

SEABIRDS AS ECOSYSTEM ENGINEERS: PROVIDING ARTHROPOD HABITAT ON OCEANIC ISLANDS

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ABSTRACT

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Seabirds play several important ecological roles on oceanic islands through their high-density breeding. Their ecosystem functions—such as nutrient cycling through excretion or terrestrial vegetation disturbance through trampling—are well known; however, little is known of their roles as ecosystem engineers. Nests and burrows can be densely concentrated in seabird colonies, by which seabirds can affect adjacent terrestrial ecosystems, especially affecting arthropods that use these structures as food or habitats. However, studies investigating the species composition of arthropods that inhabit seabird nests are limited. To characterize the arthropod faunas in seabird nests, this study surveyed and analyzed 90 nests of three seabird species nesting on the Ogasawara Islands, Japan. In total, 207 individuals of arthropods belonging to nine orders were found. In addition, we found that more arthropods occurred in the burrows of Wedge-tailed Shearwaters *Ardenna pacifica*, formed within soil, compared to nests of Brown Boobies *Sula leucogaster*, which nest on the surface. It appears that burrows, such as those of shearwaters, maintain stable temperature and humidity, and thus they can greatly influence terrestrial arthropod communities on the islands.

Key words: *Ardenna pacifica*, arthropod fauna, burrow nesters, ecosystem engineer, seabird nesting, oceanic islands, *Sula leucogaster*

INTRODUCTION

Seabirds can play a significant ecological role on oceanic islands where they breed in high densities. Seabirds forage at sea and breed on land. As a result, organic matter and nutrients such as feces, regurgitated food, carcasses, and nesting materials accumulate at breeding sites. Seabirds also disturb vegetation through their trampling or burrowing. Previous studies on the ecological function of seabirds at breeding sites have focused primarily on their effects on vegetation and nutrient cycling (Ellis, 2005; Magnússon et al., 2014). However, several studies have shown that nests made by stacking soil or plant materials or by digging burrows in the ground serve as habitats for certain insect species (Nasu et al., 2014; Sinclair & Chown, 2006).

Many studies have reported insects using bird nests, particularly in land birds (Hamao & Nasu, 2022; Hicks, 1953; Nordberg, 1936; Tryjanowski et al., 2001; Wilson & Bull, 1977; Woodroffe, 1953), suggesting that birds engineer ecosystems through their nesting. Similarly, some studies have reported that other arthropods also inhabit seabird nests (Hicks, 1959; Matsumura et al., 2024; Nasu et al., 2014; Sinclair & Chown, 2006; Wilhelm et al., 2001). Among these studies, Sinclair and Chown (2006) focused on seabird ecosystem engineering to show that the temperature in nests of Snowy Albatross *Diomedea exulans* was higher than that of the surrounding environment, creating an environment that is favorable for insects such as Tineidae. Nasu et al. (2014) reported three species of Tineidae and one species of Crambidae inhabiting the burrows of Wedge-tailed Shearwaters *Ardenna pacifica* and Bulwer's Petrels *Bulweria bulwerii*, which are

burrow-nesters on the Ogasawara Islands, and also suggested that seabird burrows were important habitats for keratin-eating Tineidae. Many procellariiform species dig burrows in soil and form tunnels up to a depth of > 1 m. These burrows formed in soil can have unique physical environments because they are not directly exposed to sunlight or rain, thus creating suitable habitats for unique arthropod fauna.

Previous studies of arthropods in seabird nests are mostly fragmentary, focusing on specific taxonomic groups such as Coleoptera, Ixodida, and Siphonaptera, and therefore the characteristics of arthropod communities, including important decomposers such as Isopoda and Diptera, remain unclear. The only studies on ecosystem engineering by seabirds and their effects on insects were conducted by Sinclair and Chown (2006) and by Nasu et al. (2014); no studies have evaluated the influence of differences in seabird nesting types on the arthropod fauna.

The Ogasawara Islands comprise many islands and islets, including islands uninhabited by humans that are important breeding sites for several seabirds (Chiba et al., 2007). These islands are among the most suitable study sites to observe and understand the characteristics of arthropod communities in seabird nests, because the arthropod fauna within nests can be compared among seabird species on different islands. To date, 21 species of seabirds have been confirmed to breed on the Ogasawara Islands, and these seabirds employ three nesting types: ground-nesting (e.g., albatrosses and boobies), burrow-nesting (e.g., shearwaters and petrels), and tree-nesting (e.g., White Terns *Gygis alba* and Red-footed Boobies *Sula sula*) (Chiba et al., 2007); however,

the latter are few in number. Among these species, Black-footed Albatrosses *Phoebastria nigripes*, Wedge-tailed Shearwaters, and Brown Boobies *Sula leucogaster* are the dominant species in the Ogasawara Islands (Chiba et al., 2007). In this study, we aimed to (1) create inventories of arthropod fauna in the nests of the three most widely distributed species of seabirds on uninhabited islands and (2) clarify the relationship between seabird nesting types (ground- or burrow-nesting) and the arthropod fauna (at the order level) in these nests. This study provides insights into the ecosystem engineering that occurs through seabird nesting on the Ogasawara Islands.

