated with population size, but Lei and Hanski (1997) have demonstrated that parasitoid

attack also influences extinction. This work shows the importance of thinking spatially.

Besides theoretical models, some applied population models have been built, which can be used as management tools. The approach for combining reconstruction with control was adopted to eradicate locust calamity in the area of the Hongze Lake. The associated dynamics equations were formulated on the basis of the generalized Lotka-Volterra-Verhulst's interaction equations, and might be solved iteratively by using the bilateral algorithm (Lan and Ma, 1981). In addition, the research on forecasting models are also very important from management aspect, for example, the mid-term predication model of cotton bollworm (Ge and Li, 1995). These models are kind of multiregression models, which can optimally select variables on the basis of the values of C_p , R^2 and $R \alpha^2$. Song and Gao (1994) developed a prediction approach for *Cryptotheta variegata* Sneuen, by the means of smooth stochastic time series. A recent paper studied the statistical relationship between outbreaks of the oriental migratory locust (*Locusta migratoria manilensis* Meyen) and El Niño episodes, and discussed how El Niño affects locust outbreaks (Zhang and Li, 1999).

3. Evolutionary and behaviour ecology

Smith (1974, 1982) introduced the fundamental notion of an evolutionarily stable strategy (ESS) in order to explain the evolution of genetically determined social behaviors within a single animal species. The concept of evolutionarily stable strategy has not only proved of practical use in the study of animal behaviors but also has generated enormous theoretical research in this area. Chinese ecologists have made some very important contribution to the theory of ESS. Tao and Zhao (1994) showed the necessary and sufficient conditions of density-dependent evolutionary stable strategy in the two-phenotype model. In their next paper (Tao and Wang 1996), the effect of time delay is investigated. This might be a step towards the continuous time ESS models with time delay.

In the aspect of reproductive strategies, using an ESS approach, Zhang and his colleagues (Zhang and Wang, 1994; Zhang et al. 1996; Zhang and Jiang, 1997; Zhang, 1998; Zhang and Jiang, 1998) have studied the reproductive strategies of sexually reproducing organisms, in particular perennial plants. Recognizing that sexual reproduction creates a conflict between individual-level and population-level adaptations, Zhang and his colleagues (Zhang and Jiang, 1995; Zhang and Lin, 1997; Zhang and Hanski, 1998) note that some traits that lead to interspecific competitive disadvantage can be selected for and maintained within a population by natural selection if they can confer intraspecific competitive advantage to individuals, thus rendering stable coexistence of identical species plausible. This is an important contribution to competition theory, having profound implications for species diversity maintenance in natural ecosystems. Zhang et al. (1999) also develop a game theoretical analysis of competitive interactions between crop plants and argue that competition often leads to overgrowth of some resource-garnering organs, which is detrimental to the yield of crop as a whole.

4. Global climate change

The global climate change is a new critical problem met by human beings. Scientists are paying close attention to the problem. Gao et al. (1996) studied the responses of northeast China transect to elevated CO_2 and climate change using vegetation index. Green biomass dynamics of the ecological transect in northeast China was modeled using spatial simulation with a process-based model, NECT. State variables of the model included green biomass of 12 vegetation categories, and soil water contents of two soil layers. The modeled monthly green biomass of all the vegetation categories was converted into normalized difference vegetation index (NDVI) of AVHRR. The result of simulation showed that with the present climate conditions, doubling atmospheric CO_2 concentration led approximately to a 20.3% increase in green biomass, 11.2% increase in non-

green biomass, 19.0% increase in green NPP, 12.8% increase in nongreen NPP and 14.9% increase in overall average NPP at steady state.

