A new model for simulating ecosystems on oceanic islands: a case study for the Ogasawara (Bonin) Islands

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Abstract:

We developed a new ecosystem model to reproduce the nutrient cycle (imaging nitrogen) in ecosystems on the Ogasawara Islands. As in the real ecosystem, the model ecosystem consisted of about 100 species with various properties. Our model, which is based on the food web system, incorporated the following three nutrient cycle processes involved in the actual ecosystem: growth of animals and plants controlled by amount of nutrient, inter-specific interactions, and detritus decomposition. The model successfully reproduced the vegetation coverage, the number of individuals of seabirds, and the total amount of biomass of feral goats in the ecosystem on Nakoudojima Island in the Ogasawara Islands. The model also successfully reproduced the vegetation coverage of Higashijima Island. However, the model could not reproduce the vegetation coverage of the ecosystem on Nishijima Island, which has been severely disturbed by humans and an invasive parasite. Nutrient content had complex effects on ecosystems. The main cause of this complexity was that the area of forest was not positively related to nutrient content. This is derived from the behavior of white popinac. Because white popinac can fix nitrogen, it can grow without competition with other plant species in the oligotrophic condition. Then, during the stage when nutrient content was low, the area of forest continued to decline. When nutrient content exceeded a certain threshold, the area of native trees became larger as nutrient content rose. This was the cause of the complex patterns in changes in biomass of animals. The model had high performance in reproducing real ecosystems on several islands, except when having an extraordinary history. The model still has several points to be improved, but it can contribute to understanding what happened in the real ecosystem, and then can contribute to establish a system for close research cooperation between the theoretical research group and the field observation group.

Keywords

Computer simulation, Ecosystem model, Insular ecosystem, Nutrient cycle

Introduction

Ecosystem management that aimed to preserve ecosystems in danger is practiced around the world. Ecosystems can be preserved effectively if we can predict whether planned ecosystem management measures will yield their intended benefits or produce undesirable results. Therefore, attempts have recently been made to predict changes in an ecosystem by computer simulations of the target ecosystem. Caut *et al*. (2007), using a model mimicking Buck Island in the US Virgin Islands, simulated the eradication of introduced species and showed that in the presence of multiple introduced species, ecosystem preservation effects become higher when such species are controlled simultaneously. Raymond *et al*. (2011) carried out a similar simulation using a model that reproduced Macquarie Island in Australia and obtained similar results. Bode *et al*. (2015) explored optimal schedules for eradicating introduced species through a simulation model reproducing the Channel Islands in the US State of California. Baker *et al*. (2017) analyzed the effects of the reintroduction of wolves to Yellowstone National Park and the effects of the reintroduction of dingoes to a national park in semi-arid Australia. Bode *et al*. (2017) extended the Baker *et al*.'s model (2017) and developed a fascinating method in which they hold workshops inviting many interested parties and build a model through consultations with them. Baker *et al*. (2019) developed a method for building ecosystem models using time-series data of multiple species. They then developed a model that reproduced the ecosystem of Booderee National Park in Australia and showed that the reintroduction of long-nosed potoroos would have very little impact on the eastern bristlebird population but that the reintroduction of eastern quolls would increase the likelihood of eastern bristlebird decline.

Such studies contribute to conservation of endangered ecosystems. These studies utilized simple models focusing on reproducing the network topology of inter-specific interactions.

However, in real ecosystems, there are phenomena too fractious to be analyzed by simple models, for example, ecosystem changes after eradication of invasive species.

The spread of invasive species is a major environmental problem for many oceanic islands (e.g., Clarke *et al*., 1984; Hadfield, 1986; Pimm, 1987; Savage, 1987; Williamson, 1996; Hasegawa, 1999; Rodda *et al*., 1999; Ruiz and Carlton, 2003). One major invasive species is feral goat, which is well known to have major effects on native vegetation on many oceanic islands (Coblentz, 1978; Leathwick *et al*., 1983; Loope & Mueller-Dombois, 1988; Hamann, 1993; Shimizu, 2003). Therefore, projects to eradicate feral goats are ongoing on several islands (e.g. Campbell & Donlan, 2005). In some cases, vegetation has been restored (Hamann, 1975, 1979; Mueller-Dombois & Spatz, 1975; Loope & Scowcroft, 1985; Bullock *et al*., 2002; Kessler, 2002; Shimizu, 2003). However, in other cases, vegetation was not restored as observed on Nakoudojima in the Ogasawara (Bonin) Islands (e.g. Stone *et al*., 1992; Courchamp *et al*., 2003; Hata *et al*., 2010, 2019; Weller *et al*., 2011; Osawa *et al*., 2016; Hata, 2020). These examples indicate that ecosystem changes after eradication of invasive species are not simple.

One reason for this unpredictability is that invasive species are frequently incorporated into complex processes in ecosystems, such as the nutrient cycle and several types of inter-specific interactions (Hata *et al*., 2014; Hata, 2020). In order to efficiently formulate conservation measures, we need to understand the complex behavior of ecosystems after eradication of invasive species. To achieve this, it is effective to analyze ecosystem behavior using an ecosystem model that reproduces the target ecosystem with high reality, that is, the model ecosystem consists of many species with various characteristics and incorporates complex processes that function in real ecosystems.

Our goal is to establish a positive feedback system of adaptive ecosystem management by (1) constructing a plan for a nature restoration project using an ecosystem model, (2) monitoring the ecosystem after the project, (3) improving the model using monitoring data, and (4) making a new plan using the improved model. This high-reality ecosystem model will be the foundation for achieving this goal. In this study, we developed a new ecosystem model reproducing the ecosystem of Nakoudojima Island in the Ogasawara Islands. Here, we introduce the model and check the performance of reproducing the target ecosystem by comparing results of simulations with actual available data (vegetation coverage, the number of individuals of seabirds, and the total amount of biomass of feral goats). In addition, using this model, we attempted to reproduce the ecosystems of individual islands of the Ogasawara Islands (i.e., Higashijima and Nishijima Islands). We examined the versatility of this model by identifying the island(s) that could or could not be reproduced using this model.

Methods

0: Outline of the ecosystem model

This model contains many processes, and their full descriptions are too long to be included in the main text. Therefore, the model is only outlined here, and the full descriptions can be found in Appendix 1. Section numbers in Method (except for 12 and 13) correspond to those in Appendix 1.

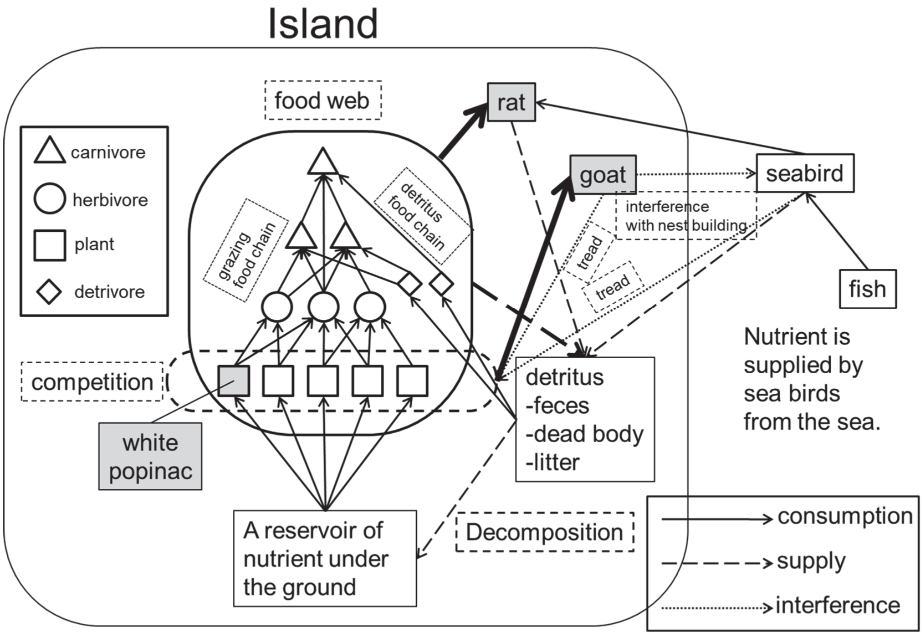

Fig. 1. Schematic figure of the nutrient cycle in the ecosystem on an oceanic island.

Terms surrounded by bold or broken lines represent components or processes in the ecosystem, respectively. Interactions among components are represented by three kinds of arrows (see the box in the bottom right of the figure).

Our model reproduces the nutrient (e.g. nitrogen) cycle in the ecosystem of Nakoudojima Island. Explicit spatial structures are not considered in this model. This is because Nakoudojima Island is small with an area of approximately 1.38 km^2 and is relatively flat with few undulations. This cycling is described schematically in Fig. 1. This island ecosystem consists of seabirds, plants (trees and grasses), and invertebrate animals [primarily arthropods, we assume that the feeding types are herbivorous, carnivorous, scavenger, litter-eating, and coprophagous (only where goat droppings are present)]. Each of these feeding groups contains multiple species. In addition, four invasive species are considered: feral goats, rats, white popinac (*Leucaena leucocephala*) for Nakoudojima and Higashijima Islands; and beefwood (*Casuarina equisetifolia*) for Nishijima Island.

Including parameters for species (e.g. growth rate, death rate, nutrient content, and feeding type), this model requires many variables to be determined (Tables 1 and 2, Appendix 1). Values for the variables were obtained from the literature, unpublished data, and experts' opinions (see Table 1 and Appendix 1). For other variables (Table 2), multiple simulations were run by assigning random values and the parameter sets that best reproduced the ecosystem of Nakoudojima Island (see Appendix 2).

Our model, which is based on the food web system, incorporates the following three nutrient cycle processes involved in the actual ecosystem: growth of animals and plants regulated by nutrients, inter-specific interactions (predator–prey, competition, and interference), and detritus decomposition (Fig. 1). The nutrient cycle on oceanic islands is characteristically a closed system in a small area. On the Ogasawara Islands, the input of nutrient from seabirds is a major nutrient source (Hiradate *et al*., 2015). Seabirds feed on fish at sea. They leave droppings and die on islands. Droppings and carcasses of seabirds decompose and are broken down into nutrients available to plants. Nutrients are stored in belowground sinks (section 9 in Appendix 1).