METHODS

Study Sites

Nest samples were collected from the Ogasawara Islands, a cluster of oceanic islands 1,000 km south of the Japanese mainland. The Ogasawara Islands contain four island groups (Mukojima,

Hahajima, Chichijima, and Volcano Islands) and three islets, and all islands except for Hahajima, Chichijima, Iwoto, and Minamitorishima are uninhabited by humans (Fig. 1).

Nest Analysis

To reveal the characteristics of arthropod faunas in the Ogasawara Islands from a broad, comprehensive perspective, we analyzed 90 seabird nests on six islands (Torishima, Nakoudojima, Minamijima, Nishinoshima, Kitaiwoto, and Minamiwoto Islands), collected from 2011 to 2019. We targeted Black-footed Albatrosses, Wedge-tailed Shearwaters, and Brown Boobies, which are widely distributed among the Ogasawara Islands. Black-footed Albatrosses and Brown Boobies are ground-nesters, whereas Wedge-tailed Shearwaters are burrow-nesters. The nests of the three species were collected, dried in an oven, and stored in plastic bags. The arthropods found in the nests were sorted by hand and identified to species level as much as possible from their morphological characteristics; their bodies were stored in plastic bags. It is

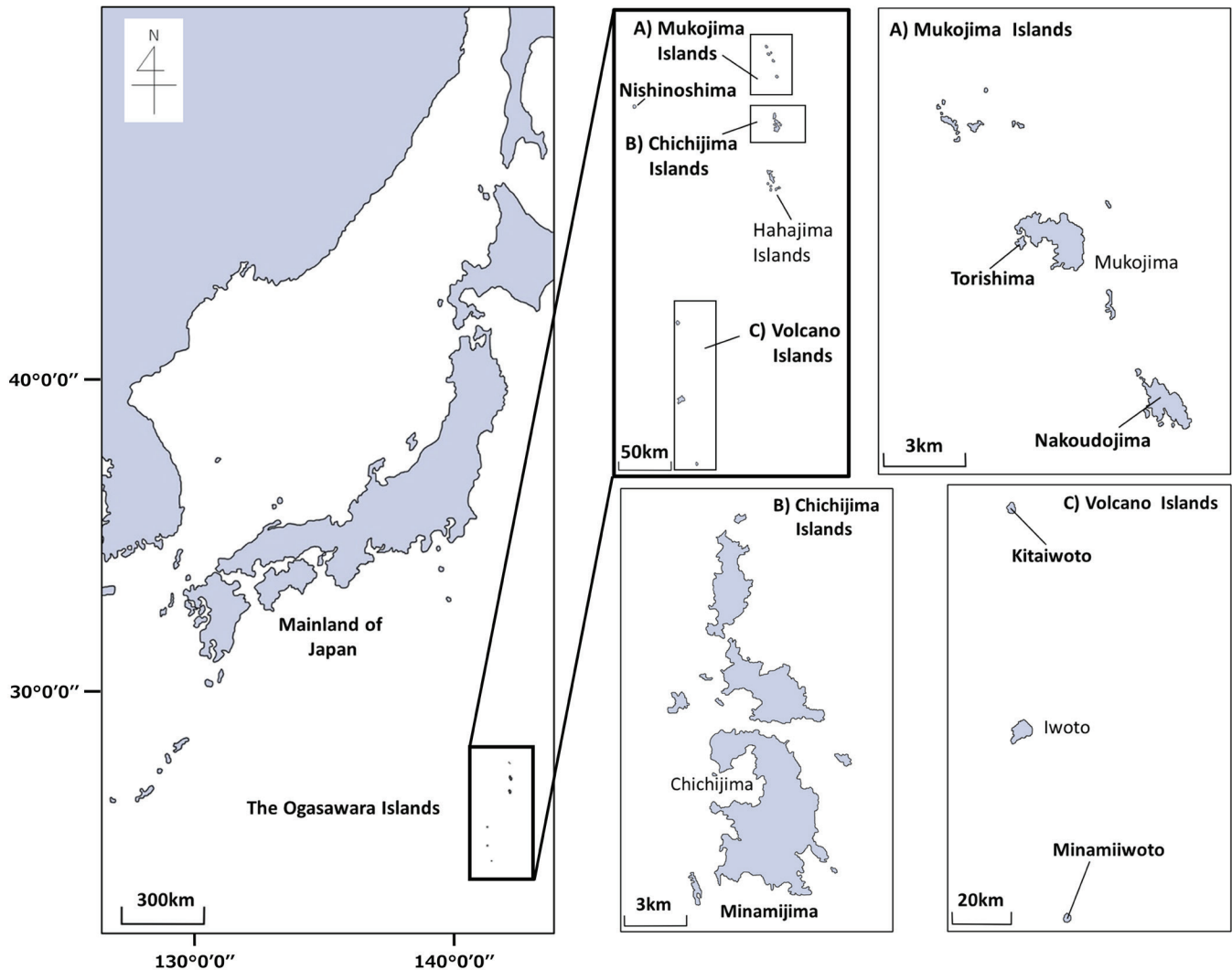


Fig. 1. Location of the Ogasawara Islands, Japan. Minamitorishima is omitted from the figure because its location is approximately 1,300 km east of Chichijima.

important to note that we could not identify all the arthropods to species level because some samples were collected over 10 years ago and had become degraded and damaged.

