Predicting Changes in Ecosystems after Eradication of Invasive Species through Computer Simulations

Katsuhiko YOSHIDA

Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies
16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan
E-mail: kyoshida@nies.go.jp

Abstract

Projects to restore ecosystems have been conducted in various regions. To assess the effects of these projects, studies have been launched to predict changes in ecosystems by constructing mathematical models to reproduce target ecosystems and performing computer simulations. When an entire ecosystem including many species is the target, models using differential equations are often used to calculate population dynamics of the species constituting the ecosystem. When interactions among species are reproduced, the types of interactions are determined based on previous studies and experts' opinions. Since it often happens that the strength of interactions cannot be measured, multiple models with randomly determined strengths of interactions are prepared to perform simulations to select a model that satisfies the requirements. After that, simulations of eradication of invasive species are performed to predict the outcome. This is the general procedure. A plurality of simulations has predicted that if there are multiple invasive species, eradicating these species simultaneously will be effective for restoring the ecosystem efficiently. However, since simultaneous eradication has a larger impact on ecosystems, monitoring must continue even after eradication and appropriate measures taken. Furthermore, since the models are still in the course of development, a framework is required to feed data obtained from monitoring into the models to improve them further.

Key words : ecosystem change, eradication, invasive species, prediction, simulation

1. Introduction

Biological Invasion is one of the most serious environmental problems. This is also true in the Ogasawara Islands. On several of these islands, the vegetation has been destroyed due to grazing damage by feral goats. Large areas of bare ground have spread (Fig. 1; Hata *et al.*, 2007; Kachi, 2010). Therefore, projects to restore the ecosystems, such as eradication of invasive species, have been conducted in various regions (in the Ogasawara Islands, eradication of feral goats is complete except for on Chichi-Jima Island). One of the most severe problems is that it is often impossible to predict with ease places where effects will appear in an ecosystem when invasive species are eradicated, because multiple species interact within the ecosystem. Several studies have pointed out that various problems may occur after eradication (e.g., meso-predator release: Courchamp *et al.*, 1999; increase of another invasive species: Osawa *et al.*, 2015; negative impacts on native species via inter-specific interactions: Ballari *et al.*, 2016). Moreover, the long-term effects of eradication are mostly unclear. Accordingly, attempts to reproduce an ecosystem to be managed on a computer and assess the effects through simulations to manipulate the ecosystem, such as removals or additions of species, have been initiated to check for unexpected harmful effects (Caut *et al.*, 2007; Raymond *et al.*, 2011; Bode *et al.*, 2015, 2017; Baker *et al.*, 2017, 2019; Yoshida *et al.*, 2019). Such studies would be useful especially for the Ogasawara Islands, because

Fig. 1 Photograph of Nakoudo-Jima Island in the Ogasawara Islands, taken in June 2012. Photographer: Katsuhiko Yoshida.

unexpected harmful effects are not acceptable in ecosystems on islands registered as a Natural World Heritage site.

Although theoretical studies on removals or additions of species have been conducted over many years (Pimm, 1980; Zavaleta *et al*., 2001; Quince *et al*., 2005), these previous studies have been conducted using relatively simple hypothetical ecosystems because the purpose was to understand the general and fundamental behavior of ecosystems. In recent years, however, several studies have tried to construct simulation models reproducing real, complex ecosystems and to predict changes after manipulation due to the necessity of ecosystem management. In this paper, such trends in recent years are reviewed and future directions are discussed.

Table 1 Combinations of positive and negative interaction coefficients and types of interactions represented by them.

a_{ij}	a_{ji}	
+	-	predator-prey
-	-	competiton
+	+	mutualism
+	0	commensalism
-	0	amensalism
0	0	no interaction

a_{ij} represents the strength of influence of species j on species i and a_{ji} represents the converse. Various types of interactions observed in ecosystems can be represented by combinations of positive and negative values of a_{ij} and a_{ji}.

