Ecological Modelling 413 (2019) 108831

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Ecosystem changes following the eradication of invasive species: Evaluation of various eradication scenarios by computer simulation

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ARTICLE INFO

Keywords:
insular ecosystem
Invasive species
Eradication
Ecosystem change
Scenario evaluation
Computer simulation

ABSTRACT

The decline of the natural ecosystem on the Ogasawara Islands caused by invasive species has been an important environmental problem and projects for eradicating invasive species are currently underway. Some invasive species have proliferated in the host environment and are affecting the material cycle in the ecosystem. If the invasive species were removed from the environment, the material cycle of the ecosystem may be altered and native species that should be protected may be negatively affected. After the introduction of invasive alien species, namely goats and rats, the vegetation declined on Nakoudojima Island, an island that belongs to the Ogasawara Islands. Therefore, in this study, a mathematical model was developed to simulate and analyze the ecosystem changes that occurred following the eradication of goats and rats. When only rats were eradicated, the island's vegetation changed to grassland but revegetation was delayed and the biomass of the native animal species did not recover significantly. When only goats were eradicated, the vegetation recovered and the biomass of the native animal species increased; however, the island became forested and many native herbaceous plant species became extinct. When goats and rats were eradicated simultaneously, the vegetation recovered and the biomass of the native animal species increased; however, the ecosystem became very unstable and two extreme results were obtained – the vegetation of the entire island changed to either forest or grassland. The results of this study suggest that instead of simply eradicating invasive species, it is necessary to monitor post-eradication changes in the ecosystem and take adaptive measures as required.

1. Introduction

In many parts of the world, invasive species are causing environmental problems. It has long been suggested that island ecosystems, especially ecosystems on oceanic islands, are susceptible to damages caused by invasive species (Elton, 1958). The Ogasawara Islands, registered in 2011 as a World Natural Heritage Site, is no exception. Following the start of human settlement in the 19th century, the unique ecosystems of the islands were severely damaged by the introduction of multiple alien species. Therefore, projects are currently underway on many of the islands in an attempt to eradicate such species.

However, invasive species cannot simply be removed from the environment because many have already established an interactive system with local native species in the host ecosystem. Removing invasive species can have a negative impact on the native species with which the invasive species interact. Human intervention can affect many native species if indirect effects are included, especially if the interactions between native and invasive species are complex. Therefore, removing component species from an ecosystem – even if they are invasive species – may disrupt the ecosystem (Pimm, 1980; Zavaleta et al., 2001; Quince et al., 2005). In addition, some invasive species may flourish in the host ecosystems and represent a large portion of the ecosystem's biomass. Goats, rats, beefwoods, white popinacs, and bishop woods are examples of this on the Ogasawara Islands.

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https://doi.org/10.1016/j.ecolmodel.2019.108831
Received 8 February 2019; Received in revised form 24 September 2019; Accepted 25 September 2019
Available online 10 October 2019

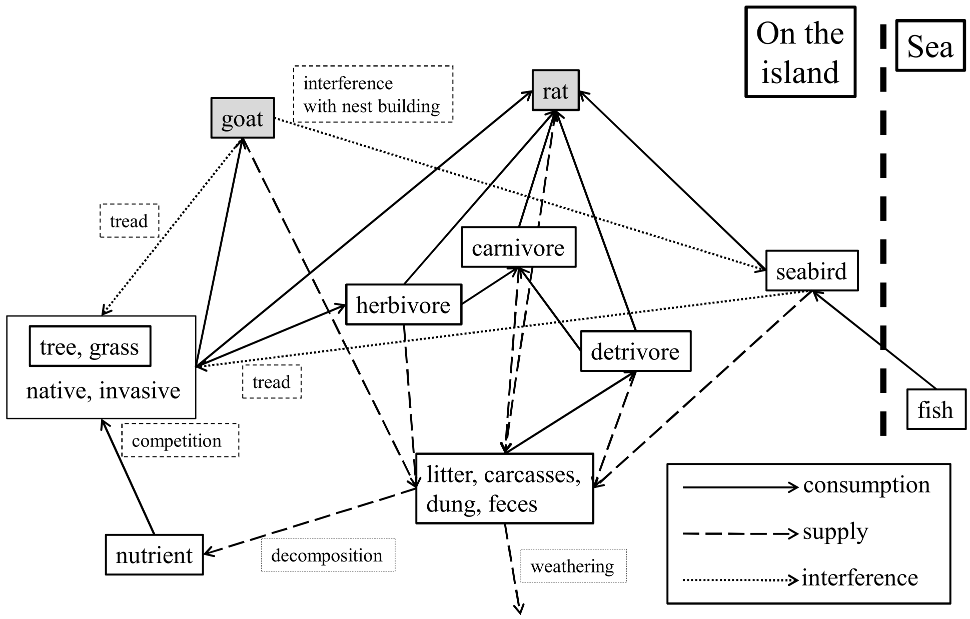

Fig. 1. Schematic diagram of the ecosystem of Nakoudojima Island.
For all species, intraspecific competition is incorporated. For plant and seabird species, intraguild competition is incorporated. These are not illustrated in the figure to avoid reducing the visual effects.

Removal of these species would greatly alter the material circulation of the ecosystem and concerns exist about the impact on native species.

It is desirable that the potential impacts of a project on the native ecosystem via material circulation are identified prior to starting an eradication project or during the early stages of an eradication project. One effective method is the use of computer simulations. This allows for the estimation of the effects of human intervention and the proposal of specific eradication methods that exert the least influence on the native ecosystem. Some theoretical studies on the effects of species removal have been conducted (Pimm, 1980; Quince et al., 2005). These studies aimed to reveal the general trends of the effect on biological communities. In cases where the target area for the computer simulation is specified, it is necessary to conduct the simulation using a mathematical model capable of representing the ecosystem of the area. Recently, several studies have been published (Raymond et al., 2011; Sahasrabudhe and Motter, 2011; Bode et al., 2015; Baker et al., 2017) that reveal interesting behavior of biological communities and can contribute to managing the target ecosystems. Such studies should continue to advance.

A potential method is to incorporate actual material cycle processes into the model ecosystem. Previous studies considered only predator-prey interactions by using simple forms of equations. However, real ecosystems are more complicated. Material cycles in real ecosystems involve several types of interactions (e.g. competition, one-handed interference) and processes. In real ecosystems, the growth of producers cannot be expressed by "*r*" alone. Even if plants receive adequate sunlight, they cannot grow without nutrients. Complicated models are not always good (Ludwig and Walters, 1985; Iwasa, 1990). However, overly simplified models cannot analyze the complex phenomena in real ecosystems. Therefore, we developed an ecosystem model incorporating material cycle processes (Yoshida et al., submitted). This model provides a good reproduction of the current state of ecosystem on the Nakoudojima Island (the target island of this study) in the Ogasawara Island Group.

The location for this study was the Nakoudojima Island in the Ogasawara Islands. The Nakoudojima Island belongs to the Mukojima Islands located 50 km north of Chichijima Island in the Ogasawara Islands.