Plants grow by absorbing nutrients from under the ground (section 1-2 in Appendix 1). Each plant species absorbs only the amount of nutrients it needs at that time. The amount of biomass growth is regulated by the amount of nutrients absorbed. In a severely oligotrophic condition, plant biomass may be reduced. In addition, inter-specific interactions and habitat area also regulate the amount of biomass of plant species (mentioned below).

The main part of this model is the food web system. Animals, except for detritivores, feed on other species with characteristics that fit their preference (section 3-1 in Appendix 1). Calculations for the food web system are based on biomass. Changes in biomass regarding predator–prey interactions are described by a Holling type III equation [eq. (12) in section 3-1 in Appendix 1]. An animal preys on other species in the order of its preference. The animal stops its predation when the nutrients contained in the assimilated biomass reach the maximum necessary amount for the species' population at that point (the amount of nutrients necessary to compensate for the biomass lost through metabolism and furthermore to realize the population's maximum growth). Retainable biomass is determined based on the amount of nutrients ingested.

Our model incorporates 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 (Fig. 1). Plants having similar characteristics compete against each other (section 1-4 in Appendix 1). Inter-specific competition between plant species is described by a process in which a taller plant encroaches the habitat area of a smaller plant. The size of the area encroached is calculated by a simple Lotka–Volterra equation [eq. (8) in section 1-4 in Appendix 1]. The size of the area encroached is larger as the difference between the height of the two plant species is greater and as the stress tolerance of the smaller plant species is lower. Our model assumes that herbaceous plants are shorter and so cannot compete with trees. Competition among seabird species is described as the same process (section 8 in Appendix 1). In this case, a bigger seabird encroaches the habitat area of a smaller seabird. Seabirds interfere with plant growth around their nests by trampling (section 8 in Appendix 1). Goats interfere with the nesting of all seabird species by trampling a wide area on an island (section 7 in Appendix 1).

Our model considers optimal foraging (section 5 in Appendix 1). Initially, a predator selectively allocates their feeding effort to prey with characteristics close to the predator's feeding preference. Predation effort changes according to changes in the available prey biomass. A predator sequentially feeds on prey according to the difference between the feeding preference of the predator and the characteristics of prey (App.1-Fig. 2). A predator stops feeding when its nutrient intake reaches the amount that they need at the time, even if there is prey remaining. Animals assimilate a part of the biomass taken in. The assimilation rates of animals were determined by referring to the literature (section 3-1 in Appendix 1).

The biomass not assimilated by a predator is expelled as droppings. In addition, animal carcasses and litter are produced constantly. A part of detritus [animal droppings (only droppings of goats), carcasses, and litter] is used by detritivores (dung feeders, scavengers, and litter feeders; section 4 in Appendix 1). Unused detritus is decomposed within a certain period, broken down into nutrients available to plants and stored in belowground sinks (section 9 in Appendix 1).

Other than nutrients, inter-specific interactions, and habitat area, factors that limit plant productivity include light, soil pH, pathogens, and water. Regarding light, the Ogasawara Islands are situated in a subtropical zone, and sunlight hours are not a limiting condition for plants, unlike in high latitude environments. In addition, all the subject islands are all flat and are not constantly covered with clouds generated due to topography. Therefore, we decided that light is not a factor limiting plant growth. Concerning soil pH, to introduce it into the model, we will need to introduce soil erosion and spatial structures as well as chemical reactions in the soil, which would make the model too complex, and so we decided not to introduce pH at this time. Regarding diseases, it can suddenly become prevalent, causing catastrophic consequences, and we cannot predict when that will happen. These characteristics of diseases differ greatly from those of other biological components of an ecosystem. We decided that they should be dealt with in other models and decided not to introduce diseases into the model at this time. Water is one of the most important elements for animals and plants. In fact, during a drought on Chichijima Island, the numbers of seedlings and juvenile trees decreased (Shimizu, 1999, 2018); and unusual defoliation and dieback were observed (Yoshimura *et al*., 2017) and plant activity decreased over a wide area (Miyoshi & Matsuyama, 2022). However, no major changes in vegetation ratio have been reported during such serious droughts, which occur once every several decades (Matsuyama, 2018). Thus, we considered that drought does not have a fatal impact on the ecosystem. We also considered that seasonal changes in the amount of precipitation do not have a severe impact on the ecosystem, because the magnitude of the seasonal change is much smaller that the drought mentioned above. In addition, all the subject islands are small and do not have large rivers, and all plant species are considered to be given equal water conditions for simplification. Because water is very important for living things, we must develop a new ecosystem model incorporating water in the future. However, it is very difficult to incorporate water into a food web model and, consequently, models incorporating both nutrient and water cycles are rare. Therefore, we decided not to incorporate water into our model.

For the purpose of this study, one round of calculations for the aforementioned processes is defined as one time step. In one time step, each species loses biomass equivalent to that lost through metabolism in one day (Yodzis & Innes, 1992). While we assume one time step to be one day, we have not been able to define this clearly; therefore, in this paper, related data are expressed in time steps.

The Ogasawara Islands, the subject of this study, are situated in a subtropical zone and do not experience winter temperatures low enough to disable the growth of animals and plants; therefore, for simplicity, seasonality is not considered in this model.

One of the characteristics of island ecosystems is that they are closed systems and limited in area (the fifth paragraph in section 1-1 in Appendix 1). This means that the total amount of plants that an island can support is limited, which in turn limits the total amount of animals that can be supported. These are essential considerations when modeling the nutrient cycle of an island. Our model assumes that the habitat area of plants and the nesting area of seabirds are finite, whereas our model does not use an explicitly specific structure but incorporates the concept of area. Then, competition among plant species and among seabird species is described in terms of competing for space. As mentioned, nutrients necessary in this ecosystem model are supplied by seabirds. Twenty seabird species are introduced at the start of the simulation (Table A.1). Seabird species commonly nest on more than one island. If a seabird population becomes locally extinct on one island as a result of simulation, individuals of the same species are able to recolonize from other islands. In this study, it is assumed that if any of an island's seabird species becomes locally extinct, one pair of the species migrates from another island. If this rule is adopted, however, seabirds will never become extinct, which would preclude considerations of diversity in the model. Therefore, it is assumed that seabirds cannot be observed unless there are at least 10 nesting pairs. Also, based on this assumption, the initial number of seabird species becomes the upper limit.

1. Plants

1-1. Plant traits

Even small oceanic islands are inhabited by diverse plant species. However, ecological data required by the model are not available for all plant species. For the purpose of modeling, virtual parameters must instead be set. In doing so, care must be taken to not give advantages to particular species. Otherwise, species with advantageous traits will quickly outcompete other species, leaving the model unable to reproduce the natural ecosystem with many coexisting species. For this study, to express multiple trade-offs based on a single rule, a method was adopted that sets data for individual plant species by applying the concept of Grime's triangle (Grime, 1974, 1979; Grime *et al*., 1988). To avoid giving advantages to particular species, all plant species are given 100 points, which are allocated across the three strategies: competitive (C), stress-tolerant (S), and ruderal (R). Ecological traits of plant species are determined based on these values (for details, see section 1-1 in Appendix 1).

Each plant species is given a height. The height of plants influences the upper limit of biomass they can retain and their competitiveness (see section 1-4 in Appendix 1). Competition among plant species). The heights of dominant plant species, such as white popinac and beefwood, are set for the model as shown in App.1-Table 1. For other plants, heights are set using uniformly distributed random numbers. Grass species are not taller than tree species.

In our model, each plant species has an exclusive habitat area (occupied area). In proportion to their occupied area, each species is given an upper limit of biomass that it could achieve. The upper limit of biomass for each plant species is determined by multiplication of current occupied area and plant height. It is assumed that plants cannot increase the area they occupy unless the biomass sufficiency rates (the ratio of the current amount of biomass to the upper limit of biomass) of them are equal to or larger than a threshold (area increase threshold; Table 1, section 1-3 in Appendix 1). It is assumed that the area a species occupies decreases when the species cannot maintain its “keep area threshold” (Table 1 in the main text) biomass as the biomass sufficient rate of the species becomes equal to this threshold. The area no longer occupied becomes bare ground.

Inter-specific competition is described by the rule that taller species take occupied space away from shorter species (for details, see section 1-4 in Appendix 1). It is assumed that a tree species becomes extinct when its biomass decreases below the biomass of an individual tree.

White popinac and beefwood are known to be able to fix nitrogen, and this model assumed that only these species could fix nitrogen. White popinac have been shown to obtain 60% to 80% of their nitrogen requirements through biological nitrogen fixation (Jayasundara *et al*., 1997). If we incorporate these nitrogen fixation rates, white popinac can grow almost freely without any supplemental nutrient, because our model considers a single kind of nutrient. In reality, of course, plants require many other nutrients besides nitrogen, such as phosphorus, for growth, and it is therefore assumed that plants can secure 30% of their nitrogen requirements by biological fixation.

1-2. Plant growth

In general, plants grow more if they absorb more nutrient. The absorption rate of nutrient increases with nutrient density but does not increase infinitely. Growth parameters are determined by the predominance of the C strategy. If nutrient density is high, C-strategy species absorb nutrient quickly and grow quickly (the rate of increase in biomass increases). At low nutrient densities, however, they cannot absorb nutrient and cannot grow. In a natural setting, a C strategy may be advantageous or disadvantageous depending on environmental conditions, but in our model, parameters are set based on rules that do not give potential advantages or disadvantages to particular species. In addition, because faster-growing plants tend to drop old leaves more quickly, it is assumed that the rate of biomass loss increases and decreases as growth rate does.

