

Research Article

Organisms associated with nests of the invasive squirrel *Callosciurus erythraeus* (Pallas, 1779): an overlooked arboreal habitat for urban pests

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Abstract

The nests of wild animals serve as habitats for a diverse range of organisms. Depending on the constructors, these nests can occur in urban environments and provide potential shelters for pest organisms harmful to human health and activities. In this context, we collected arboreal nests of Pallas's squirrel *Callosciurus erythraeus*, a non-native species that has invaded urban areas in the Kanto region of Japan, and examined their materials and associated biota. Nine nests collected from an urban green space in Kanagawa Prefecture in January 2022 were found to have one- to three-layered structures constructed using plant species from 10 orders. The inner layers were primarily composed of fibers of *Cryptomeria japonica* and *Trachycarpus fortunei*, whereas the outer layers consisted of twigs and leaves of *Padus* sp. and *Castanopsis sieboldii*, with leaves of *Prunus buergeriana* and *Quercus glauca* used for intermediate layers. From these nests, we recovered 1,467 invertebrates in 14 orders, with an average of 8.2 (5–11) orders and 163.0 (36–314) individuals per nest. Dipterans (n = 355) were the most abundant, followed by collembolans (n = 261), acarids (n = 235), and psocids (n = 226). Several dipterans were recognized as urban pests, including phorid flies, muscid houseflies, and drosophilid fruit flies associated with discomfort, food contamination, and pathogen transmission. In addition, we genetically identified larvae of a non-native noctuid moth, suggesting that the nests may provide suitable microhabitats for additional alien species. These findings support our assumption that the nests of invasive squirrels show distinctive plant use and serve as microhabitats for diverse and harmful fauna. Given that Pallas's squirrel populations are insufficiently controlled in many invaded areas, the number of such nests is likely to increase. We therefore recommend that eradication programs address not only the squirrels but also their nests as potential sources of urban pests.

Key words: invasive species, Pallas's squirrel, management, microhabitat, invertebrate

Introduction

Biological invasions exert significant impacts on recipient ecosystems (Didham et al. 2005; Ehrenfeld et al. 2010) and threaten both human health and economic activities (Pejchar and Mooney 2009; Pyšek and Richardson 2010; Gallardo et al. 2024). The associated damage and management costs continue to rise globally, making invasive species a key issue from both

ecological and societal perspectives (Simberloff et al. 2013; Cuthbert et al. 2021; Diagne et al. 2021; Heringer et al. 2024). In addition to their direct biotic interactions, invasive species often modify the physical and chemical conditions of habitats through their creation, destruction, or alteration (Jones et al. 1994; Crooks 2002; Hastings et al. 2007). These modifications can substantially affect biodiversity (Cuddington and Hastings 2004; Sousa et al. 2009; Anderson et al. 2014; Emery-Butcher et al. 2020), though the direction and magnitude of such impacts vary across cases (Gribben et al. 2013; Guy-Haim et al. 2018; Rilov et al. 2023). Understanding these context-dependent processes across diverse systems is therefore essential for building a robust evidence base.

Animal nests are known to serve as habitats for a variety of co-habiting organisms (Jaworski et al. 2021), including those inhabiting the nests of birds and small mammals (e.g., Marié 1929; Ihssen 1940; Ross 1944; Medvedev 1947; Roháček 2019). Although most documented examples come from natural habitats, nesting structures in urban environments also provide refuges for pest organisms considered harmful to human health and activities (Hicks 1959; Tomioka and Nakamura 2000; Buczek et al. 2018; Krivosheina et al. 2018). Given that bird nests have been shown to provide microhabitats for urban pests, such as housefly relatives and pigeon-associated chicken mites (Buczek et al. 2018; Krivosheina et al. 2018), it is reasonable to assume that the structures of nests constructed by invasive mammals could offer similar opportunities, particularly when constructed in proximity to areas of human habitation.