On Nakoudojima Island, two invasive species, feral goats and rats, were an issue in the 1990s (Ogasawara Islands Ecosystem Conservation Action Plan: Kanto Regional Environment Office of Japan et al., 2010). Feral goats often destruct vegetation and accelerate soil erosion by grazing and trampling (Coblentz, 1978; Coblentz and Van Vuren, 1987). This has occurred on Nakoudojima Island. On this island, grassland and denuded areas expanded, while deforestation continued (Hata et al., 2007; Kachi, 2010). In addition, feral goats interfere with seabird nesting by trampling nests (McChesney and Tershy, 1998; Chiba et al., 2007). Because black rats are known to be generalist omnivores, they have substantial effects on plants and invertebrates (Hashimoto, 2010). In particular, impacts on endemic land snails (Chiba, 2007), endemic insects (Karube, 2010), and small seabirds have been severe (Jones et al., 2008; Kawakami et al., 2010). However, a project for the eradication of invasive goats on the island ended in 1999 (Hata et al., 2007). In addition, the eradication of rats is now being planned (Ogasawara Islands Ecosystem Conservation Action Plan: Kanto Regional Environment Office of Japan et al., 2010).

Approximately 20 years have passed since the completion of the goat eradication project and it is important to identify changes in the ecosystem resulting from their removal. Consequently, a simulation model reproducing the ecosystem of Nakoudojima Island was warranted. We developed such a model, which could reproduce ecosystem conditions on Nakoudojima Island as disturbed by invasive species (Yoshida et al., submitted). Using this model, we may be able to make strong predictions regarding changes in the ecosystem of Nakoudojima Island after eradication of invasive species. In this study, simulations of the eradication of invasive goats and rats were conducted. The goals were to identify changes in the post-eradication ecosystem and propose a desirable eradication scenario.

2. Methods

2.1. Outline of the model

The ecosystem of Nakoudojima Island prior to the eradication of invasive goats (Fig. 1) was represented using an ecosystem model developed in a previous study, and the model's details and parameters are described in Appendix Method and Yoshida et al. (submitted).

The nutrient cycle on oceanic islands is characteristically a closed

Table 1
Changes in the ecosystem after the eradication of goats and rats.

	before eradication	s.d.	after eradication of goat	s.d.	**after / before**	after eradication of rat	s.d.	**after / before**	after simultaneous eradication of goats and rats	s.d.	**after / before**
Total amount											
nutrient	11.57	4.52	104.50	193.51	**9.03**	14.87	3.85	**1.29**	420.96	341.79	**36.39**
dung of goat	0.81	0.63	0.00	0.00	**0.00**	0.88	0.35	**1.08**	0.00	0.00	**0.00**
animal carcasses	0.63	0.09	1.19	0.33	**1.88**	0.61	0.05	**0.96**	0.87	0.48	**1.38**
litter	16.91	37.76	1055.57	327.38	**62.43**	6.25	19.81	**0.37**	859.74	645.09	**50.85**
species diversity											
herbivorous invertebrate	16.18	5.14	12.32	2.67	**0.76**	12.95	4.66	**0.80**	13.04	4.30	**0.81**
carnivorous invertebrate	4.70	2.07	3.23	2.05	**0.69**	3.89	1.82	**0.83**	4.44	2.01	**0.94**
seabird	15.37	2.96	12.06	3.95	**0.79**	14.46	2.53	**0.94**	16.20	4.74	**1.05**
grassland-nesting seabird	7.70	1.72	2.06	3.95	**0.27**	7.21	1.61	**0.94**	6.20	4.74	**0.81**
forest-nesting seabird	7.67	1.76	10.00	0.00	**1.30**	7.25	1.61	**0.95**	10.00	0.06	**1.30**
grass	20.41	2.16	3.72	6.82	**0.18**	20.12	2.56	**0.99**	11.84	9.43	**0.58**
tree	10.91	1.50	9.69	2.16	**0.89**	10.71	1.82	**0.98**	10.61	1.73	**0.97**
Total amount of biomass											
herbivorous invertebrate	3.53	1.39	3.04	0.87	**0.86**	5.11	1.93	**1.45**	16.92	14.56	**4.79**
carnivorous invertebrate	0.53	0.35	0.23	0.20	**0.44**	2.16	1.23	**4.04**	6.43	3.23	**12.05**
seabird	1.58	0.55	35.11	8.12	**22.23**	1.38	0.35	**0.87**	45.80	10.14	**29.00**
grassland-nesting seabird	0.79	0.29	1.91	6.21	**2.42**	0.69	0.19	**0.88**	21.19	19.85	**26.82**
forest-nesting seabird	0.79	0.30	33.20	5.10	**42.05**	0.69	0.18	**0.87**	24.61	17.91	**31.18**
grass	10.75	5.57	0.94	3.40	**0.09**	15.70	4.71	**1.46**	18.94	21.01	**1.76**
tree	20.65	20.87	354.01	75.16	**17.15**	12.01	12.03	**0.58**	201.71	183.37	**9.77**
goat	5.78	1.80	0.00	0.00	**0.00**	6.32	1.22	**1.09**	0.00	0.00	**0.00**
rat	3.57	1.35	19.71	5.00	**5.52**	0.04	0.02	**0.01**	0.13	0.04	**0.04**
white popinac	12.33	20.78	130.08	43.61	**10.55**	4.28	11.79	**0.35**	46.12	66.63	**3.74**
ratio of area (%)											
grassland	67.64	25.13	2.22	8.17	**0.03**	88.04	15.36	**1.30**	45.06	45.32	**0.67**
forest	7.61	7.28	97.75	8.22	**12.85**	4.96	4.07	**0.65**	53.87	45.20	**7.08**
white popinac	4.12	7.45	40.15	15.57	**9.74**	1.58	4.07	**0.38**	14.05	20.72	**3.41**
bare ground	24.75	25.45	0.03	0.97	**0.00**	7.00	14.91	**0.28**	1.08	9.19	**0.04**

All figures are virtual values for the model. s.d. stands for standard deviation. The figures in the far left columns indicate the state of the ecosystem prior to the eradication. Before-after comparison values are calculated by dividing post-eradication values by pre-eradication values. When the comparison value is 1, it indicates no change in the parameter. Values smaller than 1 indicate that the parameter decreased after the eradication and values larger than 1 indicate that the parameter increased after the eradication.

system in a small area that receives an input of necessary nutrient from seabirds (Hiradate et al., 2015). An island ecosystem consists of seabirds, plants (native and invasive trees and grasses), and invertebrate animals (primarily arthropods, we assume: feeding types are herbivorous, carnivorous, scavenger, litter-eating, and coprophagous [only where goat droppings are present]).

An ecosystem includes numerous species, and often not much is known about their ecology. In the model, ecological traits of some of such species are determined by several methods (Appendix Method, Yoshida et al., submitted).

In general, seabirds feed on fish at sea and leave droppings and die on islands. The droppings and carcasses decompose over time (or, are eaten by scavengers) and are broken down into nutrient available to plants and stored in below-ground sinks. Plants grow by absorbing only the necessary amount of nutrient.

Plants are classified into herbaceous and woody plants, and plants that occupy a similar niche compete against each other. The model assumes that herbaceous plants grow faster than woody plants but grow to shorter heights and so cannot compete with woody plants. Plants are used by herbivorous animals (the model assumes only herbivorous invertebrates, invasive goats and rats). Herbivores are preyed on by carnivorous invertebrates and invasive rats.