2. Basic Structure of Ecosystem Models

Many species interact with each other in any ecosystem, being intertwined like a web. To construct an ecosystem model, these interactions must be expressed mathematically. Differential equation models, often using Lotka–Volterra equations (Lotka, 1920 1922a 1922b, 1925; Volterra, 1926, 1928), have long been used for such expressions. Many ecosystem models are based on these equations (Caut *et al*., 2007; Raymond *et al*., 2011; Bode *et al*., 2015, 2017; Baker *et al*., 2017, 2019; Yoshida *et al*., 2019).

Ecosystems can be easily reproduced using a Lotka–Volterra equation. The Lotka–Volterra equation is presented in the following form:

$$\frac{dM_i}{dt} = r_i M_i + \sum_{j=1}^{N} a_{ij} M_i M_j, \tag{1}$$

where M_i and M_j are the biomass (or the number of individuals) of species i and j, respectively; r_i is the intrinsic growth rate of species i; N is the total number of species within a system; and a_{ij} is the interaction coefficient representing the strength of influence of species j on species i. This equation is often used in this form but there are many variations depending on the target ecosystem for the purpose of study as described below. When actually performing a calculation, the equation is expressed in the form of a matrix of N rows and N columns in a computer as shown below:

$$\begin{pmatrix} a_{11} & a_{12} \cdots a_{1N} \\ a_{21} & a_{22} \cdots a_{2N} \\ \vdots & \vdots \ddots \vdots \\ a_{N1} & a_{N2} \cdots a_{NN} \end{pmatrix}$$

Combinations of symmetric components allow easy expression of various types of interactions observed in an actual ecosystem (Table 1). For example, when a_{ij} is positive and a_{ji} is negative, species i derives benefit from species j but species j is damaged by species i; therefore, this combination represents a predator–prey relationship in which species i preys on species j. The diagonal component a_{ii} is the influence on itself, representing intra-specific competition.

The Lotka–Volterra equations have many variations depending on the target ecosystem or the purpose. Famous variations include Holling Type II, which takes handling time when organisms eat their prey into consideration, and Holling Type III, which introduces the effect of increasing difficulty for predators to find their prey or starting to search for other prey when the prey population decreases (Holling, 1959, 1965). Carrying capacity may be included in the equation, although not included in equation (1) above, or the equation may become complicated due to incorporation of various parameters that reproduce detailed properties of species to be handled such as proliferation of potential of constituent species and preferences of predators for certain prey. This tendency is particularly strong when an ecosystem with a small number of species, such as a system with three species, is considered (Caut *et al*., 2007; Bode *et al*., 2015). However, in studies in which ecosystems with many species are targeted, simple Lotka–Volterra equations are often used (Raymond *et al*., 2011; Baker *et al*., 2017, 2019; Bode *et al*., 2017). This is because it is difficult to actually collect detailed data of many species. Another reason is that the coexistence of all species constituting a target ecosystem is relatively easy to model using simple Lotka–Volterra equations. Although the Holling Type II function is observed most often in the real world (Begon & Mortimer, 1981), this equation is not often used when considering ecosystems with many species because it is extremely difficult to reproduce the coexistence of multiple species when simulations use the Holling Type II function (Yoshida, unpublished data). If all the species constituting a target ecosystem cannot coexist, such a model cannot be regarded as a successful one.

3. How to Reproduce Ecosystems

This section describes how to reproduce a target ecosystem with a differential equation model, the most common type used.

Procedures for reproducing an ecosystem are quite common and proceed as follows (Fig. 2): (1) set the species constituting the target ecosystem; (2) set the properties of the constituent species; (3) set the interactions; (4) calculate the population dynamics of each species by performing provisional simulations; and (5) select a model satisfying the requirements as a result of the simulation. Item (1) is determined using previous studies, literature and observations as references. Items (2) and (3) are also determined in the same way as item (1) using previous studies and literature data as references, but many species that have not been sufficiently studied are also included in an ecosystem with a large number of species. Therefore, although not published as papers, opinions of experts are often used as references to determine these items (Caut *et al*., 2007; Raymond *et al*., 2011; Bode *et al*., 2015, 2017; Baker *et al*., 2017, 2019; Yoshida *et al*., 2019). The model of Bode *et al*. (2017) was constructed with an emphasis particularly on such opinions. Bode *et al*. (2017) held workshops multiple times with the participation of not only researchers from universities but also a wide variety of experts including government officials, representatives of non-governmental organizations (NGOs) and environmental volunteers. They then summarized the opinions from the experts to determine whether interactions between species and interactions with environmental elements such as the amount of rainfall would have positive or negative effects on the respective species. Furthermore, Bode *et al*. (2017) also summarized opinions concerning how environmental changes and anthropogenic impacts influence interactions among species and interactions with environmental elements, and constructed a model to predict the effects on ecosystems.