However, researches of global climate change were mainly concentrated on the responses of terrestrial ecosystems to global change, the studies on the feed back of vegetation on climate have been seldom performed. But the study on the effect of vegetation on climate would enhance the understanding of global change, and promote the accuracy of evaluating and predicting the responses of terrestrial ecosystems to global change. Fortunately, Zhou et al. (1996) discussed the feed back of plant on climate based on the two well-known balance equations. This paper provides a long-term and region-scale based method for evaluating the effect of vegetation on climate. Another very interesting paper, we should mention, is that of Gao et al. (1996). Their results showed that the model was in very close agreement with 5 year field observations on a one-hectare fenced alkaline grassland, implying that the modeling approach used in this research is very appropriate for grassland landscape studies. From an individual level, to study the effect of global change is another very promising area. Two papers (Yu et al., 1997, 1998) should be recommended. They have proposed an ecophysiological model for individual plant under global change and studied the sensitivity analysis of individual responses of plants to global change.

5. Ecotoxicology

With the development of industry, many new chemicals are discharged into the environment. Potential endangerment brought by the chemicals for the environment and human beings have raised the attentions of Chinese ecologists. Some research work in ecotoxicology has been performed. The threshold between persistence and extinction of a population in a polluted environment was discussed (Liu and Ma, 1991; Wang and Ma, 1994). Their work was on the basis of the Kolmogorov model.

5.1. A model describing the dynamics of the concentration of toxicants in aquatic organisms

The model describes the toxicants' uptake from water and intake from food chain. The dynamics of concentration in aquatic organisms is considered as a function of the weight of body, growth rate, the efficiency of uptake and intake of toxicants and the efficiency of excretion of toxicants (Guo and Li, 1990). A model for multipredator-multiprey species system under environmental stress was developed, too, based on the Volterra Model. In order to describe the effects of toxicants to organisms by the food chain, the model considered a factor of feeding effect. The factor indicated when the action of bioconcentration was stronger than the bioassimilation, the effect of the process of predation for organisms would turn positive to negative (Guo and Li, 1990).

6. Conservation of biodiversity

Population viability analysis promises to predict for how long particular populations are expected to survive. Taking into account all the known mechanisms of extinction, these models are valuable because they go one step further than the simple examination of the mechanisms of extinction, and can be applied to specific situations and species.

The survey function for Kiang (*Asius kiang*), based upon Fourier series, was used to estimate the density of population and amount of Kiang in overall Tibet (Piao, 1994). The population viability analysis of River deer (*Hydropotes inermis*) was discussed using a stochastic simulation model (Li and Li, 1995). The models have considered demographic stochasticity, environmental stochasticity, natural catastrophes, genetic stochasticity and hunting factor.

Li and Li (1998) analyzed the current dynamics of the crested ibis population and predicted future changing by population viability analysis with the help of the computer simulation model VORTEX. The results indicated that the extinction probability of the crested ibis population was 19.7% over the next 100 years. Sensitivity analysis showed

that the extinction probabilities were sensitive to catastrophe and environmental variation, and the long-term existence of the population was most affected by the carrying capacity of the habitat and inbreeding depression. Furthermore, Li et al. (1999) have expanded these methods to spatial dynamics of crested ibis by geographical information system. Similar research work has been performed for giant panda (Li et al., 1997).

7. Sustainable use of biological resources and ecological engineering

The optimal age-specific harvesting on a fishery model was considered as an example of renewable resource management. The problem for the maximum sustainable yield of a population harvested age was analytically discussed, on the basis of Logistic matrix model (Liu et al., 1994). The values of biological resources are multiple for human. This multiplicity of value results in the multiplicity of benefits gained from biological resource. When a certain use of biological resource is carried out by harvest, the benefits provided by alive organism should be considered as factors to control yield. An approach of multi-objective satisfied sustainable use was developed, based on the principle of maximum sustainable yield (Guo, 1995). The approach gives consideration to the environmental, economic and social benefits gained from biological resource.