Statistical Analysis

To investigate the differences in the arthropod fauna, we compared the number of arthropods found in each nest among all islands and bird species using the Kruskal–Wallis test and Dunn’s post hoc test. The P value ($P < .05$) was adjusted by Holm’s correction to control the familywise error rate. Furthermore, to elucidate the differences in arthropod fauna in seabird nests caused by the difference of nesting types of birds, we compared the number of arthropods found in the Brown Booby and Wedge-tailed Shearwater nests collected on Minamijima and Nishinoshima Islands using the Wilcoxon rank-sum test ($P < .05$); the nests of these two species were collected in sympatry on these two islands.

For nest samples from Minamijima and Nishinoshima Islands, we compared the numbers of the following arthropod taxa between boobies and shearwaters—for Minamijima Island: Isopoda, Ixodida, Coleoptera, Diptera, and Lepidoptera; for Nishinoshima Island: Ixodida, Blattodea, and Coleoptera (Fig. 2). We drew up non-metric multidimensional scaling (NMDS) plots and visualized the dissimilarities of the arthropod faunas among each category of sample (Fig. 3). The dissimilarities of the arthropod fauna in seabird nests were calculated based on the average numbers of arthropod occurrences (at order level) per nest. All statistical analyses were performed using R software (R Core Team, 2024).

RESULTS

In the 90 seabird nests, we found 207 individuals of arthropods belonging to nine orders (Table 1). Isopoda, seabird-parasitic Ixodida, Coleoptera, and Diptera were the most frequently found