Opinions of experts, however, are often not quantitative and sometimes information simply cannot be obtained. In particular, it is extremely difficult to obtain actual measurement values for the strength of interactions between species. In such a case, a small number of parameter sets that can reproduce the target ecosystems well are selected from a larger number of parameter sets, the values of which are randomly determined ((4) and (5) in Fig. 2, Table 2). What is required first for selection of the parameter set is that all species constituting the

Table 2 Detailed procedure of (5) in Fig. 2.

Literature	Raymond *et al.* (2011)	Bode *et al.* (2015)	Bode *et al.* (2017)	Yoshida *et al.* (2019)
Total number of parameter sets examined	(*1)	2 million	1 billion	500 (*2)
Number of selected parameter sets	1000	15000	10000	1
Additional criteria of selection			suitable for experts' opinion	Best fit to real data

(*1): the total number of parameter sets examined is unknown. Raymond *et al*. (2011) repeated a process of confirming stability of a system by performing simulations giving the strength of interactions randomly until 1000 parameter sets that allowed stable coexistence of all the species were found. (*2): for each parameter set, 200 simulations with different interaction matrix were conducted.

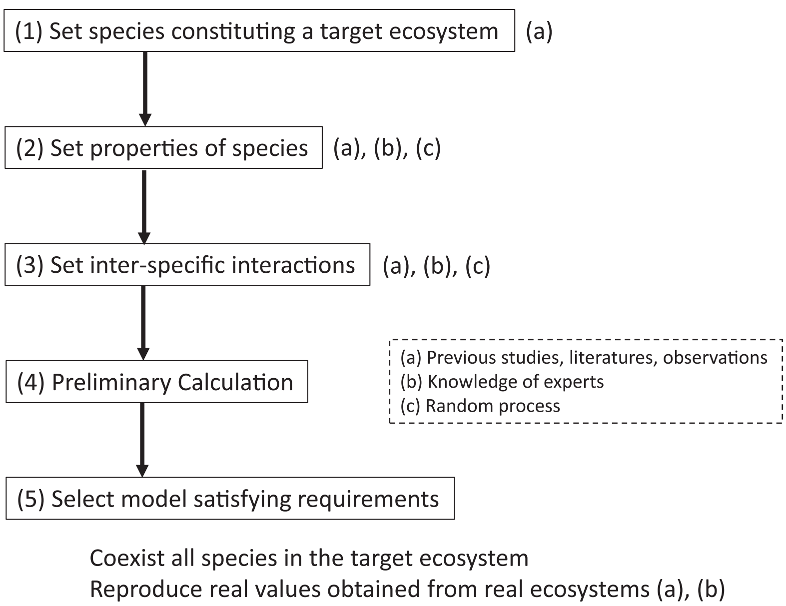

Fig. 2 Procedure for reproducing a target ecosystem.

A model to reproduce an ecosystem is created by following the procedure described in this figure. Information to be used in each step is shown in the dotted line frame. For details of procedure (5), see Table 2.

ecosystem to be reproduced can coexist. This is common to all studies

Several studies have adopted other criteria for parameter selection. Bode *et al*. (2017) selected those that showed behavior with respect to environmental changes and anthropogenic disturbances as predicted by experts who had participated in the workshops. Baker *et al*. (2017) selected parameter sets that reproduced the behavior observed in an ecosystem in Yellowstone National Park after the introduction of wolves. Yoshida *et al*. (2019) selected one parameter set with the highest ability to reproduce the actual measured values of the vegetation ratios on Nakoudo-Jima Island in the Ogasawara Islands (Hata *et al*., 2007).