The methods of loop analysis were used to study the agro-ecosystem (Li and Liu, 1988). An obvious approach to redesign the commercial agro-ecosystem is to look at the pest ecosystem interactions in a system devoid of energy and chemical inputs and compare it with the existing systems. A detailed study of these systems will yield possible design changes that can be introduced in the commercial systems. Li's paper presented an overview of this design problem and discussed a procedure and its computer implementation for obtaining alteration designs. In addition, a qualitative model for the design of ecological engineering was built, by means of loop analysis (Guo and Li, 1993). The ecological engineering was for treating eutrophication in an

aquatic ecosystem. On the basis of the result of loop analysis, the structure of the food chain can be appropriately regulated so that the ecological engineering holds a certain specific function and materials and energy can be effectively utilized.

8. Space analysis of ecological data

Geographical information system and geostatistics have opened up new avenues for analyzing spatial patterns of populations in recent years. Chinese ecologists have performed some research work in the field. Li (1992) studied the spatial dynamics of the gypsy moth in Michigan by geostatistics. The semivariograms for pheromone-trap data were built to analyze the spatial dependence of the gypsy moth distribution. Then the data at unsampled locations (between traps) were gained by Kriging method, which is a technique of making optimal, unbiased estimates of regionalized variables at unsampled locations. The results showed very clearly the spatial and temporal dynamics of this insect. The methods of the analysis of biogeographical information was introduced to the research of ecological problems (Zhou and Li, 1994; Li and Zhou, 1994). The method included spatial heterogeneous indexes, the analysis of spatial pattern, spatial interaction, spatial and time correlation, the estimation and forecast of spatial density distribution and biogeographical information analysis system.

Recently, geographic information system was used to solve ecological problems in China. A GIS was built to analyze the relationships between the outbreak of pine caterpillar and the distribution of rivers and lakes (Shi and Dong, 1994). Guo et al. (2000) applied GIS combining simulating models to assess an ecosystem service for forest regulating water flow and increasing the output of a hydroelectric power station.

Wavelets have been a very popular topic of conversation in many scientific and engineering gatherings in recent years. It is a very effective technique for time-frequency analysis with the ability of preserving local information. The sampling data of forest transects, based upon ecological spatial pattern, were processed, to identify the gap structures (He, 1995).

9. Decision support system and information system

Recently, some expert systems and decision support systems have been applied to resolve unstructured ecological problems and aid decision-makers for the management of the ecosystem, which covers several areas, from management of pest and environment to biodiversity conservation. Some information systems were constructed, too.

An expert decision support system was built to manage cotton pest (Ji and Li, 1990), which consisted of data base management system, mathematical model base system and knowledge base system. MLCES expert system was used for forecasting cotton bollworm in second generation (Hui and Hui, 1994). It was based on the experiences of experts and by means of multi-level fuzzy synthetical judgement. Chinese biodiversity information system was constructed in order to meet the needs of the conservation and sustainable use for biodiversity. Guo et al. (1995) discussed the conceptual model and basic schemes for biodiversity information system, with the principle of set theory.

10. Conclusion

The developments of ecological modeling may be classified into two categories: one is theory oriented, another is application oriented. The former emphasizes the revelation of the general laws and common properties in ecology, and the establishment of general methodologies such as the studies on the space analysis of ecological data, population dynamics models evolutionary and behaviour models and the decision support system and information system; while the latter stresses the descriptions of concrete problems, for example, the modeling for conservation biodiversity, ecological engineering and planning as well as global climate change.

In the last several decades ecological models have been used increasingly in China as in other countries. This application has clearly revealed the advantages of models as a useful tool in

ecology (Jørgensen, 1994): models are useful instruments to survey complex systems, to reveal system properties and the gaps in our knowledge. Therefore, models can be used to set up research priorities and to test scientific hypotheses.