Our model incorporates the following four processes: the growth of animals and plants, predator-prey relationship, detritus decomposition, and competition in several forms: competition among plant species and seabird species, disturbance of seabird nests by goats, and trampling of plants by goats and seabirds. For the details of the model, see Appendix Method and our previous paper (Yoshida et al., submitted).

Variables are explained in full detail below. Parameter values supported by the literature were used where possible, and where relevant literature was not available (e.g., traits of species that have not been studied in detail), values considered reasonable by an expert were estimated and iterative simulations were used to determine values that reproduce the actual island ecosystems (Appendix Method, Yoshida et al., submitted).

2.2. Simulation of eradication of invasive species

The eradication began 10,000 days after the start of the simulation. In this study, three various scenarios were used (only goats are eradicated; only rats are eradicated; both goats and rats are eradicated).

In simulating the eradication of goats, a constant amount of goat biomass was removed daily from the virtual ecosystem. In this research, we ran a simulation assuming that 40 kg of biomass was removed on a daily basis. At this removal rate, the eradication was completed in approximately 100 days. The actual goat eradication on the island was performed intermittently and completion required approximately one year. The eradication pressure used in this simulation was believed to be stronger than the actual eradication pressure used for the goat population. The adopted removal rate was chosen because a lower rate may have resulted in failure to eradicate the goats. The simulation assumed that the eradicated goats remained in the ecosystem as carcasses as it occurred in the actual eradication project.

Rats have been eradicated on many islands; however, they are difficult to eradicate and such attempts often fail (Harper and Bunburyb, 2015; Holmes et al., 2015; Keitt et al., 2015; Russell and Holmes, 2015; Amos et al., 2016). In the Ogasawara Islands, a previous attempt to eradicate rats on Nishijima Island failed. Reasons for the difficulty to eradicate rats include their high fertility, the difficulty in capturing them due to their agility, and their small size, which allows them to use hiding spaces such as gaps between rocks and reduces the catch efficiency at low population densities. The process of catching rats under these conditions can be described as a Holling III functional response (Ito et al., 1992). Therefore, in this study, the simulation assumed that workers engaging in the eradication project would remove rat biomass in accordance with the following equation (Holling III type) (Yamamura et al., 1978):

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \frac{kMm^2}{c + m^2}$$

where dE/dt: biomass removed per unit hour, k: interaction coefficient between eradication workers and rats, M: biomass of eradication workers, m: biomass of rats, c: constant (reflects handling time). In this study, k = 0.3, M = 3 (assuming the involvement of 50 workers) and c = 0.5 were used. The removed biomass remained in the ecosystem as carcasses. The efforts for eradicating rats continued until the end of the simulation. As a result, rats were not eradicated but the biomass of rats was reduced to 1.10% compared with the original status (Table 1: see the total biomass of rat after eradication of rat).

For each scenario, a 10,000-day observation period was set and the final status was compared among the scenarios. The simulation was run 1000 times for each scenario.

3. Results

3.1. Changes in the ecosystem between pre- and post-eradication

Fig. 2 shows the changes in vegetation ratio between pre- and post-eradication. Before the eradication, grassland was the dominant vegetation and approximately 24% of the island was without vegetation (Fig. 2; the value was compatible to the real data measured by Hata et al. (2007) (Yoshida et al., submitted)). When only goats were eradicated, the vegetation improved dramatically and bare ground disappeared, transforming almost the entire island into a forested area (Fig. 2). When only rats were eradicated, grassland was the dominant vegetation; however, the vegetation did not improve as much as it did for the eradication of goats, leaving 7% of the island without vegetation (Fig. 2). When both goats and rats were eradicated, bare ground disappeared almost entirely and grassland and forested areas accounted for 50% each of the island's area on average (Fig. 2). However, compared with other scenarios where goats and rats were eradicated separately, the standard deviation was considerably higher (Table 1, Fig. 2).

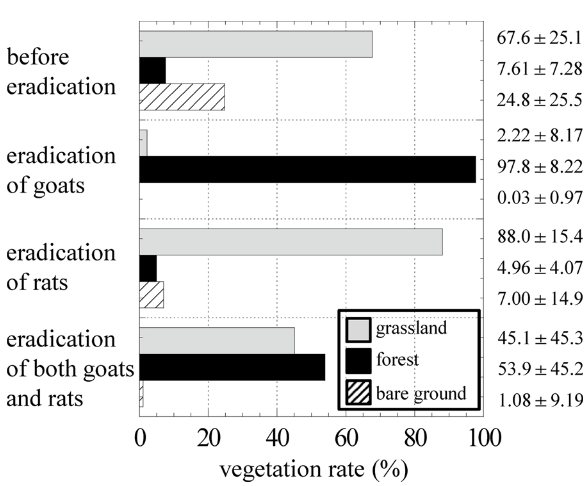

Fig. 2. Changes in vegetation ratio before and after eradication.
The figures are occupancy rates. The figures in the far right indicate average ± standard deviation.

The changes in the entire ecosystem are summarized in Table 1 and Fig. 3. When goats were eradicated, the amount of nutrient salt in the soil and the amount of litter increased noticeably (Table 1, Fig. 3a). On the other hand, both the number and biomass of invertebrate species decreased. Specifically, the number of herbivorous invertebrate species decreased by approximately 24% (Table 1, Fig. 3a). For carnivorous invertebrates, the number of species decreased by 31% and the biomass decreased by 56% (Table 1, Fig. 3a). The number of forest-nesting seabird species increased, but a decrease was observed for grassland-nesting seabird species, resulting in an overall decrease in the number of seabird species (Table 1, Fig. 3a). However, the biomass increased significantly for both grassland-nesting and forest-nesting seabirds with the latter exhibiting a more pronounced increase (Table 1, Fig. 3a). While 11% of woody plants became extinct, the number of herbaceous plant species decreased significantly to 18% compared to pre-eradication (Table 1, Fig. 3a). While the biomass of woody plants increased significantly, the biomass of herbaceous plants decreased to a near extinction level (Table 1, Fig. 3a). After the eradication of goats, the biomass of rats increased more than five-fold (Table 1, Fig. 3a). White popinacs increased significantly, with a 10-fold increase in biomass and a 14-fold increase in area (Table 1, Fig. 3a).

When rats were eradicated, the biomass of carnivorous invertebrates increased significantly (Table 1, Fig. 3b). In addition, the amount of nutrient salt, the biomass of herbaceous plants, and the biomass of herbivorous invertebrates increased slightly (Table 1, Fig. 3b). However, many parameters exhibited little recovery or worsened compared with pre-eradication (Table 1, Fig. 3b). These results indicated that it was not desirable to eradicate only rats.

When goats and rats were eradicated simultaneously, many parameters showed a marked increase (Table 1, Fig. 3c). In addition, the rate of increase in white popinacs was reduced compared to a scenario where only goats were eradicated (Table 1, Fig. 3c). These results indicated that recovery effects were highest when goats and rats were eradicated simultaneously. However, the number of herbivorous invertebrates decreased by approximately 20% and the number of herbaceous plants decreased by approximately 42% (Table 1, Fig. 3c).