4. Types of Models

Although "model" is one word, models can be divided into various types depending on the elements to be emphasized when modeling. Masuda (1991) mentioned three elements for constructing a model, likening them to the three primary colors of light (red, green and blue) (Fig. 3): realistic variables, global domain and basic understanding. "Realistic variables" (R) show correspondence to physical variables in the real world. A model emphasizing this element will necessarily introduce a process that works in the real world. "Global domain" (G) means the model constructed is of an autonomous world, i.e., not a cutaway part of a world (a cutaway part does not move autonomously), and models the target world in its entirety. "Basic understanding" (B) means being able to explain the cause-and-effect relationships in a model. This element may be restated as being able to understand the model simply and clearly.

An ideal model would have these three elements but is impossible to achieve. Therefore, two of these elements are adopted for many models. A toy model adopts G and B, and represents the entire world with a small number of variables (processes). Ecosystem models that reproduce multiple species by the Lotka–Volterra equation (Raymond *et al*., 2011; Bode *et al*., 2017; Baker *et al*., 2017, 2019) belong to this type. A process model adopts B and R, and represents cause-and-effect relationships in a cutaway portion of an ecosystem using realistic variables. Models of Caut *et al*. (2007) and Bode *et al*. (2015), which cut away a portion of a motif from within an ecosystem and adopt a plurality of realistic variables, belong to this type. A full model adopts R and G, and represents the entire world by combining realistic processes. This type of model has the advantage that it is easily seen as realistic. A representative example of this model is the global circulation model. Among the ecosystem models introduced in this paper, only the model of Yoshida *et al*. (2019) belongs to the full model type. This model includes material circulation processes such as decomposition processes of excrement, remains and dead leaves; the detritus food chain; and plant growth based on nutrient contents. It not only describes interactions among organisms simply by the Lotka–Volterra equation but also introduces many processes that actually work in ecosystems, such as preferences for prey based on characteristics of the constituent species, changes in prey menus based on the optimum foraging theory, and scrambling for places among plants or seabirds.

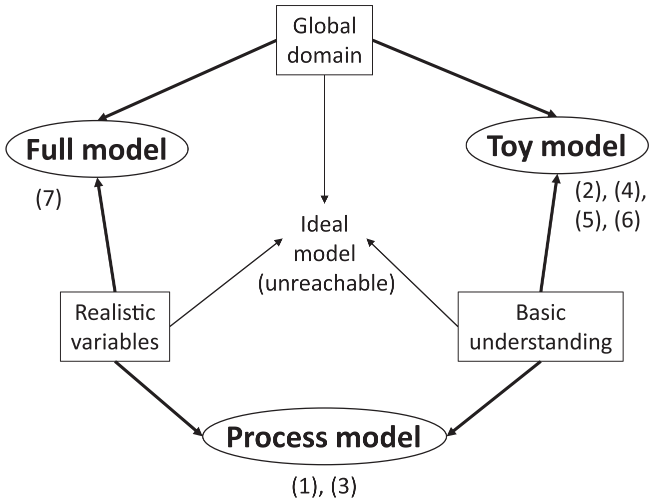

Fig. 3 Classification of simulation models (after Masuda, 1991).

The models introduced in this study are classified according to the categories of Masuda (1991). Numbers in parentheses correspond to each model: (1) Caut *et al*. (2007), (2) Raymond *et al*. (2011), (3) Bode *et al*. (2015), (4) Bode *et al*. (2017), (5) Baker *et al*. (2017), (6) Baker *et al*. (2019) and (7) Yoshida *et al*. (2019). For other items, refer to the text.

Each model has disadvantages. The toy model is necessarily an abstract model because of its structure. Therefore, it makes comparison with reality difficult, and consequently, it generally makes it difficult to gain a broad understanding. The process model is suitable for tracking modeled phenomena in a narrow range, but cannot explain behavior outside this narrow range. The full model is necessarily a complicated model, and so it makes it difficult to understand the cause-and-effect relationships of phenomena occurring within the model. Furthermore, it also causes practical problems in that a great amount of effort is required for its construction and the amount of time required for simulation becomes longer.