Scientists, on the other hand, have found that real difficulty in ecological modeling is that the ecological system, being a soft system, the structure and components of which are changed through time, essentially differs from the physical system that is a rigid system compared with soft system. There are more uncertain factors and more complex mechanisms in the ecological system than the physical system. Recent advances of three different kinds are driving a change in the way that modeling is being performed in ecology. First, the theory of chaos tells us that short-term predictions of nonlinear systems will be difficult, and long-term predictions will be impossible. Second, ecologists have started to recognize the importance of local interactions between individuals in ecological systems. And third, improvements in computer power (Judson, 1994). In the last Chinese national conference of ecological modelling, held in August of 1999, many participants noted these trends in ecological modelling and proposed the idea of 'information ecology' or 'ecoinformatics', which is mainly based on high technology for data collection, storage and transfer, high speed of data processing and mathematical modeling and artificial intelligence. This may be a solution for studying the complex ecosystem.

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References

- Gao, Q., Li, J., Zheng, H., 1996. A dynamic landscape simulation model for the alkaline grasslands on Songnen Plain in northeast China. *Landscape Ecol.* 11 (6), 339–349.

- Ge, S., Li, D., 1995. Study on mid-term numerical prediction of cotton bollworm. *Sino Zool.* 12, 6–9.
- Guo, Z., 1995. Strategy of sustainable use of biological resources. *Chin. Biodiversity* 3 (Suppl.), 79–86.
- Guo, Z., Li, D., 1990. The analysis on the dynamics of toxicant in the food chains of aquatic organisms and the design of ecological engineering for treating sewage, The thesis of M.S.
- Guo, Z., Li, D., 1993. Loop analysis for the combination of food chains in ecological engineering. *Acta Ecol. Sin.* 13 (4), 342–347.
- Guo, Z., Li, D., Wu, Y., 1995. Conceptual model and basic schemes of biodiversity information system. In: *Advances in Biodiversity Research. Proceedings of the First National Symposium on the Conservation and Sustainable Use of Biodiversity.* Chinese Science and Technology Press, Beijing, pp. 109–116.
- Guo, Z., Xiao, X., Li, D., 2000. An assessment of ecosystem services: water flow regulation and hydroelectric power production. *Ecol. Appl.* (in press).
- He, W., 1995. Spatial pattern analysis of forest community using the 1-D wavelet transform. In: *Ecological Modeling Progress to Meet the Challenge of Sustainable Development. Proceedings of the Tenth International Conference on State of the Art of Ecological Modeling (ISEM'95),* Beijing, pp. 38.
- Hui, R., Hui, C., 1994. Expert system (MLCES) for predicting quantity of two generation cotton bollworms production. In: *Proceedings of the Commemoration of the Founding 50 Years of the Entomological Society of China and Symposium,* Beijing, pp. 251.
- Huang, H., Liu, L., 1998. Attractive behavior for a logistic population with age dependent reproduction. *Commun. Nonlinear Sci. Numerical Simulation* 3 (1), 6–10.
- Ji, L., Li, D., 1990. The approach on cotton pest management expert decision support system. In: *Chen, Q. (Ed.), Advance in IPM on Cotton.* Chinese Agriculture Press, Beijing, pp. 334–337.
- Jin, W., Liu, L., 1999. Nonlinear model for gypsy moth and its dynamics. *J. Beijing Normal Univ.* 35 (2), 174–178.
- Jørgensen, S.E., 1994. *Fundamentals of Ecological Modeling,* second ed. Elsevier, Amsterdam, p. 9.