3.2. Vegetation changes for the simultaneous eradication of goats and rats

Detailed analysis was performed concerning the resulting vegetation following the simultaneous eradication of goats and rats. Grasslands and forests accounted for an average of 50% each of the total area (Fig. 2). However, results did not correspond to the average (Fig. 4). Out of 1000 simulations, nearly the entire island changed to grassland 421 times, but for 468 times, the ratio of grassland lower than 10% (Fig. 4). Out of these 468 simulations, nearly the entire island became forested 459 times and became denuded (called crashed ecosystem, see below (section 3–4)). These results showed that following the simultaneous eradication of goats and rats, the ecosystem became bistable, resulting in the entire island to become either forest- or grassland-dominated.

To examine whether it was possible to predict whether forests or grasslands became dominant after the simultaneous eradication of goats and rats, the pre-eradication characteristics of the forest and grassland ecosystems were compared. Strongly significant statistical differences (99.9%) were observed only for the number of species and the biomass of carnivorous invertebrates (Table 2). Slightly significant statistical differences (95%) were observed for the total amount of litter, that of biomass of tree, rat, and white popinac (Table 2).

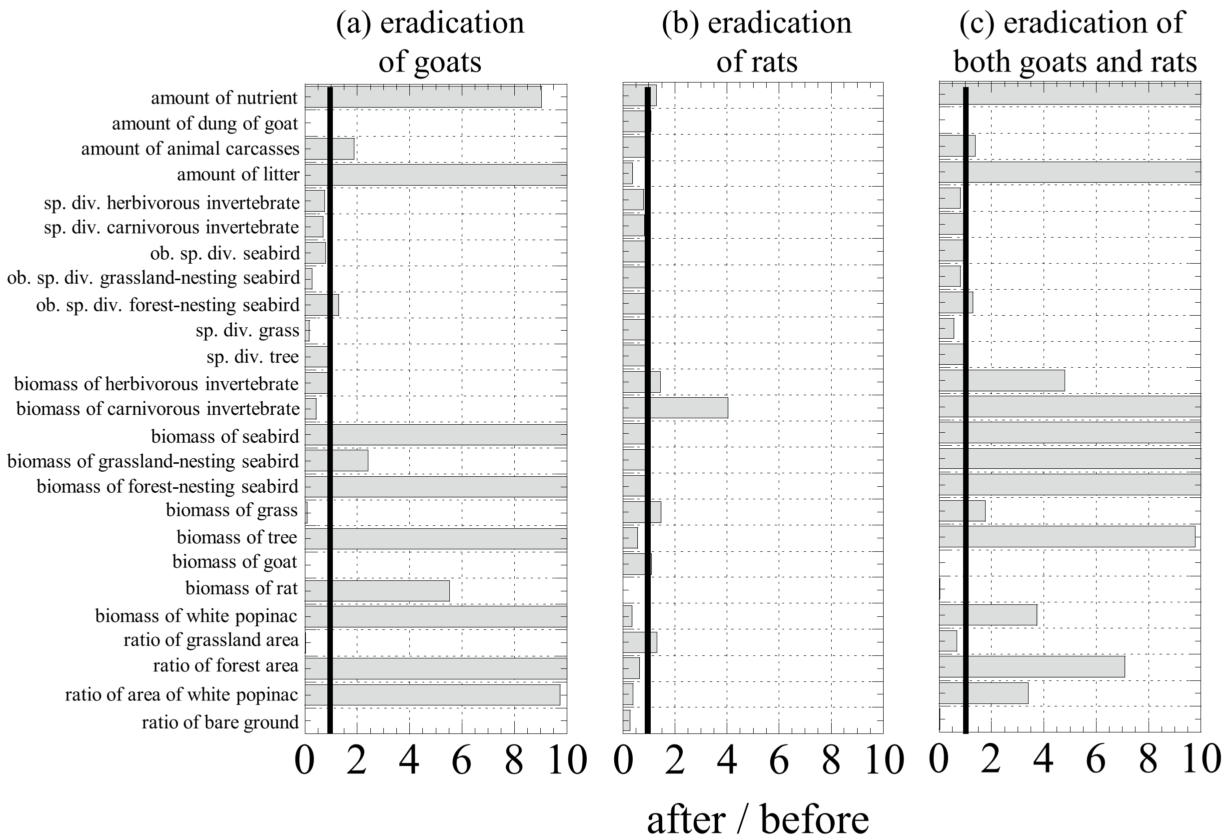

Fig. 3. Changes in the ecosystem before and after eradication.
Comparison with pre-eradication status for the three scenarios: (a) only goats are eradicated, (b) only rats are eradicated, and (c) goats and rats are eradicated simultaneously. “1” indicated by the bold line in each graph means the pre- and post-eradication levels are the same. Levels on the right side of the line indicate an increase after the eradication and levels on the left side of the line indicate a decrease after the eradication. The horizontal axis shows up to 10 times. Refer to Tables for actual figures.
Because no new species are added, the number of species does not increase except in the case of seabirds. As for seabirds, observable species (it was assumed that species with 20 or more birds could be observed) are counted; therefore, as the number of seabirds increases, the number of observable seabird species also increases.

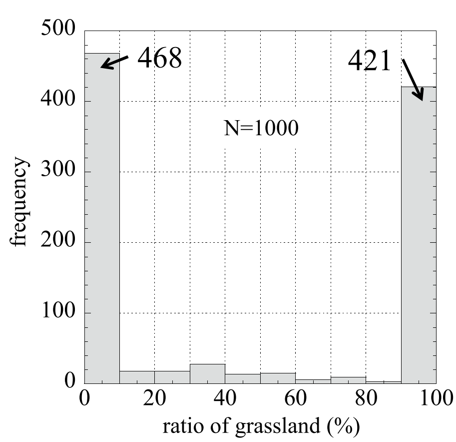

Fig. 4. Distribution of the percentage of grassland after the simultaneous eradication of goats and rats.
In most cases, if goats and rats are eradicated simultaneously, bare ground disappears, turning non-grassland areas into forests. For example, if grassland area accounts for 10%, forest area accounts for 90%. 468 ecosystems of which ratio of grassland was lower than 10% include 9 crashed ecosystems.

A comparison of the biomass of herbivorous invertebrates in the forest and grassland ecosystems after the simultaneous eradication of goats and rats indicated that the biomass of herbivorous invertebrates was twice as high in the grasslands compared to the forests (mean biomass of herbivorous invertebrates in the grassland was 22.28 [s.d. 16.67] and in the forest was 11.06 [s.d. 9.20]).

3.3. Results with large standard deviations

As with the vegetation rate mentioned in section 3–2, the amounts of nutrients and litter and biomass of herbivorous invertebrates and seabirds also had large standard deviations after the eradication of goats and rats (Table 1).