1-3. Increase in area occupied by plant species

Our model incorporates area by considering increases in occupied area as well as increases in biomass. The rates of increase in area per time step are determined using uniformly distributed random numbers. White popinac and beefwood, which are known to rapidly spread and increase their occupied area, are assumed to have the highest rate of area increase rate among woody plants. Herbaceous plants have a higher rate of area increase than woody plants. Where bare ground is available, plant species that rely more on the R strategy increase their occupied area faster. Where bare ground is not available, plants push out shorter competitors from suitable areas. For woody plants, grassland plays the same role as bare ground.

The area occupied by plants cannot exceed the area of the island. The rate of area increase per time step of native woody plants is given by uniformly distributed random numbers between the minimum and the maximum values of the rate of area increase per time step of native woody plant (Tables 1 and 2). To calculate the rate of area increase of herbaceous plants, which expand faster than woody plants, the aforementioned random numbers were multiplied by a grass coefficient (Table 2).

1-4. Competition among plant species

Competition among plant species is defined as a scramble for habitat. In plants, in essence, taller individuals remove their competitors by shading them out. Therefore, competition between species is represented by the process of taller species encroaching into the habitat of shorter species. The area of a shorter species encroached upon by a taller species is calculated using a simple Lotka–Volterra equation.

2. Traits of animal species

Each animal species is given a maximum growth rate, which is defined as the population-level biomass increase rate when food is sufficient. A biomass increase at the population level represents offspring being born and growing. The maximum growth rate of goat, rat, and seabird species are set according to the literature, unpublished data, and experts' opinions. Invertebrate animals generally reproduce quickly, but their accurate values are almost unknown. Then, in this study, maximum reproductive rate for invertebrates were chosen from 500 parameter sets (Table 2, Appendix 2), and the potential reproductive rate for each invertebrate species is determined by using a random number (Table 1).

The biomass decrease rate per time step of goat, rat, and seabird species are also set according to the literature, unpublished data, and experts' opinions (Table 1). For invertebrates, the biomass decrease rate are set assuming that species with a higher reproductive rate have a higher biomass reduction rate. Values of metabolism efficiency of animal species are estimated by the equation in Yodiz & Innes (1992).

The body weights of animal species are also set according to the literature, unpublished data, and experts' opinions (Table 1). The weights of invertebrate species are determined using randomly distributed random numbers.

3. Grazing food chain

The species combinations for which predator–prey relationship has been confirmed (Fig. 1) are reproduced in our model. The species combinations for which predator–prey relationships have not been confirmed, especially relationships involving invertebrates, are established virtually based on the Niche Model proposed by Williams & Martinez (2000) (see the former half of section 3-2 in Appendix 1). A predator allocates more predation effort to prey species with characteristics closer to its preferences (see the latter half of section 3-2 in Appendix 1). Once the species has filled its requirements for nutrient (becomes satiated), it stops eating for the time step. Predatory animals prey on animals smaller than them (Vézina, 1985; Warren & Lawton, 1987; Cohen *et al.*, 1993; Pahl-Wostl, 1997; Neubert *et al.*, 2000; Jennings *et al.*, 2001; Brose *et al.*, 2005). Because homoiothermic animals are highly mobile, they can spend more effort on eating (the total of their interaction coefficients is high). The totals of interaction coefficients for individual animal species are shown in Table 2. Black rats feed on all species in the ecosystem including seabird, however, they cannot feed on seabirds larger than a certain size (Jones *et al.*, 2008, for details, see section 6 in Appendix 1). Goats feed on all plant species. Korean lawn grass grows from low down the stem and so is not fatally damaged by goats' feeding (Kachi, pers. obs.). Seabirds do not forage on the islands but feed on fish out at sea, absorbing necessary nutrient there. Interaction coefficients for fish are set as constant (Table 1). In this model. invertebrate is divided into carnivore, herbivore, dung feeder, litter feeder, and scavenger. Herbivore is divided into two groups; one grazes tree and the other grazes grass. Resources and animals consuming them are listed in App.1-Table 2.

Seabirds concentrate their feeding effort on fish out at sea. Litter feeders, dung feeders, and scavengers concentrate their feeding effort on their own resources. Herbivores (including goat) and carnivores usually feed on two or more species. In this case, consumers distributed their feeding effort (the total of their interaction coefficients). Black rats feed on all species. Moreover, they also feed on animal carcasses.

Changes in biomass are calculated by using the Holling type III function in Yamamura *et al.* (1978). Assimilation rates are defined mainly based on literatures (Begon *et al.*, 1996; Li *et al.* 2003) and are listed in App.1-Table 2. The assimilation rate varies according to a combination of consumer and prey or resource type.

4. Detritus food chain

Our model also considers the detritus-based food chain, which includes invertebrates that use plant litter, animal droppings, and animal carcasses. The only animal droppings available are goat droppings; on the Ogasawara Islands, no animals have been observed to use droppings other than those of goats. Plant litter, droppings, and carcasses are decomposed into nutrient over given periods of time.

5. Optimal foraging

Our model considers optimal foraging so that predation efforts change according to changes in the amount of prey available.

6. Interactions involving black rats

Rats are omnivorous animals, feeding on both animals and plants including white popinacs (Hashimoto, 2009) and seabirds (Jones *et al*., 2008; Scofield, 2009; Yabe *et al.*, 2009; Croxall *et al.*, 2012; Ringler *et al.*, 2015). Moreover, they also feed on animal carcasses.

7. Interactions involving goats

Goats eat a wide variety of plant species including introduced species (Osawa *et al*., 2016). Lawn grasses are not critically damaged through herbivory by goats as their growth points are so close to the ground. Goats are known to disrupt ecosystems not only through what they eat but also by physically damaging plants (e.g., trampling) and interfering with seabirds' nesting activity, among other things (Coblentz, 1978, Stone & Loope, 1987, de la Luz *et al*., 2003).

8. Interactions involving seabirds

Seabirds do not eat other organisms on an island, as they do not forage there, but rather feed on fish at sea. In this study, seabirds are classified as forest-nesting or grassland-nesting, and seabirds belonging to the same nesting type compete for nesting sites. Scrambling for nest sites occurs between seabirds with similar traits, i.e., similar nest site preferences. Further, scrambling for nest sites is one-sided, not interactive interference competition, such that larger birds chase away smaller birds. Whether scrambling for nest sites occurs is determined by using the same framework shown in the former half of section 3-2 in Appendix 1. Seabirds do not walk far but are known to trample plants around their nests. Whether trampling of plants by seabirds occurs is determined by using the same framework shown in the former half of section 3-2 in Appendix 1. Grassland-nesting seabirds trample herbaceous plants and forest-nesting seabirds trample woody plants.

9. Decomposition and weathering

Our ecosystem model includes detritus (animal feces/carcasses/litter) and its decomposition is modeled. Carcasses and litter contain the same nutrient as their producers. Animals excrete as feces the food that they could not assimilate. For simplicity, it is assumed that the nutrient content of feces is the same as that of the ingested food. Detritus is decomposed over a given time and reverts to nutrient. It is known that animal detritus tends to decompose more quickly than plant detritus (Briggs, 1995; Sansom *et al.*, 2010; Hata *et al.*, 2012; Klompmaker *et al.*, 2017). Detritus produced on a given time step is stored in detritus pools, which are defined separately for goat feces, feces of other animals (including seabirds), animal carcasses, and animal litter. The proportion of nutrient contained in the detritus pools is re-calculated each time more detritus is added. Detritus in each pool, excluding feces of invertebrates and seabirds, is used by detritus-feeding animals every time step, and thus the size of the pools decreases (detritus food chain). Detritus is lost not only through use by organisms but also through leaching out of the system due to rainfall and wind. After a set period has passed since detritus production, nutrient contained in the remaining detritus move to the ecosystem-level nutrient pools. Actual decomposition comprises complex biological and chemical processes involving microorganisms such as soil bacteria. However, since the bacterial ecosystem is largely unknown and the main objective of this study is to characterize the ecosystem of large terrestrial organisms, a very simple decomposition process is adopted for the model in order to avoid using excessively complicated models.

10. Target islands

This study targets the ecosystems of Nakoudojima Island, Higashijima Island, and Nishijima Island of the Ogasawara Islands. Nakoudojima Island is suitable for investigating effects of invasive species on ecosystems on oceanic islands, because it has been heavily impacted by goats, and vegetation is disappearing from the whole island. Higashijima Island has a relatively undisturbed ecosystem, as goats were eradicated from it a long time ago (Kanto Regional Environment Office of Japan *et al.*, 2010). Nishijima Island has a unique history; its major vegetation was plantations of luchu pines (*Pinus luchuensis*) and beefwood until the 1970s (Abe *et al.*, 2011). However, pinewood nematodes were introduced to the island, eliminating the pines and stripping it of vegetation (Shimizu, 1986). Consequently, beefwood quickly expanded its distribution to the newly bare areas and formed beefwood forests. Although reproducing the ecosystem on this island may be difficult, we faced this challenge to determine the limits of our model.

At first, we tried to reproduce the ecosystem on Nakoudojima Island. Then we used the model in an attempt to reproduce the other two islands to check performance and versatility of the model (for details, see section 12 in Method, section 10 in Appendix 1, and Appendix 2).

11. Other assumptions

The model assumes nitrogen contents of approximately 2% for plants, 11% for invertebrates (insects: Schoonhoven *et al.*, 1998), and 12% for mammals (goats and rats: Takahashi, 1984) and, by analogy, for seabirds.

Seabird species commonly nest on more than one island. If a seabird population becomes locally extinct on one island, individuals of the same species are able to recolonize from other islands. In this study, it is assumed that if any of an island's seabird species becomes locally extinct, one pair of the species migrates from another island.

If this rule is adopted, however, seabirds will never become extinct, which would preclude considerations of diversity in the model. Therefore, it is assumed that seabirds cannot be observed unless there are at least 10 nesting pairs.

Our model offers special considerations to the following introduced species: goats, rats, white popinacs, beefwood, and Korean lawn grass (an endemic dominant grassland species). Presence or absence of each of these species on each island is determined based on the current status of each island (Table A.1 in the main text).

Simulation run time is 10,000 time steps, and after this period, the status of the modeled ecosystem is analyzed. Simulations are run 1000 times for each island.