- Judson, P.O., 1994. The rise of the individual-based model in ecology 9 (1), 9–14.
- Lan, Z., Ma, S., 1981. System ecological basis of combining reconstruction with control on eradicating locust calamity. *Acta Ecol. Sin.* 1 (1), 30–36.
- Lei, G., Hanski, I., 1997. Metapopulation structure of *Cotesia meliteaarum* a specialist parasitoid of the butterfly *Melitaea cinxia*. *OIKOS* 78, 91–100.
- Li, D., 1993. General simulation models of insect population. *Pol. Ecol. Stud.* 19, 7–14.
- Li, Y., Li, D., 1995. The stochastic simulation model and its application on river deer (*Hydropotes inermis*) on zhoushan archipelago. In: *Advances in Biodiversity Research. Proceedings of the First National Symposium on the Conservation and Sustainable Use of Biodiversity,* Chinese Science and Technology Press, Beijing, pp. 154–159.
- Li, D., Li, X., 1998. Population viability analysis for the Crested Ibis (*Nipponia nippon*). Proceeding of the first international symposium on the geoenvironmental changes and biodiversity in the Northeast Asia, Seoul, November 16–19.
- Li, D., Liu, C., 1988. Application of loop analysis to agro-ecological engineering. In: *Ma, S. (Ed.), Proceedings of the International Symposium on Agro-Ecological Engineering,* Beijing.
- Li, D., Xie, B., 1991. Dynamic models for cotton aphids (*Aphis gossypii*) population. In: *Chen, Q. (Ed.), Advance in IPM on Cotton.* Chinese Agriculture Press, Beijing, pp. 300–305.
- Li, Y., Zhou, G., 1994. Studies on spatial auto-correlation and index of spatial disturbance. *Acta Ecol. Sin.* 14 (3), 327–331.
- Li, X., Li, D., Yong, Y., Zhang, J., 1997. A preliminary analysis of population viability analysis for Grant Panda in Foping. *Acta Zool. Sin.* 43 (3), 285–293.
- Li, X., Li, D., Ding, C., 1999. A preliminary evaluation of habitat quality of the Crested Ibis (*Nipponia nippon*). *Chin. Biodiversity* 7 (3), 161–169.
- Liu, H., Ma, Z., 1991. The threshold of survival of systems of two species a polluted environment. *J. Math. Biol.* 30, 40–61.
- Liu, L., Chen, K., 1988. Stochastic dynamics of insect population with stage-age structure: a randomized generalized leslie matrix model. *Appl. Math. — JCU,* (3), 327–338.
- Liu, L., Cohen, J.E., 1989. Equilibrium and local stability in a logistic matrix model for age-structure populations. *J. Math. Biol.* 25 (1), 73–88.
- Liu, L., Gong, B., 1995. The discrete dynamics for competitive population of Lotka-Vilterra type. *Appl. Math. J. Chin. Univ.* 10B, 419–426.
- Liu, L., Liu, J., 1994. The optimal age specific harvesting for renewable resources. In: *Lan, Z., Li, D. (Eds.), Progress on Mathematical Ecology.* Chengdu Science and Technology University Press, Chengdu, pp. 173–177.
- Liu, Z., Liu, L., 1994. Intensity of mare reproduction in Brandt's vole *Microtus brandti*. *Acta Theriol.* 39 (4), 389–397.
- Liu, L., Wang, J., 1991. Survival analysis of multi-stage development in insect species. *J. Biomath.* 16 (2), 41–44.
- Liu, L., Zhou, Y., 1989. Dynamic behavior of age-structured Ricker model. *Chin. Sci. Bull.* 34 (21), 1811–1814.
- Ma, S., Ding, Y., Li, D., 1965. Study on long-term prediction of locust population fluctuations. *Acta Entomol. Sin.* 14 (4), 319–338.
- Piao, R., 1994. Fourier series estimation for the richness of population of Kiang. In: *Lan, Z., Li, D. (Eds.), Progress on Mathematical Ecology.* Chengdu Science and Technology University Press, Chengdu, pp. 33–44.
- Shi, G., Dong, Y., 1994. Geographical information system and management of forest pest. In: *Proceedings of the Commemoration of the Founding 50 Years of the Entomological Society of China and Symposium,* Beijing, pp. 424.