The total seabird biomass after eradication was widely distributed from 0 to 90 (Appendix Fig. 1a). As a result, it exhibited a large standard deviation (Table 1). In addition, it had a strong peak in the interval from 40 to 45 (Appendix Fig. 1a). Appendix Fig. 1b represents the distribution of the biomass of grassland-nesting seabirds. This distribution had two peaks, the interval from 40 to 45 and that from 0 to 5 (Appendix Fig. 1b). When the entire area of the island was covered by grassland in the model, the biomass of grassland-nesting seabirds reached a maximum carrying capacity (approximately 45), and that of forest-nesting seabirds was 0. Conversely, when the island was covered by forest, the biomass of grassland-nesting seabirds was 0, and that of forest-nesting birds reached the maximum value. Because the ecosystem became bi-stable (Fig. 4), the “total” biomass of seabirds was approximately 45 in most cases (Appendix Fig. 1a).

In 111 cases of 1000 simulations, forest and grassland coexisted (neither coverage ratio exceeded 90%). In such cases, the total biomass of seabirds was greater than 45, because the two types of seabirds coexisted (the maximum biomass of seabirds was 85.6).

In rare cases, vegetation on the island was not restored and a wide denuded area remained (in 9 cases of 1000 simulations, the ratio of

Table 2
Comparison of pre-eradication status between the ecosystems that became forested and the ecosystems that became grassland after the simultaneous eradication of goats and rats.

	become forested		become grassland		forested / grassland	U-test	
	mean	s.d.	mean	s.d.		P	significance
Total amount							
nutrient	11.52	4.52	11.69	4.53	0.986	0.742	
dung of goat	0.85	0.65	0.80	0.61	1.062	0.106	
animal carcasses	0.63	0.09	0.64	0.09	0.997	0.708	
litter	17.66	38.26	16.35	37.82	1.080	0.016	*
species diversity							
herbivorous invertebrate	16.04	5.21	16.56	5.10	0.969	0.172	
carnivorous invertebrate	5.47	1.93	3.87	1.98	1.414	< 0.0001	***
seabird	15.45	2.97	15.26	2.90	1.012	0.253	
grassland-nesting seabird	7.74	1.77	7.66	1.65	1.010	0.304	
forest-nesting seabird	7.71	1.74	7.60	1.75	1.014	0.294	
grass	20.42	2.08	20.47	2.17	0.997	0.408	
tree	11.03	1.29	10.83	1.65	1.019	0.393	
Total amount of biomass							
herbivorous invertebrate	3.56	1.42	3.58	1.38	0.997	0.719	
carnivorous invertebrate	0.63	0.35	0.43	0.32	1.472	< 0.0001	***
seabird	1.58	0.54	1.58	0.58	0.999	0.584	
grassland-nesting seabird	0.79	0.28	0.79	0.30	0.993	0.741	
forest-nesting seabird	0.79	0.29	0.79	0.30	1.005	0.557	
grass	10.77	5.53	10.87	5.64	0.990	0.870	
tree	21.51	20.99	19.84	20.62	1.084	0.010	*
goat	5.80	1.86	5.78	1.76	1.004	0.959	
rat	3.48	1.32	3.70	1.41	0.940	0.039	*
white popinac	12.89	20.87	11.74	20.57	1.097	0.028	*
ratio of area (%)							
grassland	67.20	24.94	68.40	25.39	0.983	0.180	
forest	7.78	7.14	7.51	7.47	1.035	0.075	
white popinac	4.18	7.34	4.09	7.61	1.022	0.099	
bare ground	25.02	25.26	24.09	25.67	1.039	0.454	

Mean values, standard deviations, and values of “forest / grassland” are shown. “U-test P” represents the result of Mann-Whitney’s U-test, and “significance” represents its significance, *: 95%, ***: 99.9%, respectively.

vegetation area did not exceed 80%, as mentioned below). In such cases, the seabird biomass declined (the minimum was 3.97). Therefore, seabird biomass was widely distributed (from near 0 to 90).

The distribution of the amount of nutrients after eradication of goats and rats had two peaks, with intervals from 0 to 100 and from 500 to 700 (Appendix Fig. 2). Then, we compared the two types of ecosystems, for which the amount of nutrients after eradication was less than 100 or was larger than 500. Ecosystems having a low amount of nutrients had a larger ratio of forest (Appendix Table 1). Such ecosystems had smaller numbers of grass species and grassland nesting seabird species (Appendix Table 1), indicating forest expansion. Such ecosystems also had greater species diversity and biomass of carnivorous invertebrates, and a lower biomass of herbivorous invertebrates. These features are compatible with those of forested ecosystems after eradication (Table 2). These results indicate that nutrients in forested ecosystems were stored in aboveground parts of the forest and not in belowground reservoirs because forests had a much larger biomass aboveground than did grasslands. In fact, the amount of nutrients in forested ecosystems was negatively related to tree biomass (Appendix Fig. 3). As mentioned above, after eradication of goats and rats, vegetation and seabird biomass in ecosystems were restored (Fig. 3 and Table 1). Consequently, the nutrient supply was increased. In the case of grassland ecosystems, nutrient supply was stored in belowground reservoirs. Then, the value of the amounts of nutrients increased. Conversely, in the case of forest ecosystems, nutrients were converted from the belowground reservoirs to tree biomass. Then, the value of the amounts of nutrients decreased.

The distribution litter after eradication exhibited two peaks at intervals from 0 to 400 and from 1000 to 1500 (Appendix Fig. 4). We compared two types of ecosystems for which the amount of litter after eradication was less than 400 or was greater than 1000 (Appendix Table 2). The most remarkable difference between them was in the vegetation. Ecosystems having a small amount of litter were covered by grasslands. On the other hand, those having a large amount of litter were covered by forests. Other differences in characteristics between ecosystems with small or large amounts of litter were similar to the aforementioned case for amounts of nutrients (Appendix Table 1). It appeared that forests produce greater amounts of litter than grasslands, because forests have a large amount of biomass per unit area. Then, we analyzed the relationship between the amount of plant biomass and that of litter (Appendix Fig. 5). The amount of litter was positively related to that of plant biomass. In addition, it was obvious that forested ecosystems had greater amounts of plant biomass and litter, and grassland ecosystems have smaller amounts. This result clearly indicated that the amount of litter was strongly controlled by vegetation type.

The amount of biomass of herbivorous invertebrates also exhibited a large standard deviation (Table 1). The distribution of biomass of herbivorous invertebrates exhibited a peak in the interval from 5 to 10 and was skewed to the right. Then, we compared the two types of ecosystems for which the biomass of herbivorous invertebrates was in the interval from 5 to 10 or was greater than 30 (Appendix Table 3). Ecosystems having a smaller biomass of herbivorous invertebrates had a lower diversity of grass species, greater diversity and biomass of carnivorous invertebrates, and a smaller ratio of grasslands. Their features were similar to those of ecosystems that had small amounts of nutrients (Appendix Table 1) and a large amount of litter (Appendix Table 2); that is, ecosystems covered by forest after eradication of goats and rats (Table 2). In fact, of 337 ecosystems for which the biomass of herbivorous invertebrates was in the interval from 5 to 10, 225 ecosystems were almost completely covered by forest (the ratio of forest

Table 3
Properties of crashed ecosystems before eradication of goats and rats.