12: Procedure to reproduce the Nakoudojima Island ecosystem

For components and the characteristics of the ecosystem of Nakoudojima Island, see Fig. 1, Table A.1, and Appendix 1. As mentioned above, values for the variables were obtained from the literature, unpublished data, and experts' opinions (Table 1 and Appendix 1). For other variables (Table 2), we chose the parameter sets that best reproduced the vegetation ratio (Hata *et al*., 2007) and the biomass of goats (Japan Wildlife Research Center, 2000) of the ecosystem of Nakoudojima Island from 500 parameter sets, of which values were determined randomly, via 200–1,000 iterations of simulation (see Appendix 2).

While the initial number of seabird species was set at 20 (Table A.1), simulations were also performed using a lower species abundance (i.e. two species), because seabirds play an important role in supplying nutrients to island ecosystems.

13: Model ecosystem without invasive species (original state of ecosystem)

To check that the model could reproduce the original state of the ecosystem on Nakoudojima Island, we conducted simulations using the model in the condition without invasive species (i.e. goats, rats, white popinac, and beefwood), that is the biomass of invasive species are set to 0.

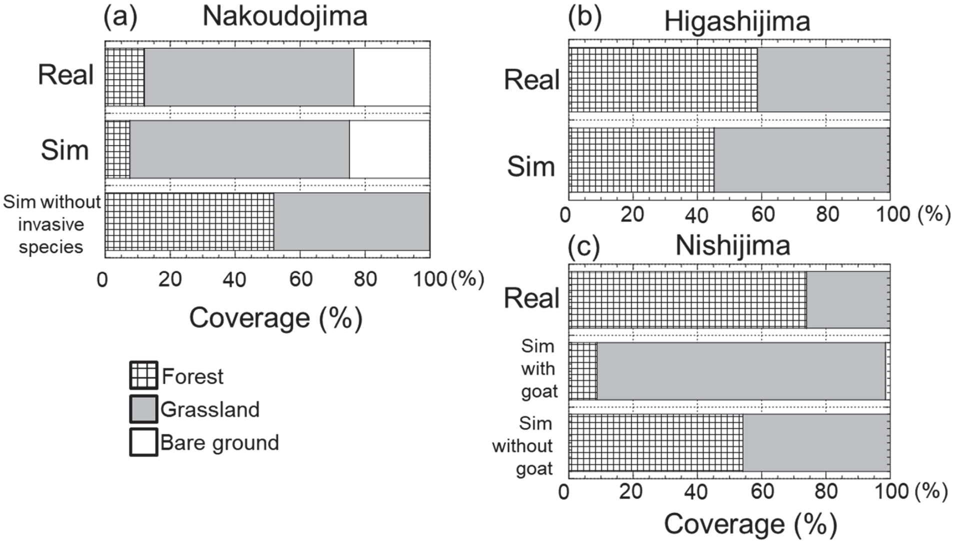

Fig. 2. Comparison between simulation results (Sim) and actual data (Real).

Ratios of each vegetation type are shown by %. Values of simulation results and real ratios of each vegetation type on each island are shown in Table A.1. Real data for Nakoudojima Island are based on Hata *et al*. (2007). Real data for the other two islands are based on the Ogasawara Islands Ecosystem Conservation Action Plan.

Results

Reproducing island ecosystems with the model

Figure 2 and Tables 3 and A.2 show results of simulations of Nakoudojima Island compared with the actual data. This model well reproduced the ratios of grassland and bare ground. In particular for the area of denuded land, the real value was within the 95% confidence interval from the mean value of simulations (Table A.2); and for grassland, the real value was near the edge of the lower confidence interval from the mean value. The simulated proportion of forests was half of the actual proportion, but the actual proportion of forests was small and, therefore, the difference in actual area was also small. Nakoudojima Island was inhabited by about 417 goats immediately before the goat eradication project (Japan Wildlife Research Center, 2000). Among these, 409 goats were weighed, making a total weight of 9.35 tons (average weight 22.93 kg, standard deviation 5.88 kg, maximum weight 40.00 kg, minimum weight 1.20 kg). This value was only 1.62 times the simulation result (average, 5.78 ton; 95% confidence interval, 0.10 ton; Table 3).

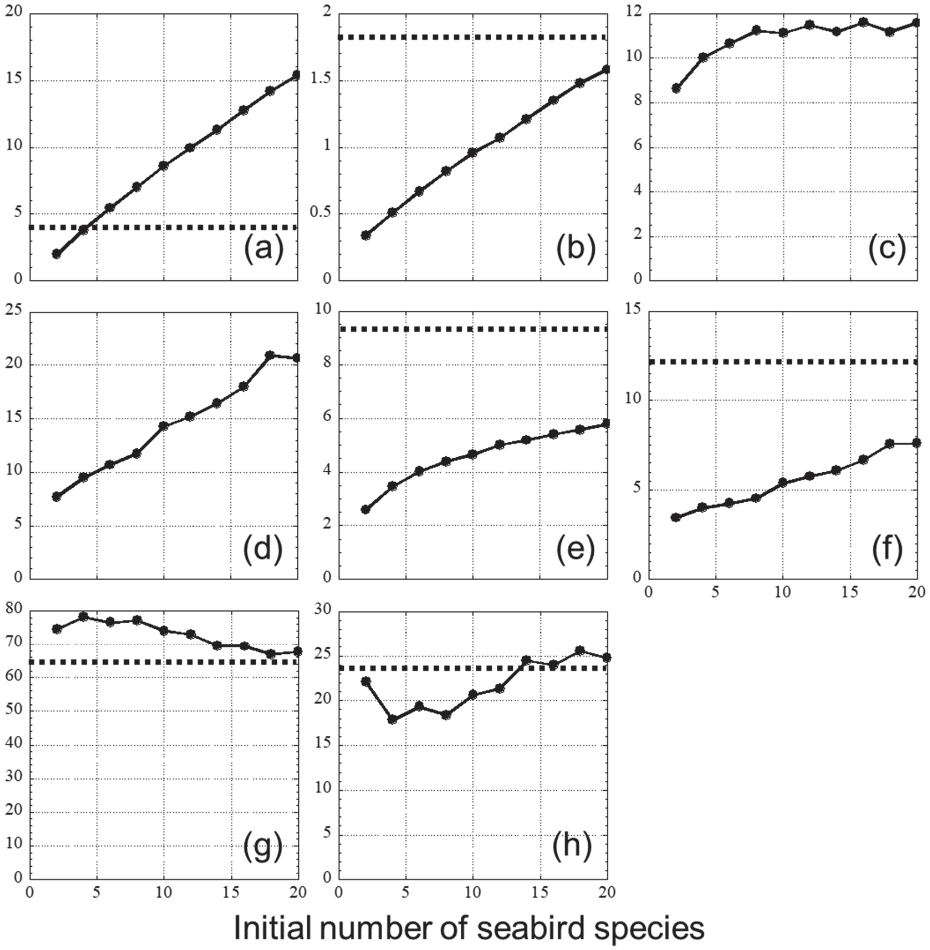

Fig. 3. Relationship between the initial number of seabird species and ecosystem characteristics.

(a) simulated number of seabird species, (b) total biomass of seabirds (ton), (c) amount of nutrient (ton), (d) total amount of tree biomass (ton), (e) biomass of feral goats (ton), (f) ratio of forest area (%), (g) ratio of grassland area (%), (h) ratio of denuded area (%). The values are the averages of 1,000 simulations. Refer to Tables A.3 and A.4 for exact values and standard deviations, respectively. The bold horizontal dotted lines in (a), (b), and (e)–(h) indicate actual values for Nakoudojima Island. Horizontal axes represent the upper limit of the number of seabird species.

Our model predicted that the total biomass of seabirds was 1.58 tons (standard deviation, 0.55 ton; 95% confidence interval, 0.034 ton; Table 3), which corresponded to about 780 individuals (standard deviation, 275 individuals; 95% confidence interval, 17 individuals)—mean biomass of individual seabirds in the model was 2.0 kg (the last paragraph of section 2 in Appendix 1). 3 years after the goat eradication on the real Nakoudojima Island, 904 individual seabirds were observed: black-footed albatross, 117 nests (234 individuals); brown booby, 326 nests (652 individuals); and Bulwer's petrel, 9 nests (18 individuals) (Suzuki *et al*., 2019). Then, this result indicates that our model had excellent ability to reproduce seabird biomass.

However, our model could not reproduce seabird species diversity. Our model yielded 15.7 ± 2.6 observable seabird species, representing an overestimate, as surveys have only recorded four species on Nakoudojima Island (Suzuki *et al*., 2019). In response, we performed simulations in which smaller numbers of initial seabird species were used to get the model outputs closer to the observed number. When a smaller value was used as the initial number of seabird species, the simulated number of seabird species became smaller (Fig. 3a, Table A.3). For the initial number of four species, the simulated number of seabird species was almost the same as the actual number of species found on Nakoudojima Island. In this case, the biomass of seabirds also became smaller (Fig. 3b, Table A.3). When the simulated number of seabird species was four (i.e. the same as the actual number on Nakoudojima Island), the biomass of seabirds was 0.51 tons. This is equivalent to approximately 250 birds, which is only 30% of the actual number. Because the biomass of seabirds is directly linked to the amount of nutrients supplied to the ecosystem, when the initial number of seabird species decreased, the amount of nutrients also decreased (Fig. 3c, Table A.3). With small initial numbers of seabird species, the numbers of carnivorous and herbivorous animals greatly decreased, whereas the number of plant species did not change significantly (Table A.3). In both animals and plants, biomass decreased greatly (Fig. 3d and e for trees and goats, respectively; Table A.3). When the initial number of seabird species was four, the biomass of goats was approximately 60% of that when the initial number was 20. This is approximately one-third of the actual value on Nakoudojima Island. When a small initial number of seabird species was used, forest coverage was greatly reduced, becoming approximately one-third of the actual value (Figs. 2a and 3f, Tables A.2 and A.4). However, grassland coverage increased and bare ground decreased, and the gaps between these areas and from their respective observed values widened compared with when the initial value was 20 (Figs. 2a, 3g and h, Tables A.2 and A.4).