- Smith, J.M., 1974. Theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47, 209–221.
- Smith, J.M., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Song, J. and H. Gao, 1994. Long-term quantity prediction of *Cryptotheta variegata* Sneuen. In: Proceedings of the Commemoration of the Founding 50 Years of the Entomological Society of China and Symposium, Beijing, pp. 257.
- Tao, Y., Wang, Z., 1996. The necessary and sufficient conditions of density-dependent evolutionary stable strategy (DDESS) in the two-phenotype model. *J. Theor. Biol.* 167, 257–262.
- Tao, Y., Zhao, S., 1994. Resource-dependent selection. *J. Theor. Biol.* 159, 387–395.
- Wang, W., Ma, Z., 1994. Permanence of population in a polluted environment. *Math. Biosci.* 122, 235–248.
- Zhai, L., Li, D., 1991. Time-varying distributed delay process and modeling dynamics of *Heliothis armigera*. In: Chen, Q. (Ed.), *Advance in IPM on Cotton*. Chinese Agriculture Press, Beijing, pp. 305–308.
- Zhang, D.-Y., 1998. Evolutionarily stable reproductive strategies in sexual organisms. IV. Parent-offspring conflict and selection of seed size in perennial plants. *J. Theor. Biol.* 192, 143–153.
- Zhang, D.-Y., Hanski, I., 1998. Sexual reproduction and stable coexistence of identical competitors. *J. Theor. Biol.* 193, 465–473.
- Zhang, D.-Y., Jiang, X.-H., 1995. Local mate competition promotes coexistence of similar competitors. *J. Theor. Biol.* 177, 167–170.
- Zhang, D.-Y., Jiang, X.-H., 1997. Evolutionarily stable reproductive strategies in sexual organisms. III. The effects of lottery density dependence and pollen limitation. *J. Theor. Biol.* 185, 123–131.
- Zhang, D.-Y., Jiang, X.-H., 1998. Evolutionarily stable reproductive strategies in sexual organisms. V. Joint effects of parent-offspring conflict and sibling conflict in perennial plants. *J. Theor. Biol.* 192, 275–281.
- Zhou, G., Li, Y., 1994. Spatial autocorrelation method used for the estimation of insect population density. *Scisilvae Sin.* 27 (4), 475–478.
- Zhang, Z., Li, D., 1999. A possible relationship between outbreaks of the oriental migratory locust (*Locusta migratoria manilensis* Meyen) in China and the El Niño episodes. *Ecol. Res.* 14, 267–270.
- Zhang, D.-Y., Lin, K., 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? *J. Theor. Biol.* 188, 361–367.
- Zhang, D.-Y., Wang, G., 1994. Evolutionarily stable reproductive strategies in sexual organisms: an integrated approach to life history evolution and sex allocation. *Am. Nat.* 144, 65–75.
- Zhou, H., Zhu, Z., 1994. Study on the dynamic model of metapopulation. In: Lan, Z., Li, D. (Eds.), *Progress on Mathematical Ecology*. Chengdu Science and Technology University Press, Chengdu, pp. 33–44.
- Zhang, D.-Y., Jiang, X.-H., Zhao, S., 1996. Evolutionarily stable reproductive strategies in sexual organisms. II Dioecy and optimal resource allocation. *Am. Nat.* 147, 1115–1123.
- Zhang, D.-Y., Sun, G.-J., Jiang, X.-H., 1999. Donald's ideotype and growth redundancy: a game theoretical analysis. *Field Crops Res.* 61, 179–187.

Further Reading

- Gao, Q., Zhang, X., 1997. A simulation study of responses of the northeast China transect to elevated CO₂ and climate change. *Ecol. Appl.* 7 (2), 470–483.
- Guo, Z., Li, D., Yan, J., 1994. Optimal control strategy for managing an ecological engineering for turning polluted water into resource. *Acta Ecol. Sin.* 14 (Suppl.), 28–34.
- Ma, Z., Cui, G., Wang, W., 1990. Persistence and extinction of a population in a polluted environment. *Biosciences* 101, 75–97.
- Mei, Y., Gao, Q., 1997. An ecophysiological model for individual plant under global change. *Acta Bot. Sin.* 39 (9), 811–820.