	crashed		crashed / forested	crashed / grassland
	mean	s.d.		
Total amount				
nutrient	8.642	2.527	0.754	0.739
dung of goat	0.629	0.620	0.748	0.791
animal carcasses	0.596	0.094	0.942	0.938
litter	14.154	21.983	0.804	0.866
species diversity				
herbivorous invertebrate	13.000	2.550	0.813	0.785
carnivorous invertebrate	4.000	1.414	0.736	1.034
seabird	15.556	3.609	1.007	1.019
grassland-nesting seabird	7.333	2.550	0.949	0.957
forest-nesting seabird	8.222	1.716	1.065	1.082
grass	18.667	2.784	0.916	0.912
tree	11.111	1.054	1.007	1.026
Total amount of biomass				
herbivorous invertebrate	2.620	1.392	0.739	0.733
carnivorous invertebrate	0.398	0.337	0.639	0.933
seabird	1.625	0.488	1.028	1.028
grassland-nesting seabird	0.798	0.241	1.011	1.005
forest-nesting seabird	0.828	0.274	1.045	1.051
grass	6.735	4.460	0.630	0.619
tree	21.950	22.499	1.020	1.106
goat	5.324	1.658	0.920	0.921
rat	3.170	1.307	0.913	0.857
white popinac	15.664	20.305	1.210	1.334
ratio of area (%)				
grassland	46.203	20.233	0.692	0.676
forest	7.522	7.343	0.968	1.001
white popinac	4.758	7.339	1.134	1.162
bare ground	46.275	22.729	1.820	1.921

Data on 9 crashed ecosystems before eradication are shown. The properties of crashed ecosystems are compared to those that became forest or grassland, for which values are shown in Table 2. For abbreviations, see Table 2.

was greater than 90%), and 169 ecosystems were completely covered by forest (the ratio of forest was 100%).

3-4. Crashed ecosystems

Of 1000 simulated ecosystems, vegetation of 9 ecosystems was not restored after the eradication of goats and rats (these are called crashed ecosystems). It is very important to predict such undesirable results before eradication. Thus, we analyzed the properties prior to eradication for these crashed ecosystems. As compared with other ecosystems, crashed ecosystems had small amounts of nutrients, low diversity of grass species, a small ratio of grassland areas, low diversity and biomass of animal species, a large ratio of denuded areas, and a high ratio and biomass of white popinac forest (Table 3). These results indicated that crashed ecosystems before eradication were destroyed by invasive species to a greater extent than were other ecosystems.

We investigated changes in 9 crashed ecosystems after eradication of goats and rats. After eradication, the forest area fluctuated rapidly and strongly (Fig. 5a). Such fluctuation was never observed in ecosystems that did not crash. The first pulse of forest primarily consisted of white popinac (Fig. 5b, forest area = 30.93%, area of white popinac = 27.80%). The fluctuation pattern of biomass of herbivorous invertebrates was similar but slightly delayed relative to that of forest areas (Fig. 5a, c). This result indicated that the fluctuation pattern of forest areas was mainly controlled by herbivorous invertebrates. When the ecosystem was completely covered by forest (approximately the 14,500th time step; Fig. 5b), grass species went extinct. After that, the forest rapidly declined once more, but the rapid and strong fluctuation in forest area ceased, and forest area increased very slightly (Fig. 5a). Then, large denuded areas remained.

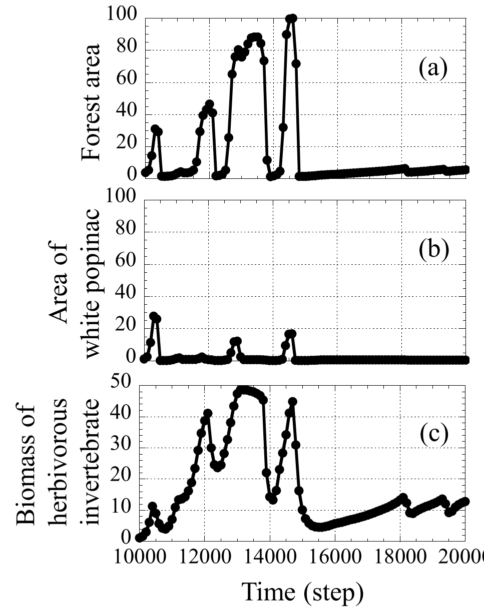

Fig. 5. Changes in a crashed ecosystem after eradication of goats and rats. Temporal changes in (a) the ratio of forest area, (b) that of white popinac area, and (c) the biomass of herbivorous invertebrates in a crashed ecosystem. Data are shown from the 100000th step (the timing of eradication of goats and rats) to the 200000th step (the end of the simulation). Data are plotted every 1000 steps.

4. Discussion

4.1. Implications for the behavior of the model system

It is well known that invasive mammals severely disturb species in invaded ecosystems (e.g., Elton, 1958; Williamson, 1996; Courchamp et al., 2003; Kachi, 2010). Then, after eradication of invasive mammals, the biomass and observable number of species were increased as compared with the pre-eradication state (plants: Hamann, 1975, 1979; Hata et al., 2007, 2010, 2014; seabirds: Robertson et al., 1994; Kawakami et al., 2010; invertebrates: Lorvelec and Pascal, 2005). The same tendencies were observed in the simulations in this study (Table 1, Fig. 3). From these results, it is considered that the model in this study could reproduce substantial properties of natural ecosystems.

Fig. 6 shows a simplified schematic diagram of the interactions in the ecosystem represented in the model. If only goats are eradicated, their feeding pressure decreases, thereby improving the vegetation (Fig. 6b). In addition, the disturbance of nesting sites caused by goats decreases, facilitating the reproduction of seabirds (Table 1, Fig. 3). As a result, the supply of nutrient salts increases significantly due to the increase in seabirds' feces and carcasses (Table 1, Fig. 3), thereby accelerating revegetation. If goats are eradicated, the biomass of rats that compete with goats for food increases (Table 1, Figs. 3 and 6b). If rats increase, their feeding pressure on invertebrates increases (Fig. 6b), thereby reducing the number and biomass of invertebrate species (Table 1, Fig. 3). If herbivorous invertebrates decrease, their feeding pressure on plants decreases (Fig. 6b), further promoting revegetation.

Some organisms are affected negatively by an increase in rats. While rats prey on seabirds, they eat only small birds (Kawakami et al., 2010). In other words, the biomass of seabirds as a whole is not greatly affected. Therefore, if goats are eradicated, the supply of nutrient salts increases significantly (Table 1, Fig. 3) and becomes the driving force behind revegetation. Rats, being omnivorous, feed on plants and the rats' feeding pressure on plants naturally increases. However, because rats also prey on other animals, their feeding pressure on plants does not increase significantly. Because herbivorous invertebrates also decrease, it is believed that the feeding pressure on plants would decrease

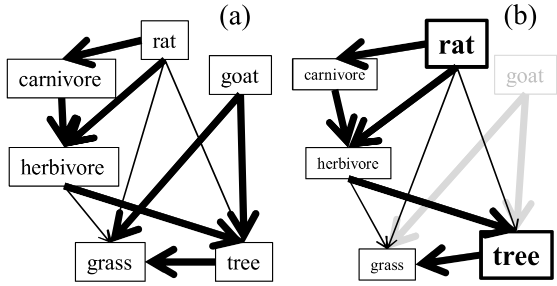

Fig. 6. Schematic diagram of interactions within the ecosystem.
(a): before eradication, (b) after eradication of goats, (c) after eradication of rats, (d) after eradication of both goats and rats. A component of the starting point of an arrow depresses the biomass of the counterpart on the end point. The thickness of arrows represents the strength of the depression. Changes in the size of font in (b) and (c) represent changes in biomass of each component after the eradication of goats and rats, respectively.

compared to when goats are present.