Results of simulations for Higashijima Island are shown in Fig. 2 and Table A.2. Compared to the actual values, the ratio of grassland of the model ecosystem was a little larger and that of forest was a little smaller. However, a remarkable feature of Higashijima Island, that it has no bare ground, was well reproduced.

Simulation results for Nishijima Island are shown in Fig. 2 and Table A.2. There were about 100 feral goats on the simulated Nishijima Island, whereas the real island had 41 (Bureau of Environment, Tokyo Metropolitan Government, 2023)—2.5 times the observed number. The ratio of forest on the simulated Nishijima Island was only about 3%, which was far from the real value (about 75%, Fig. 2 and Table A.2). In order to increase the ratio of forest, we simulated Nishijima Island without feral goats, although this was unrealistic. In this simulation, the ratio of forest reached 54.2% (Fig. 2 and Table A.2), which was still much lower than the real value. These results indicate that the expansion of beefwood on the island may be achieved by processes not incorporated into the model.

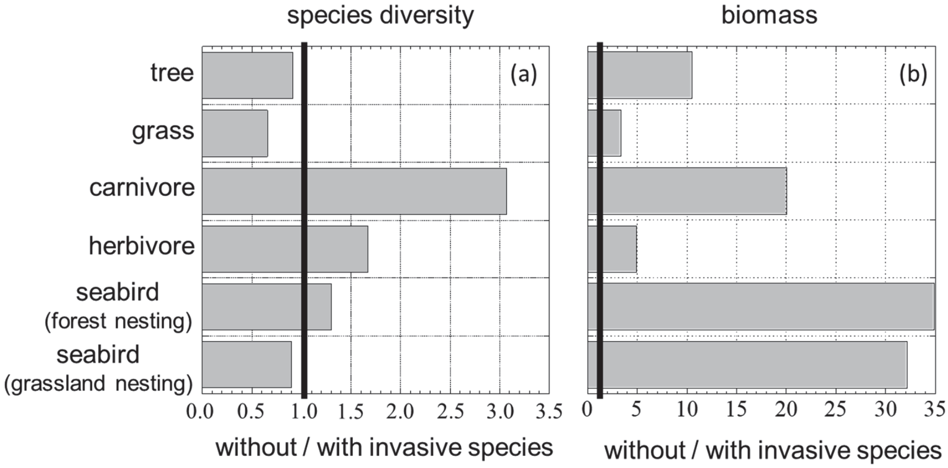

Fig. 4. Comparison between results of simulation models of Nakoudojima with and without invasive species.

(a) species diversity and (b) biomass. Mean values of both simulations are compared. “1.0” indicated by the bold line in each graph means there is no difference between the models with and without invasive species. Levels on the right side of the line indicate that the value of the model without invasive species is greater than for the model with invasive species. For actual values, see Table 3.

Ecosystem without invasive species (original state)

We tried to reproduce the ecosystem without invasive species (original state) and to compare this with invasive species incorporated. We succeeded in reproducing the ecosystem without invasive species (the biomass of invasive species was set to 0), which was characterized by abundant biomass of native species (Figs. 2 and 4, Tables 3 and A.2). The ecosystem without invasive species was fully covered by vegetation as previously reported (Kittlitz, 1844; Shimizu, 1993, 2003; Suzuki *et al*., 2019). The total biomass of tree and grass species was 10 and three times for the ecosystem without invasive species than that with them, respectively (Fig. 4, Table 3). The diversity and total biomass of animal species were much larger in the ecosystem without invasive species than that with them. The species diversities of herbivorous and carnivorous invertebrates were about two and three times larger in the ecosystem without invasive species than that with them, respectively (Fig. 4, Table 3). The total amounts of biomass of herbivorous and carnivorous invertebrates were about 5 and 20 times larger in the ecosystem without invasive species than that with them, respectively (Fig. 4, Table 3). The total biomass of seabird species exhibited a similar tendency. The total biomasses of forest- and grassland-nesting seabird species were about 35 and 30 times larger in the ecosystem without invasive species than that with them, respectively (Fig. 4, Table 3). However, only the average number of grassland-nesting seabird species decreased (Table 3). This result was influenced by the results for simulations without invasive species in which the entire island was covered with forests (293/1,000). When the entire island is covered with forests, the grassland area becomes 0, which then makes the number of grassland-nesting seabird species 0. These cases reduced the average species abundance.

Effects of content of nutrient on the ecosystem

We investigated effects of nutrient content on the ecosystem. Figure 5 presents the relationship between nutrient content and vegetation coverage. As expected, the grassland area increased and the denuded area decreased as nutrient content increased (Figs. 5a and b). However, the forest area decreased as nutrient content increased (Fig. 5c). This result was derived from the behavior of the area of white popinac, which rapidly decreased as the nutrient content increased for nutrient content below about 12.5 tons/ha (Fig. 5d). In contrast, the area of native trees gradually increased as nutrient content increased (Fig. 5e).

Figure 6 presents effects of nutrient content on biomass of animals. In all cases, the tendency changed at the point of nutrient content of about 12.5 tons/ha, that is, the area of white popinac was close to 0. Then, in each animal category, we analyzed the data under the following conditions: all data of 1,000 simulations, the area of white popinac smaller and larger than 5%, and nutrient content smaller and larger than 12.5 (the former is the oligotrophic condition, and the latter is the eutrophic condition).

When all data of 1,000 simulations were analyzed, the total biomass of carnivores was not significantly related to nutrient content (Fig. 6a, Table A.6). When the area of white popinac was below 5%, the total biomass of carnivores was positively related to nutrient content. In contrast, when the area of white popinac exceeded 5%, the total biomass of carnivores was negatively related to nutrient content. The total biomass of carnivores was negatively related to nutrient content in the oligotrophic condition; however, in the eutrophic condition, it was not significantly related to nutrient content (Table A.6).

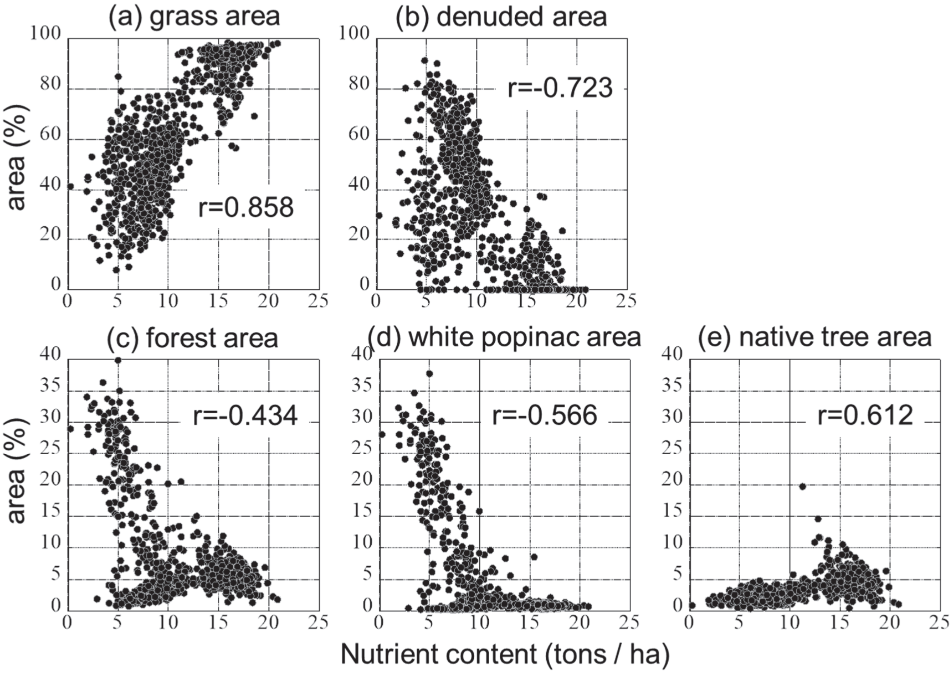

Fig. 5. Relationship between nutrient content and vegetation coverage area.

Results of statistical tests for correlation coefficients are shown in Table A.5.

When all data of 1,000 simulations were analyzed, the total biomass of invertebrate herbivores was positively related to nutrient content (Fig. 6b, Table A.7). When the area of white popinac was below 5%, the total biomass of herbivores was positively related to nutrient content, and the correlation coefficient was larger than in the case of the whole data analysis; however, when the area of white popinac exceeded 5%, total biomass of herbivores was not significantly related to nutrient content. In the oligotrophic condition, the total biomass of herbivores was negatively related to nutrient content, but was positively related in the eutrophic condition (Table A.7).

The relationship between the total biomass of seabirds and nutrient content differed from the other animal categories. When all data of 1,000 simulations were analyzed, total biomass of seabirds was negatively related to nutrient content (Fig. 6c, Table A.8). When the area of white popinac was below 5%, the total biomass of seabirds was negatively related to nutrient content;

however, when the area of white popinac exceeded 5%, it was positively related to nutrient content (Table A.8). In the oligotrophic condition, the total biomass of seabirds was positively related to nutrient content but was negatively related in the eutrophic condition (Table A.8).