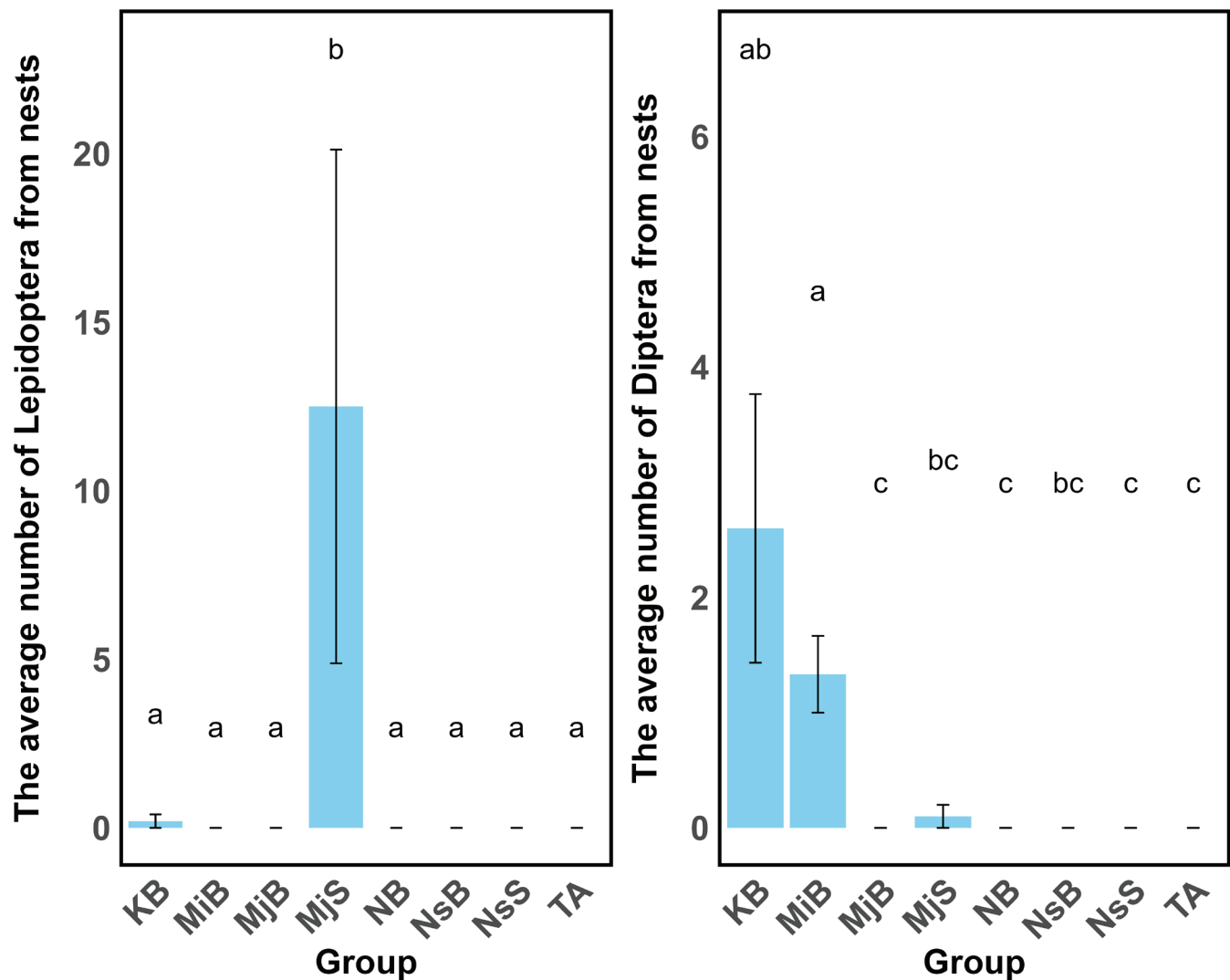


Fig. 2. Bar graphs showing the average number of individuals of Lepidoptera and Diptera found in seabird nests sampled from three bird species found in the Ogasawara Islands study area, Japan. Each abbreviation on the x-axis indicates the nest-sampling islands (indicated by the first one or two letters) and host bird species (the second capital letter); islands: K (Kitaiwoto), Mi (Minamiiwoto), Mj (Minamijima), N (Nakoudojima), Ns (Nishinoshima), T (Torishima); birds: A (Black-footed Albatross *Phoebastria nigripes*), B (Brown booby *Sula leucogaster*), S (Wedge-tailed Shearwater *Ardenna pacifica*). The lowercase letters “a,” “b,” and “c” above each bar indicate significance groups: groups that share any letters are not significantly different from each other.