Why does the entire island become forested when goats are eradicated? This is due to the decrease in the feeding pressure on plants (Fig. 6b), creating conditions where both herbaceous and woody plants can increase. As a result, herbaceous and woody plants compete with each other and the taller woody plants outcompete the herbaceous plants. As a result, the entire island becomes dominated by forest.

Compared with the case where only goats are eradicated, the ecosystem does not improve if only rats are eradicated (Table 1, Fig. 3). The most important reason for this outcome is that the number of goats remains the same. Goats feed on a wide range of plants and disturb seabird nesting sites (Fig. 1). Therefore, the vegetation is damaged and the number of seabirds – the driving force behind the improvement in the ecosystem – does not increase. If rats are removed, invertebrates increase (Table 1, Fig. 3) and an increase in herbivorous invertebrates has a negative effect on revegetation. As a result, the vegetation does not improve entirely, leaving bare patches of land (Table 1, Figs. 2 and 3).

If both goats and rats are eradicated simultaneously, on average, most parameters will improve significantly (Table 1, Fig. 3). Compared with the case where only goats are eradicated, the rate of increase in white popinacs is reduced. Therefore, it is desirable to eradication goats and rats simultaneously. However, there is a possibility that as forests improve, the grassland area decreases, which reduces the number of herbaceous plant species and grassland-nesting seabird species. These potential problems may call for the implementation of additional measures, as pointed out by Okochi (2009).

The problem with the simultaneous eradication of goats and rats is that the post-eradication ecosystem is likely to progress to one of two extreme outcomes – either grassland or forested (Fig. 4). This likely results from several parameters (amounts of nutrients and litter, biomass of herbivorous invertebrates, and that of seabirds), which had large standard deviations (see Results 3-3 and Table 1) because the amount of litter and biomass of seabirds were directly influenced by vegetation, and the amount of nutrients were directly affected by the biomass of seabirds (regarding the biomass of herbivorous invertebrates, see below). The difficulty in predicting the final state of the ecosystem can pose a significant problem for managing the ecosystem. Therefore, the resulting grassland and forest ecosystems were analyzed in terms of the pre-eradication differences between the two; the only strongly significant differences (99.9%) found were the number and biomass of carnivorous invertebrate species (Table 2). If goats and rats are eradicated simultaneously, plants and invertebrates do not experience the feeding pressure (Fig. 6d). The point is that following the eradication, the herbivorous invertebrates directly control whether the island becomes forest or grassland, and the woody plants outcompete the herbaceous plants due to their slow growth that makes them susceptible to feeding damage caused by the animals (Fig. 6d).

Prior to the eradication of goats and rats, the invertebrates lived under rather harsh conditions on the island. Due to the high feeding pressure of rats and low plant biomass, the herbivorous invertebrates cannot increase (Table 1: before eradication state). This means that carnivorous invertebrates also cannot increase in biomass. As a result, when goats and rats are present, the number of invertebrate species decreases rather significantly. How the carnivorous invertebrates survive under these conditions determines the fate of the ecosystem (Fig. 7). If goats and rats are eradicated, the island's vegetation begins to improve. Herbivorous invertebrates start reproducing as the availability of prey improves and as they are free from the feeding pressures of rats. If a sufficient number of carnivorous invertebrates remain, the reproduction of herbivorous invertebrates is suppressed. As a result, woody plants and herbaceous plants propagate without being affected by herbivorous invertebrates and compete with each other (Fig. 6d). As a result, woody plants outcompete the herbaceous plants and the island becomes forested (Figs. 6d, 7). If a sufficient number of carnivorous invertebrates are not present after the eradication of goats and rats, the opposite process occurs (Fig. 7). If only a small number of carnivorous invertebrates are present after the eradication of goats and rats, the propagation of herbivorous invertebrates cannot be suppressed (Fig. 5, 6d, 7). As a result, while plants experience strong feeding pressure, woody plants are more susceptible to feeding damage due to their lower proliferation potential. Therefore, forests decline, turning almost the entire island into grassland.

What does control the number of species and the amount of biomass of carnivorous invertebrate? The total amount of biomass of rat may control them (It is not a clear conclusion, because the difference was small (Table 2)). Carnivorous invertebrates were prone to go extinct by the feeding pressure of rats, because the biomass per single species of carnivorous invertebrate is much smaller than that of herbivorous invertebrate (carnivore: 0.114, herbivore: 0.218; calculated from Table 1). Therefore, the number of species of carnivorous invertebrate became smaller when the total biomass of rat was large.

The difference in the total amount of biomass of tree in Table 2 was mainly depended on that of white popinac. Tree species other than white popinac could not increase by the strong feeding pressure of goats

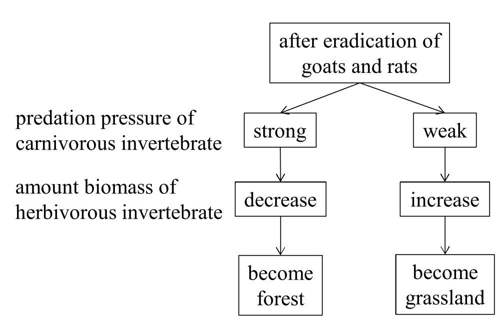

Fig. 7. Flowchart of ecosystem change after eradication of goats and rats.
The fate of an ecosystem after eradication of goats and rats depends on the strength of predation pressure of carnivorous invertebrates.

and rats. However, because white popinac has a large growth rate (Yoshida et al., submitted), it could slightly increase its biomass by the process shown in Fig. 7. The difference in the total amount of litter may be the result.

4.2. Crashed ecosystems

Although it was rare, the model ecosystem could crash after eradication of goats and rats (Fig. 5). For formulation of an ecological restoration plan, it is very important to avoid such unfavorable results. Before eradication, crashed ecosystems had a lower amount of nutrients, low species diversities for invertebrates and plants, a smaller area of grasslands, and a larger area of white popinac (Table 3). In most cases, ecosystems with a low species diversity for invertebrates became grasslands (Table 2). However, in crashed ecosystems, white popinac rapidly increases after eradication of goats and rats (Fig. 5). White popinac is a pioneer tree species that has the ability to fix nitrogen (Jayasundara et al., 1997). Therefore, white popinac can rapidly increase before the eradication state of crashed ecosystems leaving a large denuded area and a small amount of nutrients (Table 3). This rapid increase is considered a perturbation in crashed ecosystems that is strong enough to overcome the resilience of the ecosystems, and then, a so-called regime shift (e.g., Scheffer et al., 2001) occurred. Therefore, in the crashed ecosystems, there were rapid fluctuations with strong magnitudes in forest areas and in the biomass of herbivorous invertebrates (Fig. 5a, c). When the forest area reached 100%, grass species went extinct. After that grassland never expanded, even when forest declined. Then, a large denuded area remained.