5. Changes in Ecosystems after Eradication of Invasive Species

This section introduces knowledge for eradication of invasive species obtained from studies using the ecosystem simulations introduced above.

As in the Ogasawara Islands, there are many known cases of multiple invasive species. Thus, whether it would be better to eradicate each of the species individually or multiple species simultaneously must be clarified. Therefore, several simulation studies have targeted such cases (Caut *et al*., 2007; Raymond *et al*., 2011; Bode *et al*., 2015; Yoshida *et al*., 2019). A conclusion common to these studies is that there is a greater restorative effect on ecosystems when multiple invasive species are simultaneously eradicated. If invasive species are eradicated individually, there is a possibility that the remaining species will become unconstrained and increase in biomass, causing unnecessary disturbances to the ecosystem (Raymond *et al*., 2011; Yoshida *et al*., 2019). These results from simulations are also corroborated by actual observations (Zavaleta *et al*., 2001; Coomes *et al*., 2003; Johnson *et al*., 2007; Hoare *et al*., 2007; Griffiths, 2011; Innes & Saunders, 2011; Glen *et al*., 2013; Osawa *et al*., 2015).

However, since eradication of invasive species itself is a disturbance to an ecosystem, the intensity of the disturbance increases when multiple species are eradicated at the same time. Therefore, it may become difficult to predict the behavior of the ecosystem after eradication. In an example by Yoshida *et al*. (2019), the restorative effect on the ecosystem certainly became larger when non-native goats and rats were eradicated simultaneously from Nakoudo-Jima Island, but the ecosystem entered a bi-stable state, that is, there was a possibility of completely opposite results, in which the whole island following eradication would change to forest or grassland (Fig. 4). Furthermore, although rare, it was also suggested that, in an ecosystem containing a large area of invasive white popinac (*Leucaena leucocephala*), where the overall diversity level was low and oligotrophication was advancing, the vegetation could be destroyed as a consequence of simultaneous eradication of goats and rats (Yoshida *et al*., 2019). Therefore, monitoring should be continued, and the ecosystem appropriately managed to prevent extreme events.

It generally takes time, effort and money to eradicate multiple species simultaneously, so this can be impossible in some cases (Bode *et al*., 2015). In fact, on Nakoudo-Jima Island, only goats have been eradicated, while rats and white popinac have not yet been eradicated. Furthermore, if the order of eradication is mistaken, species to be conserved could be adversely affected (Okochi, 2009). In such a case, it is necessary to determine a schedule of the best order for eradication. For example, Bode *et al*., (2015) showed that it was better to eradicate the predator side first when the invasive species were in a predator–prey relationship. However, a phenomenon called meso-predator release (Courchamp *et al*., 1999), in which a rapid increase in intermediate predators caused by eradication of top predators causes secondary damage to the ecosystem, may be assumed in some cases; thus, careful responses are required according to the circumstances of the target ecosystem. It is very important in actual eradication projects to maximize the effects of eradication and ecosystem restoration with a limited budget, so this will be a main theme in modelling studies.

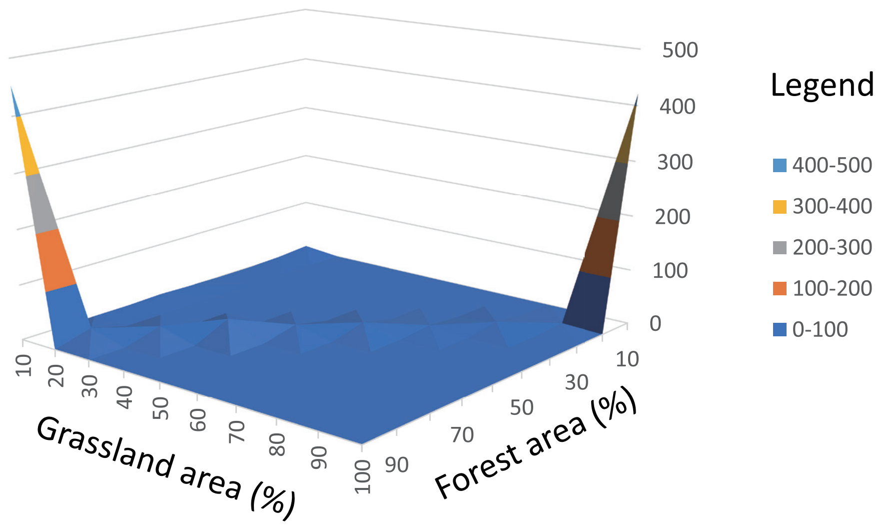

Fig. 4 Frequency distribution contour map for combinations of grassland and forest areas.