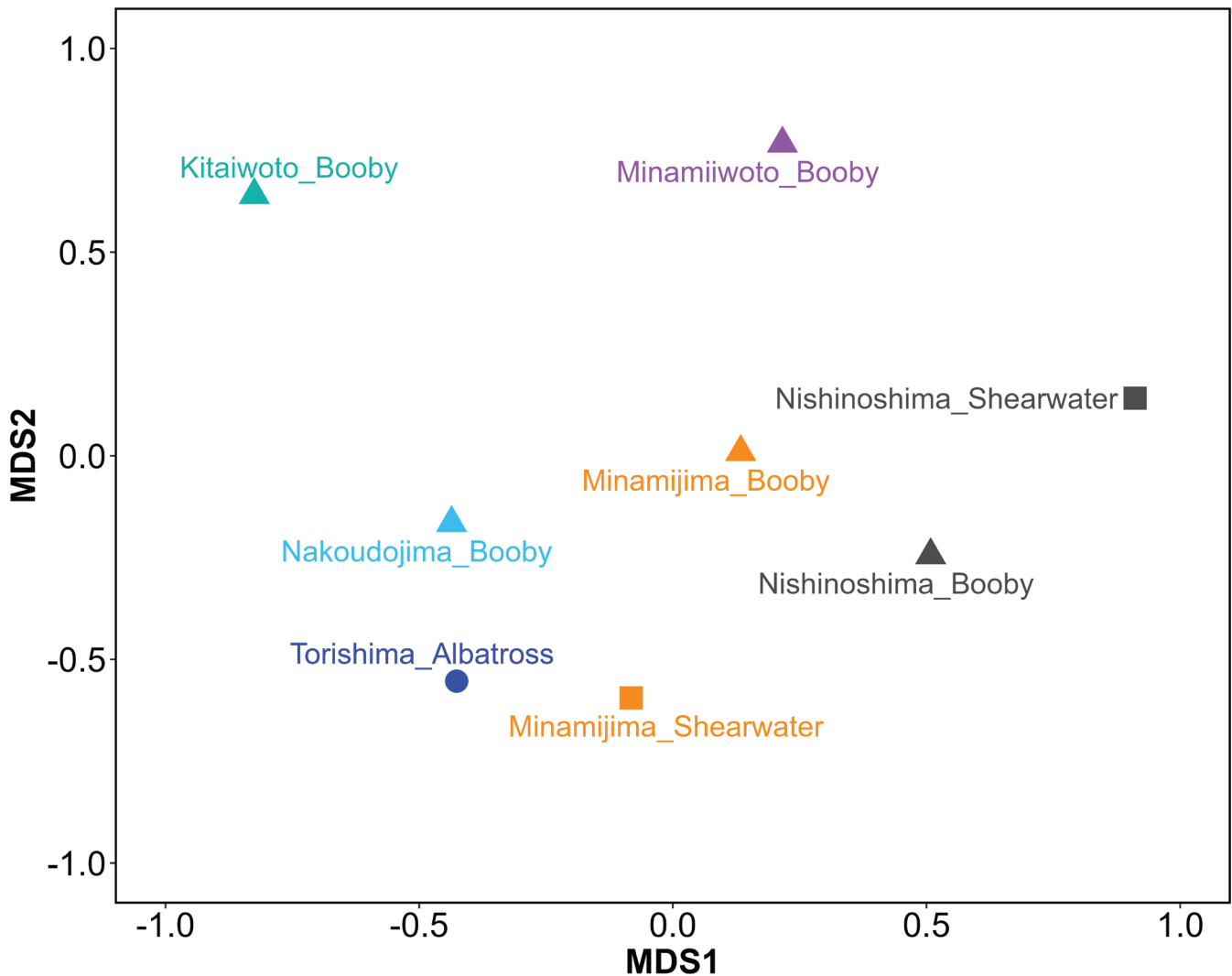


Fig. 3. A non-metric multidimensional scaling (NMDS) plot showing dissimilarities of the arthropod faunas in seabird nests, calculated based on the average number of arthropod individuals per nest. The color of each point corresponds to the island at which the nest sample was collected, and the shape of each point corresponds to the species of the host seabird; the circle, triangle, and square represent the Black-footed Albatross *Phoebastria nigripes*, Brown Booby *Sula leucogaster*, and Wedge-tailed Shearwater *Ardenna pacifica*, respectively. The NMDS ordination axes (MDS1 and MDS2) do not have inherent ecological meanings, as the analysis is based on rank orders of dissimilarities. Instead, the relative distances between points in the ordination space reflect differences in community composition, with closer points indicating more similar communities.

arthropod taxa; they were each found on four of the six islands (Table 1). Lepidoptera (123 individuals), followed by Diptera (32 individuals) and Isopoda (15 individuals), had the highest number of individuals among the arthropod taxa found in the seabird nests. Shearwater nests collected on Minamijima Island included the largest number of arthropods per nest (12.8 individuals per nest, Table 1). For the total number of arthropods found in nests, the Kruskal–Wallis test showed a significant difference among groups ($H = 52.714$, $df = 7$, $P < .05$), while a post hoc Dunn’s test did not indicate any significant differences among the groups. However, focusing on the number of individuals of each arthropod taxon, some significant differences were found in the number of Lepidoptera and Diptera. For the number of Lepidoptera, the Kruskal–Wallis test showed a significant difference among groups ($H = 18.526$, $df = 7$, $P < .001$), and a post hoc Dunn’s test with

Holm correction indicated that nests of shearwaters on Minamijima had significantly more Lepidoptera than all other groups (adjusted $P < .01$); however, no significant differences were found among the remaining groups (Fig. 2). By comparison, for the number of Diptera, the Kruskal–Wallis test showed a significant difference among groups ($H = 47.297$, $df = 7$, $P < .01$), and post hoc Dunn–Holm tests showed that nests of boobies on Minamiiwoto had significantly more Diptera than nests of boobies on Minamijima, Nakoudojima, and Nishinoshima; than nests of shearwaters on Minamijima and Nishinoshima; and than nests of albatrosses on Torishima (adjusted $P < .01$, Fig. 2). Nests of boobies on Kitaiwoto also contained more individuals of Diptera than nests of boobies on Minamijima and Nakoudojima, shearwaters on Nishinoshima, and albatrosses on Torishima (adjusted $P < .05$, Fig. 2). No other pairwise differences were significant.

TABLE 1
Arthropods found in seabird nests on six of the Ogasawara Islands

Arthropods	Mukojima Islands			Chichijima Islands			Nishinoshima Island			Volcano Islands			
	Torishima	Nakoudojima		Minamijima			Brown Booby <i>Sula leucogaster</i>	Wedge-tailed Shearwater <i>Ardeanna pacifica</i>	Brown Booby <i>Sula leucogaster</i>	Wedge-tailed Shearwater <i>Ardeanna pacifica</i>	Kitaiwoto	Minamiwoto	
	No. of arth. ^a	Freq. ^b arth. ^a	No. of arth. ^a	Freq. ^b arth. ^a	No. of arth. ^a	Freq. ^b arth. ^a	No. of arth. ^a	Freq. ^b arth. ^a	No. of arth. ^a	Freq. ^b arth. ^a	No. of arth. ^a	Freq. ^b arth. ^a	
ORDERS	SPECIES												
Isopoda	2(0.15)	0.15	5(0.39)	0.15	5(0.21)	0.17	2(0.20)	0.20	-	-	1(0.10)	0.30	-
Oribatida	-	-	-	-	-	-	-	-	-	-	9(0.90)	0.30	-
Ixodida	2(0.15)	0.077	-	-	4(0.17)	0.083	-	-	1(0.14)	0.14	5(0.50)	0.20	1(0.33)
Pseudoscorpionida	-	-	-	-	-	-	-	-	-	-	2(0.20)	0.10	-
Blattodea	-	-	-	-	-	-	-	-	-	1(0.10)	0.10	-	-
<i>Dermeestes ater</i>	-	-	-	-	-	-	-	-	1(0.14)	0.14	-	-	1(0.33)
<i>Torishimazo lineatus</i>	-	-	-	-	1(0.042)	0.042	-	-	-	-	-	-	-
<i>Dryophthorus ogasawaraensis</i>	2(0.15)	0.15	-	-	-	-	4(0.40)	0.10	-	-	-	-	-
Coleoptera	-	-	-	-	1(0.042)	0.042	-	-	-	-	-	-	-
Hymenoptera (Formicidae)	2(0.15)	0.077	-	-	-	-	-	-	-	-	-	-	-
Diptera	-	-	1(0.077)	0.077	-	-	1(0.10)	0.10	-	-	26(2.6)	0.40	4(1.3)
<i>Praeacedes atomosella</i> ^c	-	-	-	-	-	-	98(9.8)	0.60	-	-	-	-	-
<i>Crypsithyris</i> spp. ^c	-	-	-	-	-	-	14(1.4)	0.20	-	-	-	-	-
Crambidae spp.	-	-	-	-	-	-	9(0.90)	0.50	-	-	2(0.20)	0.10	-
Total no. of arthropods	8(0.62)		6(0.46)		11(0.46)		128(12.8)		2(0.29)		6(0.60)		6(2.0)