Why did the fluctuations in forest area stop? The fluctuations in forest area was strongly controlled by the amount of herbivorous invertebrates (Fig. 5a, c). These were also affected by carnivorous invertebrates and grasses. If forest area increases (Fig. 8a), the biomass of herbivores increases (Fig. 8b). In this situation, carnivorous invertebrates shift their feeding effort to herbivores of trees (Fig. 8c). The forest area decreases because of the high grazing pressure by herbivores of trees (Fig. 8d). The biomass of herbivores of trees is reduced by predation pressure by carnivores and the lack of food (Fig. 8e). If forest area decreases, and the grassland area can expand (Fig. 8d). Then, the biomass of herbivores of grasses increases (Fig. 8e). Therefore, carnivorous invertebrates shift their feeding effort to herbivores of grasses (Fig. 8f). If the biomass of herbivores of trees is reduced, forest can expand again (Fig. 8a). If forest area reaches 100%, grasses go extinct (e.g., approximately the 14,500th step in Fig. 5a). At that time, the cycle shown in Fig. 8 is stopped and the fluctuation of forest area does not occur again.

4.3. Today's Nakoudojima Island and further work

On the real Nakoudojima Island, only goats were eradicated. In this case, this study predicted that the island would be covered by forest (Table 1, Figs. 2, 3). This was also observed on the Galapagos Islands (sample plots test: Hamann, 1975, 1979). In fact, the forest area on the island is expanding, but the main component of the forest is white popinac (Osawa et al., 2015). In addition, the vegetation has not yet recovered, although over 15 years have passed since the eradication of goats. One of the reasons for the slow pace of vegetation recovery is soil erosion (Hata et al., 2019). Colonization of seedlings is directly interfered with by soil erosion. In addition, soil erosion exposes the subsoil, which has a high value for soil exchange acidity and a smaller amount of nutrients. Under such conditions, it is difficult for most plants to grow, except for white popinac, which has the ability to fix nitrogen (Jayasundara et al., 1997).

Today's Nakoudojima is in a condition similar to that of crashed ecosystems; that is, there is an increase in white popinac area and a small amount of nutrients (Table 3, Fig. 5b). However, strong fluctuations in forest area (Fig. 5a) have not been observed. Thus, the ecosystem on Nakoudojima Island may not have crashed.

This study suggests that invasive goats and rats should be eradicated simultaneously (Table 1, Figs. 2, 3). Similar results were obtained in several previous studies (Caut et al., 2007; Griffiths, 2011; Innes and Saunders, 2011; Glen et al., 2013). Thus, this is considered to be a general conclusion. However, this is not always possible because of

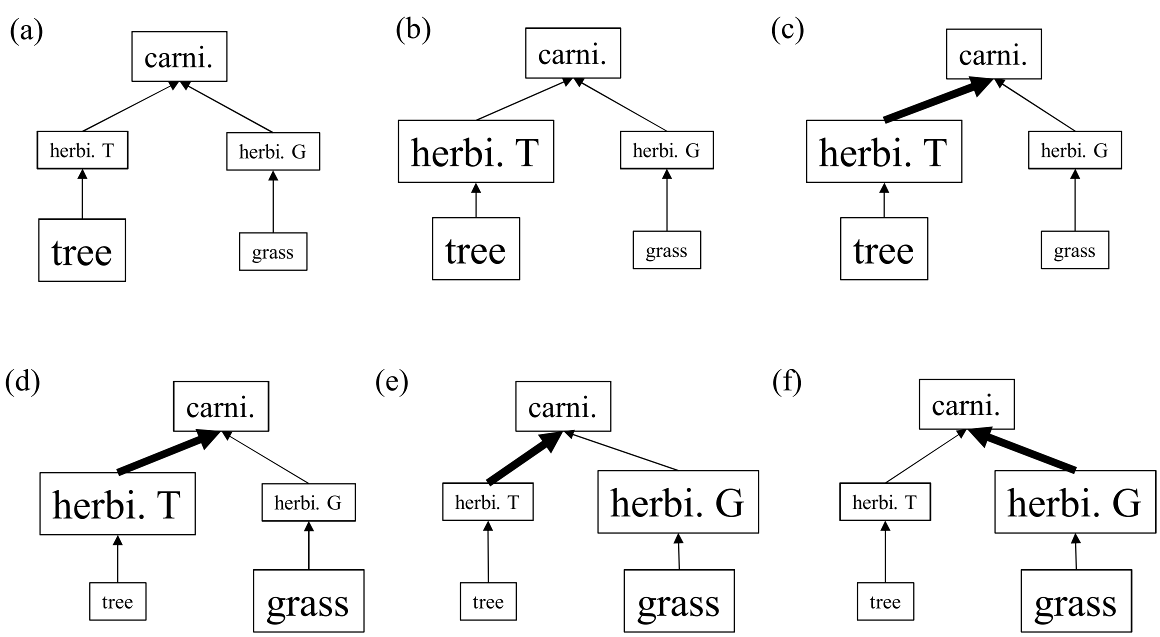

Fig. 8. Schematic diagrams of changes in a crashed ecosystem during strong fluctuations in forest area.
Fig. 8a–f represent the sequential changes of interspecific interactions in a crashed ecosystem: (a): forest expands, (b): the biomass of herbivores of trees increases, (c): predation effort of carnivores shifts to herbivores of trees, (d): forest degrades, and grasslands expand, (e): the biomass of herbivores of trees decreases, and that of herbivores of grasses increases, (f): predation effort of carnivores shifts to herbivores of grasses. The size of font represents the amount of biomass of each component, and the width of lines connecting components represents the magnitude of the interaction. carni: carnivorous invertebrates, herbi. T: herbivorous invertebrates of trees, herbi. G:, herbivorous invertebrates of grasses.

multiple reasons (e.g., the budget limitation). In this case, it is very important to determine an adequate schedule for eradication, because if an inadequate schedule is adopted, native species may be in a critical situation (Okochi, 2009). As the number of related species increases, determining an eradication schedule becomes more difficult. In such cases, computer simulation is one of the most helpful methods, and this study has already begun (e.g., Bode et al., 2015). To make more practical plans for eradication of invasive species, the issue of an eradication schedule should be considered in further studies.

5. Conclusion

In this study, three scenarios for eradicating invasive goats and rats were examined. The results showed that while some level of ecosystem recovery could be expected from eradicating only goats, it was desirable to eradication goats and rats simultaneously. However, in this scenario, it may be necessary to give special care to herbaceous plants and grassland-nesting seabirds. In addition, when goats and rats were eradicated simultaneously, one of two extreme outcomes occurred – the entire island became dominated by forest or grassland. Therefore, it is suggested that instead of only setting the goal of eradicating the invasive species to conserve the island's ecosystem, it is necessary to monitor post-eradication changes in the ecosystem while taking adaptive measures as required.

Acknowledgement

This study was supported by grant-in-aid for scientific research A (No. 24710038, 25241025, 16H01794) from the Japan Society for the Promotion of Science. We thank Yukiko Aoyama, Kyoko Sugai, Mari Kohri, Kiyoshi Satake for comments regarding features of ecosystems on the Ogasawara Islands, Hiroyuki Yokomizo for comments on the manuscript, Kenji Takamura, Noriko Takamura, Hiroya Yamano and other members of Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental studies for supporting this study.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2019.108831.

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