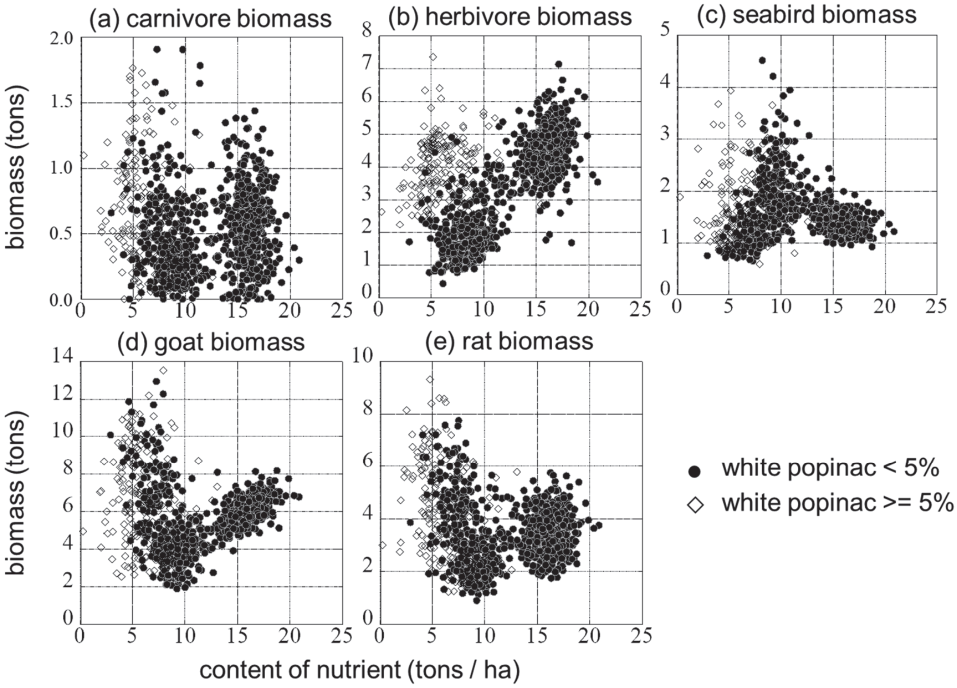

Fig. 6. Relationship between nutrient content and biomass of animals.

Data for white popinac area below 5% are shown by black circles, and for white popinac equal to or larger than 5% by white diamonds. Results of statistical tests for correlation coefficients are shown in Tables A.6–A.10.

Although goats are also herbivores, the relationship between total biomass of goats and nutrient content was not the same as in the case of invertebrate herbivores. In contrast to the case of invertebrate herbivores, the total biomass of goats was not significantly related to nutrient content, when all data of 1,000 simulations were analyzed (Fig. 6d, Table A.9). In addition, for the area of white popinac exceeding 5%, the total biomass of goats was negatively related to nutrient content (Table A.9). The maximum total biomass of goats was 8.16 tons in the eutrophic condition compared to 13.5 tons in the oligotrophic condition (Fig. 6d). In addition, in 87 cases in the oligotrophic condition, the total biomass of goats exceeded the maximum total biomass of goats in the eutrophic condition (Fig. 6d). Such results were not seen in the case of invertebrate herbivores (Fig. 6b). With respect to the mean value, an opposite tendency was observed. The mean of the total biomass of goats in the eutrophic condition was 6.12 tons (standard deviation 0.696 tons). In contrast, the mean total biomass of goats in the oligotrophic condition was 5.49 tons (standard deviation 2.33 tons). The difference between the mean values was significant (U-test, $p < 0.0001$). This result indicated that although the oligotrophic condition was severe for goats, the goat population grew explosively under some conditions. In other cases, the relationship between total biomass of goats and nutrient content was similar to the case of invertebrate herbivores (Fig. 6d, Table A.9).

The total biomass of rats was negatively related to nutrient content, when all data of 1,000 simulations were analyzed (Fig. 6e, Table A.10). For the area of white popinac below 5%, the total biomass of rats was not significantly related to nutrient content. However, for the area of white popinac exceeding 5%, the total biomass of rats was negatively related to nutrient content (Table A.10). The total biomass of rats was negatively related to nutrient content in the oligotrophic condition (Table A.10), but not significantly related to nutrient content in the eutrophic condition (Table A.10).

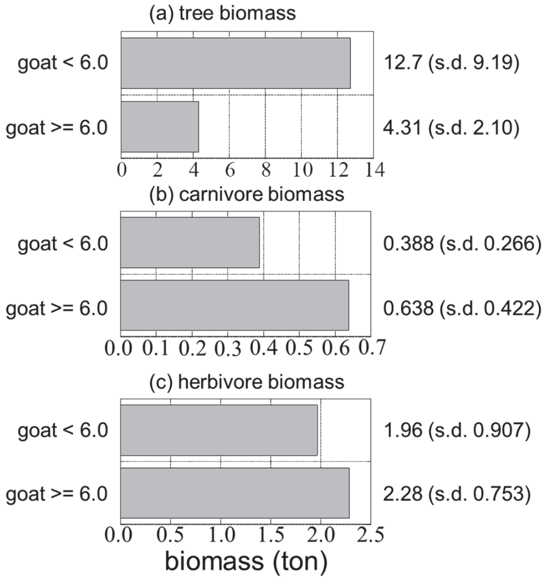

Fig. 7. Comparison between ecosystems for total biomass of goat smaller than 6.0 tons and greater than or equal to 6.0 tons.

The numbers of ecosystems for which total biomass of goats was smaller than 6.0 tons and greater than or equal to 6.0 tons are 264 and 96, respectively. In all graphs, the differences were significant (U-test, $p < 0.0001$).

One of the most characteristic features in the relationship between nutrient content and total biomass of goats was that goat total biomass was very high although the white popinac area was below 5% and nutrient content was below 12.5 tons/ha (oligotrophic condition), that is, there was little amount of plant biomass (Fig. 6d). This was also observed for biomass of rats (Fig. 6e).

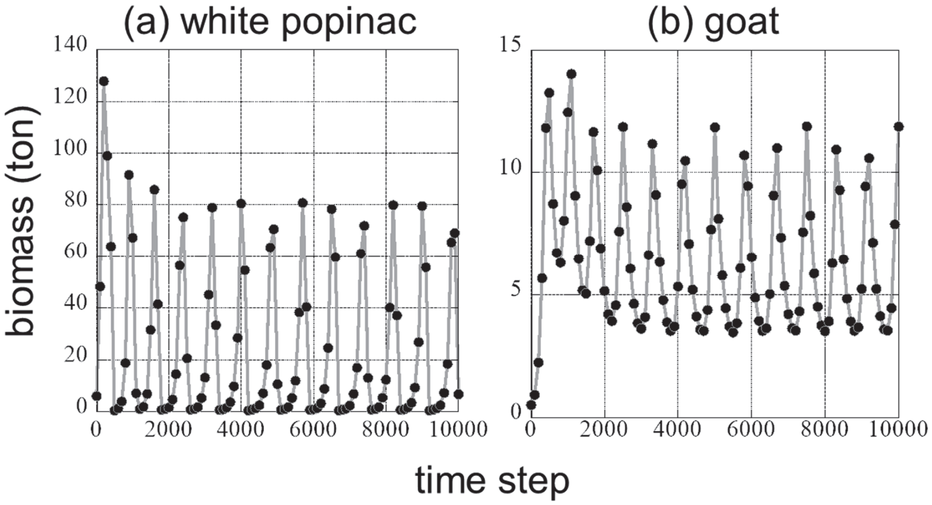

Fig. 8. An example of fluctuations in biomass of white popinac and goat.

Data are plotted every 100 steps.

Then, we compared ecosystems with total biomass of goats below 6.0 tons to ecosystems with total biomass of goats equal to or above 6.0 tons under the conditions of the white popinac area below 5% and nutrient content below 12.5 tons/ha. The ecosystems with large total biomass of goats had large biomass of herbivores and carnivores, although the total biomass of trees was low (Fig. 7)—this was a very strange result. Then, we investigated the behavior of such ecosystems and revealed that the total biomass of white popinac and goats oscillated violently (Fig. 8). The relationship between the fluctuation patterns of the total biomass of white popinac and goats was very similar to that between the biomass of predator and prey (Fig. 9). These results indicated that the total biomass of goats varied under the influence of the fluctuation of the total biomass of white popinac (in the oligotrophic condition, white popinac was the only food for goats), and that at the end of the simulation (10,000th time step), it just so happened that the total biomass of goats was large and the total biomass of white popinac was small.

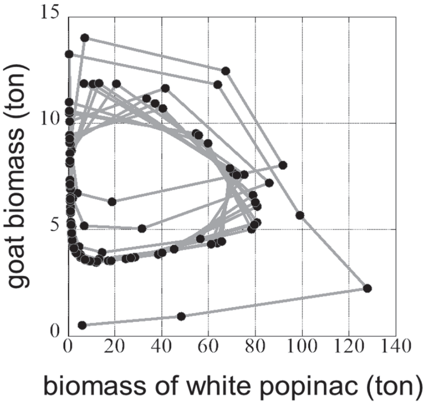

Fig. 9. Relationship between the biomass of white popinac and of goats.

This diagram is drawn using the same data as Fig. 8. Data are plotted every 100 steps.

Discussion

Performance of the model in reproducing real island ecosystems

The model reproduced the vegetation ratio and the total biomass (number of individuals) of goats (Fig. 2a, Tables 3 and A.2) in the ecosystem of Nakoudojima Island. In addition, it is noteworthy that this model precisely reproduced the number of seabird individuals (Table 3), which was not a criterion for parameter search (Appendix 2). Therefore, the model exhibited high performance in reproducing the nutrient cycle process in the ecosystem on Nakoudojima Island just before eradication of invasive species.

This model reproduced not only the ecosystem on Nakoudojima Island, an island severely disturbed by invasive species, but also for undisturbed Higashijima Island (Fig. 2b, Table A.2). This result is important, as it shows that this model, with its established parameter set, is highly versatile and capable of reproducing multiple islands.

In their original state (before invasive species colonized), the Ogasawara Islands were fully covered by vegetation (Kittlitz, 1844; Shimizu, 1993, 2003; Suzuki *et al*., 2019). In this period, the species diversities and the total biomass of plants and animals were considered to be very rich as they are in today's islands without invasive species. The model in this study succeeded in reproducing this rich ecosystem (Figs. 2a and 4, Tables 3 and A.2).

The vegetation on several islands has been destroyed by invasive species, and bare ground has appeared (Shimizu, 1993, 2003; Kawakami, 2019; Suzuki *et al*., 2019). In this period, seabird populations were severely suppressed (Chiba *et al*., 2007; Kawakami, 2008; Emura *et al*., 2013, 2015). As mentioned above, the model well reproduced the condition of the invaded island (Fig. 2a, Tables 3 and A.2). Therefore, these results indicate that the model has sufficient potential to reproduce the transition from the original rich to the poor ecosystem caused by invasive species.