^a The number of arthropods found per bird species, per island; the number in parentheses represents the average number of arthropods per nest sample.

^b Appearance frequencies were calculated as follows: the number of times that arthropod type appeared (not the number of individuals), divided by the number of nests.

^c The genera *Praeacedes* and *Crypsithyris* are members of the Tineidae family.

Focusing on shearwater nests collected on Minamijima Island and booby nests collected on the Volcano Islands, each of which contained one or more arthropods per nest on average (Table 1), arthropod faunas composed mainly of animal decomposers were found in these nests. Some of the Lepidoptera species found only in shearwater nests from Minamijima Island were *Praeacedes atomosella* and *Crypsithyris* spp., which belong to Tineidae. In our study, the number of Tineidae accounted for 87.5% of the total number of arthropods found in shearwater nests on Minamijima Island. By contrast, in the Volcano Islands, the number of Diptera accounted for 65% of the total number of arthropods found in booby nests on Kitaiwoto Island and 66.7% of the total number of arthropods found in booby nests on Minamijima Island.

Referring to the differences among nests collected on Minamijima Island, the total number of arthropods found in the shearwater nests was significantly higher than the number found in booby nests ($W = 57, P < .01$), and the number of Lepidoptera was significantly higher in the shearwater nests than in the booby nests ($W = 36, P < .01$). On Nishinoshima Island, there were no significant differences in the number of arthropods between the nests of boobies and shearwaters, either in total ($W = 30, P = .581$) or in terms of taxonomic levels.

An NMDS plot shows that the arthropod faunas in seabird nests were similar among islands in proximity, regardless of the host bird species (Fig. 3).

DISCUSSION

In total we found nine orders of arthropods from the nests of Black-footed Albatrosses, Wedge-tailed Shearwaters, and Brown Boobies collected on six uninhabited islands of the Ogasawara Islands. Notably, this is the world's first study that has comprehensively investigated arthropod fauna in the nests of seabirds.

Characteristics of Arthropod Fauna in the Nests of Seabirds Breeding on the Ogasawara Islands

The characteristic arthropods found from seabird nests in this study were Isopoda, Tineidae, and Diptera (Table 1). Isopoda play an important role as decomposers on the Ogasawara Islands (Shinobe et al., 2017). Diptera larvae found in booby nests on Kitaiwoto and Minamiwoto Islands also serve as decomposers and fill the niche of vertebrate scavengers on these two Volcano Islands (Mori et al., 2018). Several studies have reported that Tineidae larvae, which are keratin eaters, inhabit seabird nests (Wandering Albatross: Sinclair & Chown, 2006; Wedge-tailed Shearwater and Bulwer's Petrels: Nasu et al., 2014). The Tineidae larvae found in the shearwater nests were *Praeacedes atomosella* and *Crypsithyris* spp., both of which are decomposers that consume the feathers or feces of animals containing keratin (Robinson & Nielson, 1993; Zimmerman, 1978). Decomposers (Tineidae larvae, Diptera, and Isopoda) accounted for 76.8% of the total number of arthropods found in this study (Table 1). Yahiro et al. (2013) investigated the arthropod fauna in the nests of cormorants, which form open nests near water, and found that communities were dominated by corrosive insects, such as Coleoptera. Decomposer-dominated arthropod communities also occur in the nests of land birds and freshwater waterfowl (Nasu et al., 2007, 2011; Takizawa et al., 2013).