The horizontal axes on the left and the right sides show the grassland (%) and forest (%) areas, respectively. The frequency is indicated by the colors shown in the legend on the right side. The distribution is concentrated in two places: an extremity where grassland accounts for less than 10% and forest accounts for 90% or higher; and an extremity where grassland accounts for 90% or higher and forest accounts for less than 10%.

6. Future Directions

Future prediction studies using ecosystem models have just started. The models are not perfect yet and, in some cases, the actual changes in ecosystems are not consistent with the predictions. For example, Yoshida *et al*. (2019) predicted that all of Nakoudo-Jima Island would revert to forest when only goats were eradicated. Although the forested area has increased, it is at a much slower rate than predicted by the model and bare ground still remains (Hata *et al*., 2019). Furthermore, the invasive white popinac has been increasing. In this regard, inhibition of seedling colonization due to soil erosion and effects such as exposure of oligotrophic subsoil have been indicated (Hata *et al*., 2019). These elements were not included in the model used by Yoshida *et al*. (2019).

However, I never recommend adding processes and parameters to models indiscriminately. It is not always true that a correct model can be constructed by making a complex model with the introduction of many realistic processes (Iwasa, 1990). In a well-known example, the behavior of a model became unstable and the accuracy of its predictions was actually lower when the model was made more complex (Ludwig & Walters, 1985). On the other hand, models that are too simple sometimes produce incorrect results (Matsuda, 1996). A good model is one with the degree of complexity appropriate for the purpose (Akçakaya *et al*., 1999). We should keep this in mind.

Models are still being developed, so would be desirable to construct a research system including a positive feedback loop by which feedback of information obtained from monitoring can be provided to models to improve them and make their predictions more accurate (Fig. 5). If a positive feedback loop like this can be constructed, it will help us conserve ecosystems effectively and be able to understand them better.

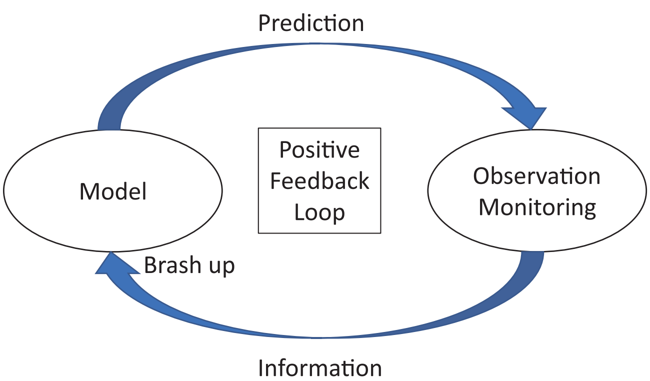

Fig. 5 Expected study framework.

Acknowledgments

I give special thanks to Naoki Kachi for giving me this opportunity and guiding me to the Ogasawara Islands, Hiroyuki Yokomizo for helping prepare this manuscript, and Kenji Hata, Kazuto Kawakami, Syuntaro Hiradate, and Takeshi Osawa for guiding me to the Ogasawara Islands. This study was partly supported by grant-in-aid for scientific research A (No. 24710038, 25241025, 16H01794) from the Japan Society for the Promotion of Science.

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Katsuhiko YOSHIDA

Katsuhiko Yoshida, Ph. D., is a senior researcher at the National Institute for Environmental Studies (NIES). His research field is mathematical ecology. He is developing original models for various types of ecosystem including those of the Ogasawara Islands. By means of computer simulations, he is trying to reveal ecosystem changes after various kinds of disturbance. He currently manages a research project for NIES on the sustainability of ecosystems of the Ogasawara Islands.

(Received 29 October 2019, Accepted 27 December 2019)