Limit and further improvement of the model

The model developed in this study is not perfect and there are several points for improvement. Although the total biomass (number of individuals) of seabirds was compatible with the observations (see the previous section), the species diversity of seabirds in the model (about 15 species, Table 3) differed from the observations (four species: black-footed albatross, brown booby, wedge-tailed shearwater, and Bulwer's petrel; Suzuki *et al*., 2019). It is possible to match the number of seabird species in the model ecosystem with the actual number by setting a small initial number of seabird species (Fig. 3a, Table A3). In that case, however, the differences widened between the simulation results (number of seabird individuals, vegetation ratio, and biomass of goats) and their actual values for Nakoudojima Island (Fig. 3b and e–h, Table A3). As the biomass of seabirds is directly linked to the amount of nutrients, if the simulated seabird biomass diverges from the actual value, it is likely that ecosystem behavior cannot be reproduced. If so, it is likely that correct results will not be obtained when various future numerical experiments are conducted using this model. At this point, it is appropriate to focus on the number of seabirds (biomass) rather than the number of seabird species.

The number of sympatric seabird species is a future issue to be solved. The problem is mainly derived from the assumption in the model regarding colonization by new seabird species. In the model, when a species becomes extinct, a pair of a new seabird species immediately colonizes. This assumption unrealistically increases the number of seabird species. Our model assumed that the species diversity in seabirds was variable. This assumption is correct on a time scale of hundreds to thousands of years (Kawakami and Horikoshi, 2022). However, on the real Nakoudojima Island, the seabird species diversity was constant for about 15 years following eradication of goats (Suzuki *et al*., 2019). For the purpose of analyzing ecosystem change within decades, incorporating a fixed number of seabird species as observed may be appropriate.

Another cause of the difference is the criterion of observable seabird species. In the model, a seabird species is observable when it has only 10 nesting pairs (section 11 in Appendix 1). If the criterion is changed, the number of observable seabird species can be adjusted to the real value. However, we did not do this, because such manipulation is unscientific.

The model did not reproduce the vegetation coverage on Nishijima Island, even if an unrealistic assumption (without goats) was adopted (Fig. 2, Table A.2). This result may be derived from the extraordinary history of this island. As mentioned in section 2.2 in the main text and section 11 in Appendix 1, plantations of luchu pines were widely developed on Nishijima Island and these suddenly disappeared following invasion by the pine wood nematode (Shimizu, 1986; Abe *et al*., 2011). After that, the beefwood forest rapidly expanded on this bare ground (Abe *et al*., 2011).

This expansion might have been too rapid for feral goats to have any influence on it. Moreover, it can be assumed that the ecosystem on Nishijima Island was severely damaged when the luchu pines were established and when beefwood rapidly expanded. Therefore, the nutrient cycle processes in the Nishijima ecosystem may have been quite different from those assumed in the model. This model did not reproduce ecosystems that have been too devastatingly disturbed.

The model reproduced the original state of the ecosystem of Nakoudojima Island without invasive species, and with rich species diversity and biomass (Figs. 2a and 4, Table 3). However, this reproduction was not perfect. Although the Ogasawara Islands were fully covered by forest (Kittlitz, 1844; Shimizu, 1993, 2003; Suzuki *et al.*, 2019), this state was achieved only in 293 of the 1000 simulations (see the last paragraph of section 3.2), and the mean ratio of forest in the model ecosystem was only about 50% (Fig. 2a, Table A2). The model should be modified in the future to more effectively reproduce a forest-dominated ecosystem in the condition without invasive species.

Effects of the content of nutrient on properties of ecosystems

Nutrient content had complex effects on ecosystems. The main cause of this complexity was that the area of forest (related to the amount of primary production) was not positively related to nutrient content (Fig. 5c). This is derived from the behavior of white popinac. Because white popinac can fix nitrogen (Jayasundara *et al.*, 1997), it can grow without competition with other plant species in the oligotrophic condition. Then, when the area of native trees became larger as nutrient content rose (Fig. 5e), the area of white popinac rapidly declined (Fig. 5d). Then, during the stage when nutrient content was below 12.5 tons/ha (Fig. 5d), the area of forest continued to decline (Fig. 5c). When nutrient content exceeded 12.5 tons/ha, the area of forest became larger as nutrient content rose (Fig. 5c). This was the cause of the complex patterns in changes in biomass of animals (Fig. 6). For example, the biomass of carnivores and goats was not significantly related to nutrient content for the analysis of all data (Tables A.6 and A.9). However, when divided into cases based on nutrient content, the biomass of carnivores and goats was significantly related to nutrient content (Tables A.6 and A.9). These patterns were reflected in the behavior of white popinac and native trees as mentioned above.

The pattern of change in biomass of goats was not the same as that for invertebrate herbivores, especially in response to the change in biomass of white popinac. In the oligotrophic condition (nutrient content below 12.5 tons/ha), the biomass of goats was frequently greater than that in the eutrophic condition (Fig. 6d). In contrast, such phenomena were not observed for invertebrate herbivores (Fig. 6b). This difference may be derived from the difference in response to white popinac between goats and invertebrate herbivores. As observed in reality (Osawa *et al.*, 2016), goats always graze on white popinac in the model. However, only invertebrate herbivores that prefer white popinac graze on it. Therefore, it is considered that the change in the area of white popinac did not strongly influence biomass of invertebrate herbivores.

The biomass of rats was not significantly related to nutrient content in the eutrophic condition and when the area of white popinac was below 5% (Fig. 6e, Table A.10). This may be due to the relationship between the area of native trees and nutrient content. Although the area of native trees was positively related to nutrient content, the slope was very small (Fig. 5e, Table A.5). Therefore, the relationship between the total biomass of rats and the area of native trees may be disturbed by other factors, for example, the amount of animal food available.

The change in the biomass of seabirds differed from those for other animals (Fig. 6c, Table A.8). One reason is that seabirds do not feed on other species on the island. Of course, they do not graze on white popinac. When the area of white popinac increased in the oligotrophic condition, the potential area for seabird nesting increased. However, in the oligotrophic condition, the biomass of white popinac frequently oscillated violently. Therefore, area of white popinac did not influence the biomass of seabirds. It is remarkable that, in the eutrophic condition, the biomass of seabirds was negatively related to nutrient content. In the eutrophic condition, the biomass of goats was positively related to nutrient content (Fig. 6d, Table A.9). Goats interfere with seabird nesting activity (Coblentz, 1978; Stone & Loope, 1987; de la Luz *et al*., 2003; section 7 in Appendix 1). Therefore, in the eutrophic condition, the biomass of seabirds was negatively related to nutrient content. These results suggests that the ecosystem of Nakoudojima Island may not be restored unless invasive species are eradicated, because seabirds are considered to be the main source of nutrients for the ecosystem of these islands (Hiradate *et al*., 2015).

On the real Nakoudojima Island, the native tree forest was not restored, although about 20 years have passed since the eradication of feral goats (Hata *et al*., 2014, 2019; Osawa *et al*., 2016; Hata, 2020), and the forest of white popinac is gradually expanding (Osawa *et al*., 2016)—the oligotrophic condition of the soil of Nakoudojima Island is considered to be one of the main causes (Hata *et al*., 2014, 2019; Hiradate *et al*., 2015; Hata, 2020). The results of this study also support this hypothesis. On the real Nakoudojima Island, rapid expansion of the forest of white popinac has not occurred, indicating that the oligotrophic condition may not be very serious. However, improving the oligotrophic condition may restore the island’s ecosystem.

Concluding remarks

The model developed in this study incorporated a number of realistic processes working in a real complex ecosystem. Then, as shown in Appendix 1, the model became very complex. As Ludwig & Walters (1985) and Iwasa (1990) pointed out, complex models are not always superior to simple ones, because complex models are difficult to control to reproduce target ecosystems. However, our model reproduced the ecosystems of some of the Ogasawara Islands with reasonable accuracy. In addition, our model exhibited a certain level of versatility.

The model developed in this study did not incorporate water. However, water is one of the most important resources for living things. This may be one cause of the differences between the model results and observations. Although this is a very difficult issue, we must develop a new ecosystem model incorporating water in the future.

The results of simulations suggest that nutrient content influenced ecosystem behavior via the behavior of white popinac. Especially, the violent oscillations in the biomass (area) of white popinac strongly influenced the ecosystem. Fortunately, such violent oscillations have not been observed on the real Nakoudojima Island. However, we should carefully monitor behavior of the white popinac forest.

This model is applicable for various future uses. While requiring the incorporation of necessary elements in accordance with simulation purposes, this model can be used for simulations under various conditions, for example, the effect of eradication of introduced species or the introduction of new species and the effects of climate change on an ecosystem. Through these applications, by presenting what will happen in the actual ecosystem, this model will contribute to the development of a positive feedback system between theoretical research and demonstration research.

Acknowledgements:

This work was supported by JSPS KAKENHI Grant Numbers JP 22241055, JP 25241025, JP 16H01794. We thank Yukiko Aoyama, Kyoko Sugai, Mari Kohri, and Kiyoshi Satake for comments regarding features of ecosystems on the Ogasawara Islands; Akio Takenaka for comments on the model; and Kenji Takamura, Noriko Takamura, Hiroya Yamano, and other members of the Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, for supporting this study.

Appendices

The appendices can be accessed from the following data repository link:
https://doi.org/10.34462/0002000005.

Table A.1. Components of ecosystems on each island and the number of species at the beginning of simulation.

Table A.2. Comparison of vegetation coverage rates (%) between real and simulation data.

Table A.3. Relationship between the initial number of seabird species and ecosystem characteristics (average values).

Table A.4. Relationship between the initial number of seabird species and ecosystem characteristics (standard deviations).

Table A.5. Relationship between content of nutrient and vegetation coverage.

Table A.6. Relationship between nutrient content and total biomass of carnivores.

Table A.7. Relationship between nutrient content and total biomass of herbivores.

Table A.8. Relationship between nutrient content and total biomass of seabirds.

Table A.9. Relationship between nutrient content and total biomass of goats.