On Nishinoshima Island, the number of individuals and species of arthropods per nest were the lowest among the study islands, which may be due to Nishinoshima Island being an actively erupting volcano. However, some decomposers, such as Blattodea and Coleoptera, and seabird parasites, such as Ixodida, did occur in seabird nests collected on Nishinoshima. In 2019, when nest samples were collected, most vegetation of Nishinoshima Island had been destroyed by an eruption that had been occurring since 2013. Decomposers appear to provide an important ecosystem function on this barren island by processing marine-derived organic matter that seabirds bring into nests, which will later contribute to soil formation, important in the restoration of the Nishinoshima ecosystem. Seabird nests may be more important as habitats for arthropods in areas with low biodiversity than in areas with high biodiversity.

Differences in Environmental Engineering Functions Based on Nesting Types

Boobies accumulate nesting materials on the ground, whereas shearwaters dig burrows or nest in rock crevices. The number of arthropods found in nests of shearwaters was significantly higher than in booby nests. Tineidae larvae, especially, were significantly more abundant in shearwater nests compared to booby nests. On Minamijima Island, which is covered by grassland, nests on the ground surface are exposed to high temperatures from direct sunlight, rain, and wind. By contrast, burrows or rock crevices are shielded from these factors (Nasu et al., 2014). Tineidae larvae have low mobility and are vulnerable to desiccation despite having pupal cases; thus, burrows, with their higher humidity, are superior habitats for these arthropods. Species such as the Snowy Albatross build elevated nests and use their bodies to maintain the temperature and humidity in their nests during incubation, which can also create a suitable environment for the growth of Tineidae larvae when birds are present (Sinclair & Chown, 2006). However, seabird burrows can easily maintain their internal temperature and humidity regardless of host birds' presence, making them invaluable habitats for arthropods.

The arthropod faunas in seabird nests were similar within each of the island groups regardless of host bird species (Fig. 3). In particular, the arthropod faunas of booby nests collected on Kitaiwoto and Minamiwoto Islands (the Volcano Islands) were dominated by Diptera and indicated different trends compared to the other islands. Nesting types of seabirds affect arthropod faunas in the nests, and furthermore, the local biota and environmental factors of each region are also thought to affect them.

CONCLUSIONS

Seabirds accumulate nest materials—such as plants, feathers, and regurgitated food—that provide decomposers with suitable habitat. In addition, seabird burrows can maintain temperature and humidity conducive to arthropod presence. Most previous studies have focused on seabird ecosystem functions such as nutrient cycling or seed dispersal, but our study revealed another ecosystem function: maintenance of arthropod communities on oceanic islands. Particularly underestimated thus far has been the contribution of burrow-nesters in the presence of insular arthropod fauna.

To elucidate the mechanisms by which arthropods establish themselves in seabird nests, future studies should measure

temperature and humidity conditions in burrows and analyze the feeding habits of arthropods in the nests. Furthermore, it will be revealing to determine any symbiotic relationships with host seabirds by evaluating not only the value of seabird nests for arthropods but also the arthropods' functions, such as cleaning.

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AUTHOR CONTRIBUTIONS

KM: Conceptualization, funding acquisition, sample collection, investigation, writing—original draft, writing—review & editing. KK: Conceptualization, funding acquisition, sample collection, investigation, project administration, writing—original draft, writing—review & editing, supervision. TK: Funding acquisition, investigation, statistical analysis, writing—review & editing, supervision.