Table A.10. Relationship between nutrient content and total biomass of rats.

Appendix 1: Detailed explanation of the ecosystem model

Appendix 2: Constructing Nakoudojima ecosystem

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Table 1. Parameters assigned fixed values.

	value	unit	brief explanation
For all species			
virtual trait	[0–1.0]	-	(Section 3-2 in App. 1)
For plant species			
area increase threshold	0.5	-	Plants cannot increase the area they occupy unless the biomass sufficiency rates of them are equal to or larger than this value. (4th paragraph in section 1-3 in App. 1)
keep-area-threshold	0.25	-	The area a species occupies decreases when the species cannot maintain its “keep area threshold” biomass as the biomass sufficient rate of the species becomes equal to this threshold. (line 26-29 on page 2 in App. 1)
value of T' in App.1-Fig.1.	0.1	ton / ha	The minimum nutrient density that a plant species of which C-value = 100 (the upper limit of C-value) can absorb nutrient. (line 15 on page 4 to line 7 on page 5, App.1-Figure 1)
minimum absorption rate	0.00001	ton / time step	The absorption rate when the nutrient density is lower than the minimum nutrient density at which nutrient become available to absorb (line 31-33 on page 4 in App. 1).
minimum value of the area increase rate of native woody plant per time step	0.0001	-	The lower limit of the random number which is utilized to determine the daily rate of area increase of native woody plant. For the upper one, see Table 2. (The third paragraph in section 1-3 in App. 1)

Table 1. Continued.

attacking range for native plant species	[0.1–0.5]	-	Plant species compete with other plants of which virtual trait fall within the range. (the first paragraph in section 1-4 in App.1, the last paragraph in section 3-2 in App.1)
attacking range for invasive plant species	0.45	-	Because invasive woody plants are widely distributed in various places on the island (Osawa *et al.*, 2016), they would compete with many species. Then, the attacking range of them are set to be very large. (section 1-4 in App. 1)
For animal species			
population growth rates per time step			
goat	0.0012	-	Assuming that two parent goats produce one offspring that matures in one year. (the first paragraph in section 2 in App. 1)
rat	0.01	-	Because black rats have a very high reproductive rate, it is assumed that a biomass increase rate 10 times that of goats is set for black rats. (the first paragraph in section 2 in App. 1)
sea bird	0.0022	-	Assuming that two parent birds produce one offspring during one nesting period (200 time steps). (the first paragraph in section 2 in App. 1)

Table 1. Continued.

invertebrate	[0.5MRR – MRR]	-	The potential reproductive rate for each invertebrate species is determined by using a random number uniformly distributed from 0.5MRR to MRR. (MRR: Maximum Reproductive Rate for invertebrate, Table 2) (the first paragraph in section 2 in App. 1)
biomass decrease rate per time step			
goat	0.001577	ton / time step	Because goats have a lifespan of eight years (Watts and Conley 1984), the daily biomass reduction rate of goats is set assuming that the biomass of the entire population would decrease to one hundredth of its original size after eight years. (from line 5 to line 7 on page 9 in App. 1)
rat	0.004206	ton / time step	Lifespan is set at three years and their biomass reduction rate is set accordingly. (from line 7 to line 9 on page 9 in App. 1)
sea bird	0.0005	ton / time step	Kawakami, unpubl. data (from line 9 to line 10 on page 9 in App. 1)
"*a*" in eq. (11)			$T = aM^{-0.25}$ (Yodiz and Innes, 1992)
endothermic vertebrates	54.9	$(kg^{0.25})$/year	(from line 23 to line 25 on page 9 in App. 1)
invertebrates	0.5	$(kg^{0.25})$/year	(from line 23 to line 25 on page 9 in App. 1)

Table 1. Continued.

Body weight			
goat	30	kg	(from line 32 to line 33 on page 9 in App. 1)
rat	0.2	kg	(from line 33 to line 34 on page 9 in App. 1)
sea bird	[0.05–4.00]	kg	(from line 34 on page 9 to line 1 on page 10 in App. 1)
invertebrate	[0.001–0.050]	kg	(from line 2 to line 3 on page 10 in App. 1)
carnivorous invertebrate	[0.025–0.050]	kg	(from line 3 to line 7 on page 10 in App. 1)
Interaction			
the value of interaction coefficients for seabird	0.2	-	Seabirds feed on only fish outside the model island (section 8 in App. 1)
range of feeding preference	[0.1–0.5]		
learning period	10	time step	
interaction coefficient between goat and bird	0.01	-	
Mfish	1	ton	Amount of fish outside the model island
CSBF	0.2	-	Interaction coefficient between seabird and fish (section 8 in App. 1)
hSBF	1	-	Handling constant when seabirds eat fish (section 8 in App. 1)
absolute value of interaction coefficient between birds	[0–M_{bcomp}]	-	For M_{bcomp}, see Table 2 (the last paragraph in section 8 in App. 1)

Table 1. Continued.

For the process of decomposition			
time steps for litter to revert to nutrient	100	time step	(section 9 in App. 1)
time steps for animal carcasses to revert to nutrient	10	time step	(section 9 in App. 1)
time steps for animal feces to revert to nutrient	10	time step	(section 9 in App. 1)

Parameters with “-” in the “unit” column do not have a unit. A brief description of each parameter is given in the rightmost column. For detailed descriptions, refer to the corresponding Appendix 1 sections given in that column.

Table 2. Parameter sets for the model from random parameter sets.

for plant species			
	basic growth rate for tree		0.05
	grass coefficient for growth rate		5
	grass coefficient for area increase		5
	H. threshold ND		0.7
	maximum assimilation rate		0.003
	maximum value of the daily rate of area increase		
		native tree	0.0005
		invasive tree	0.001
	absolute value of intra-specific competition of plant species		0.0003
	basic rate of biomass loss of plant species		0.0025
for animal species			
	maximum reproductive rate for invertebrate		0.05
	rate of biomass loss of invertebrate animal species		0.005
	total of interaction coefficients		
		homeothermic vertebrate (goat, rat, and seabird)	0.25
		invertebrate	0.15
	absolute value of inter-specific competition between birds		0.005
	absolute value of intra-specific competition of animal species		0.0003
	absolute value of interference		
		from goat to seabird	0.01
		from goat to plant	0.00001
		from bird to plant	0.00001
	h in eq. (12)		1.7

For details, see Appendix 1 and 2.

Table 3. Results of simulations for Nakoudojima Island.

		with invasive species		without invasive species	
Types and names of species		Number of species	Amount of biomass (tons)	Number of species	Amount of biomass (tons)
tree		10.91 (0.06)	20.65 (1.38)	9.96 (0.02)	217.20 (10.55)
grass		20.41 (0.11)	10.75 (0.35)	13.46 (0.56)	36.14 (2.04)
invertebrate					
	carnivore	4.70 (0.13)	0.53 (0.02)	14.42 (0.15)	10.61 (0.18)
	herbivore	16.18 (0.33)	3.53 (0.09)	27.06 (0.44)	17.46 (0.67)
	dung feeder	19.88 (0.02)	1.23 (0.03)	0.00 (0.00)	0.00 (0.00)
	scavenger	20.00 (0.00)	4.04 (0.03)	20.00 (0.00)	4.95 (0.07)
	litter feeder	20.00 (0.00)	1.97 (0.04)	20.00 (0.00)	3.55 (0.22)
seabird	total	15.37 (0.18)	1.58 (0.03)	16.94 (0.28)	53.00 (0.84)
	tree nesting	7.67 (0.11)	0.79 (0.02)	10.00 (0.00)	27.58 (1.05)
	grass nesting	7.70 (1.65)	0.79 (0.24)	6.94 (4.58)	25.42 (19.74)
feral goat		1.00 (0.00)	5.78 (0.10)	0.00 (0.00)	0.00 (0.00)
rat		1.00 (0.00)	3.57 (0.07)	0.00 (0.00)	0.00 (0.00)
white popinac		1.00 (0.00)	12.3 (1.36)	0.00 (0.00)	0.00 (0.00)

Mean numbers of coexisting species and the biomass of each type, at the end of simulations, are shown. The left column represents types and names of species. Values in parenthesis represent 95% confidence intervals. The category of trees includes white popinac.

ABSTRACT IN JAPANESE

新しい海洋島生態系モデル：小笠原諸島のケーススタディー

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本研究において、小笠原諸島の生態系を再現する新しい生態系モデルを開発した。実際の生態系と同様に、このモデル生態系は様々な性質を持つ 100 種以上の種で構成される。このモデルは食物網を基盤としており、実際の生態系で働く以下の 3 つの物質循環に関するプロセス、つまり取り入れる物質の量にコントロールされた動植物の成長、種間相互作用、デトリタスの分解プロセスが導入されている。このモデルは小笠原諸島の媒島の植生比、海鳥の個体数、野生化したヤギのバイオマスの実測値を精度良く再現することに成功した。また、このモデルは東島の植生比も再現出来た。しかし、人間活動と侵入寄生生物によって激しく撹乱された西島の植生比は再現出来なかった。このモデルの挙動は栄養元素の濃度に強く影響される。その原因は、森林面積が栄養元素の濃度と正の相関を持たないことであり、これはギンネムの挙動に由来する。ギンネムは窒素固定能を持つため、貧栄養環境ではギンネムだけが増殖できる。そのため、貧栄養環境では栄養塩濃度が高くなるほどギンネムの面積が急激に減少し、その結果森林面積が急激に減る。栄養塩濃度がある閾値よりも高くなると、今度は栄養塩濃度が高くなるほど森林面積が増加するようになる。これは動物のバイオマスに見られる複雑なパターンの原因となる。このモデルは、特異な歴史を持つ島を除き、複数の島の生態系を再現する汎用的な能力を持つと言える。まだ改良すべき点は残されているが、このモデルは「実際の生態系で何が起こっているのか」を理解することに貢献できる。そして、理論研究者と実証研究者が有機的に連携して共同研究を行えるようなシステムの構築に貢献することが期待される。

キーワード

コンピュータシミュレーション、生態系モデル、島嶼生態系、物質循環