REFERENCES

- Chiba, Y., Kawakami, K., Suzuki, H., & Horikoshi, K. (2007). The distribution of seabirds in the Bonin Islands, southern Japan. *Journal of the Yamashina Institute for Ornithology*, 39(1), 1–17. <https://doi.org/10.3312/jyio.39.1>
- Ellis, J. C. (2005). Marine birds on land: A review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecology*, 181(2), 227–241. <https://doi.org/10.1007/s11258-005-7147-y>
- Hamao, S., & Nasu, Y. (2022). Tori no su to konchu no kankei: Tori no hanshoku katsudo ga konchu no seisoku basho o tsukuridasu [Relation between bird nests and insects: Evidence that breeding activities of birds create a habitat for insects]. *Japan Journal of Ornithology*, 71(1), 13–20. <https://doi.org/10.3838/jjo.71.13>
- Hicks, E. A. (1953). Observations on the insect fauna of birds' nests. *Journal of the Kansas Entomological Society*, 26(1), 11–18. <https://www.jstor.org/stable/25082031>
- Hicks, E. A. (1959). *Check-list and bibliography on the occurrence of insects in birds' nests*. Iowa State College Press. <https://doi.org/10.5962/bhl.title.6819>
- Magnússon, B., Magnússon, S. H., Ólafsson, E., & Sigurdsson, B. D. (2014). Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. *Biogeosciences*, 11(19), 5521–5537. <https://doi.org/10.5194/bg-11-5521-2014>
- Matsumura, R., Shirai, M., Mizutani, Y., Koyama, S., Takeda, W., Yashiki, C., Fujioka, M., Kobayashi, D., Yamamoto, T., Kasai, S., Yoda, K., Isawa, H., & Itoyama, K. (2024). Survey of tick distribution in two seabird species: The black-tailed gull (*Larus crassirostris*) and the streaked shearwater (*Calonectris leucomelas*) colonies on Kabushima, Toshima, and Awashima islands, Japan in 2022. *Medical Entomology and Zoology*, 75(3), 177–183. <https://doi.org/10.7601/mez.75.177>
- Mori, H., Karube, H., & Kishimoto, T. (2018). Minamiwoto no konchuso to sono tokushusei [Insect fauna on Minami-Iwo-To Island]. *Ogasawara Research*, (44), 251–288.
- Nasu, Y., Murahama, S., Matsumuro, H., Hashiguchi, D., & Murahama, C. (2007). First record of Lepidoptera from Ural owl nests in Japan. *Applied Entomology and Zoology*, 42(4), 607–612. <https://doi.org/10.1303/aez.2007.607>
- Nasu, Y., Murahama, S., Matsumuro, H., Ueda, K., Hirowatari, T., & Yoshiyasu, Y. (2011). Fukuro no su kara hakken sareta Shirahoshi hanamuguri (Shoshimokura, Koganemushi-ka) [*Protaetia brevitarsis* (Lewis) (Coleoptera, Scarabaeidae) from the Ural Owl nests in Japan]. *Strix*, 27(4), 67–72. https://doi.org/10.51056/strix.27.0_67
- Nasu, Y., Sakai, M., Kawakami, K., & Aoyama, Y. (2014). Ogasawara shoto de hanshoku suru 3 shurui no chorui no su ni seisoku suru rinshirui [Lepidoptera from nests of three bird species breeding in the Ogasawara Islands, Japan]. *Lepidoptera Science*, 65(2), 73–78. https://doi.org/10.18984/lepid.65.2_73
- Nordberg, S. (1936). Biologisch-ökologische untersuchungen über die Vogelnidicolen [Biological and ecological studies of bird nests]. *Acta Zoologica Fennica*, 21, 1–168.
- R Core Team. (2024). *R: A language and environment for statistical computing* (Version 4.4.2) [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Robinson, G. S., & Nielsen, E. S. (1993). *Tineid genera of Australia (Lepidoptera)* (Vol. 2). CSIRO Publishing.
- Sinclair, B. J., & Chown, S. L. (2006). Caterpillars benefit from thermal ecosystem engineering by wandering albatrosses on sub-Antarctic Marion Island. *Biology Letters*, 2(1), 51–54. <https://doi.org/10.1098/rsbl.2005.0384>
- Shinobe, S., Uchida, S., Mori, H., Okochi, I., & Chiba, S. (2017). Declining soil Crustacea in a World Heritage Site caused by land nemertean. *Scientific Reports*, 7(1), Article 12400. <https://doi.org/10.1038/s41598-017-12653-4>
- Takizawa, K., Hotta, M., Kusama, Y., & Kusama, R. (2013). Iizuna kogen no fukuro no su kara hakken sareta zetsumetsu kigu-shu Shirahoshi hanamuguri to sonota no konchu-ru [An endangered beetle *Protaetia brevitarsis* (Lewis) and other beetles from Ural Owl *Strix uralensis* nests in Iizuna Heights]. *Bulletin of Nagano Environmental Conservation Research Institute*, 9, 85–89.
- Tryjanowski, P., Baraniak, E., Bajaczyk, R., Gwiazdowicz, D. J., Konwerski, S., Olszanowski, Z., & Szymkowiak, P. (2001). Arthropods in nests of the red-backed shrike (*Lanius collurio*) in Poland. *Belgian Journal of Zoology*, 131(1), 69–74.
- Wilhelm, S. I., Larson, D. J., & Storey, A. E. (2001). Habitat preference of two burying beetles (Coleoptera: Silphidae: *Nicrophorus*) living among seabirds. *Northeastern Naturalist*, 8(4), 435–442. [https://doi.org/10.1656/1092-6194\(2001\)008\[0435:HPOTBB\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2001)008[0435:HPOTBB]2.0.CO;2)

- Wilson, N., & Bull, E. L. (1977). Ectoparasites found in the nest cavities of Pileated Woodpeckers in Oregon. *Bird-Banding*, 48(2), 171–173. <http://www.jstor.org/stable/20699086>
- Woodroffe, G. E. (1953). An ecological study of the insects and mites in the nests of certain birds in Britain. *Bulletin of Entomological Research*, 44(4), 739–772. <https://doi.org/10.1017/S0007485300024706>
- Yahiro, K., Kameda, K., Nasu, Y., & Murahama, S. (2013). Kawai no su no konchuso [Insect fauna of Great Cormorant (*Phalacrocorax carbo*) nests]. *Japanese Journal of Entomology (New Series)*, 16(1), 15–23. https://doi.org/10.20848/kontyu.16.1_15
- Zimmerman, E. C. (1978). *Insects of Hawaii: Vol. 9. Microlepidoptera*. University of Hawaii Press.
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