Pallas's squirrel *Callosciurus erythraeus* (Pallas, 1779) is a small arboreal mammal native to eastern India, Myanmar, parts of the Malay and Indochina peninsulas, southeastern China, and Taiwan (Thorington et al. 2012), but it has been introduced into Japan, France, Hong Kong, Argentina, the Netherlands, Belgium, and Italy (Bertolino and Lurz 2013; Mazzamuto et al. 2021). A population in the Netherlands has been successfully eradicated in 2015 through intensive campaigns involving local citizens (La Haye et al. 2023), whereas management efforts to control populations are still underway in other countries. In Japan, this squirrel was first introduced into Izu Ōshima Island in the 1930s, and subsequently dispersed to multiple regions, mainly in western Japan from the Kanto region to Kyushu (Udagawa 1954; Tamura 2015; Tamura and Yasuda 2023; Eguchi et al. 2025). Besides potential impact on native ecosystems and damage to crops and trees (Tamura 2002), individual squirrels are concerned to serve as infective carriers of epizootic and zoonotic pathogens that pose health risks to both native mammals and humans (e.g., Eguchi et al. 2022; Katahira et al. 2022; Masuda et al. 2022, 2025).

Arboreal squirrels, including Pallas's squirrels, generally construct their nests in the forks of trees or in tree cavities (Figure 1a-c; Farentinos 1972; Wauters and Dhondt 1990; Halloran and Bekoff 1994). These nests serve



Figure 1. Representative examples of the nest of Pallas's squirrels (Photographs were taken by Yuya Eguchi). (a) A nest of which the outer layer comprises only branches (Maioka Park, Kanagawa Prefecture; March 9, 2025). (b) A nest with leaf and branches intertwined in the outer layer (Maioka Park, Kanagawa Prefecture; March 9, 2025). (c) A nest of which the outer layer comprises only leafy branches (Maioka Park, Kanagawa Prefecture; December 18, 2022). (d) An enlarged view of the nest entrance in a bilayered nest.

not only as sites to facilitate breeding, resting, and predator avoidance but also contribute to mitigating the adverse effects of summer heat and winter cold (Farentinos 1972; Wauters and Dhondt 1990; Halloran and Bekoff 1994). They typically have a bilayer structure consisting of outer and inner layers, or sometimes a three-layered structure incorporating an intermediate layer, all of which provide insulation, waterproofing, and protection from the wind (Layne 1954). Similarly, Pallas's squirrels construct nests comprising two or three distinct layers (Figure 1d), although in some cases, the boundaries between these layers are somewhat indistinct, and more complex types have also been found (Okubo et al. 2005).

Among the introduced and human-mediated populations of this squirrel in Japan, those in the Kanto region have successfully colonized urban environments, within which their nests are frequently found in urban green spaces and even in human dwellings (Ono 2001; Okubo et al. 2005). These nests may therefore serve as shelters for pest organisms in ways analogous to the pest-harboring bird nests documented in urban environments. To verify this assumption, we collected nests of Pallas's squirrels from an urban green space in Kanagawa Prefecture, which is part of the greater Tokyo area of Japan, and examined the cohabiting organisms co-habiting within the nest materials. In this paper, we report the composition of the fauna recovered and consider certain overlooked problems associated with the management programs currently in place to control the populations of this squirrel.

Materials and methods

Nest sampling and sorting

A total of nine squirrel nests were collected from an urban green space in Yokohama City, Kanagawa Prefecture, Japan, on January 6 and 14, 2022. Pallas's squirrels have been present in Kanagawa Prefecture since around 1950, and invasion records from Yokohama City date back to the late 1960s (Eguchi et al. 2025). The study site, like much of the surrounding

Kanto region, has been heavily modified by human activities and land development. As a result, no other squirrel species, including the Japanese squirrel *Sciurus lis* Temminck, 1844 and the Japanese giant flying squirrel *Petaurista leucogenys* (Temminck, 1827), occur in this area. Therefore, all collected nests can be confidently attributed to construction by Pallas's squirrels in the present study.

The urban green space from which the nests were collected consists of a mixed forest of evergreen and deciduous broad-leaved species, together with conifers. The site adjoins a residential area and is managed by the municipality. However, detail of the precise location is withheld in this study to protect the privacy of the land manager and residents.

The nests, collected with the aid of a ladder (1.6 m in length, Hasegawa Kogyo Co., Ltd), were placed in plastic bags (45 L in volume and 0.012 mm in thickness; ASKUL Corporation) and subsequently transported to the Environmental Biology Laboratory at Azabu University, wherein they were frozen prior to further analysis. The nest materials were dried at room temperature (ca., 20–25 °C) for a few days and thereafter weighed using an electronic scale (± 2 g, CS-5000S; CUSTOM Corporation). Arthropod specimens were subsequently separated using two sieves of different mesh size (2.00 mm and 0.15 mm apertures; SANPO Co., Ltd). Large-sized individuals were extracted using forceps, and the contents remaining on the sieves were examined under an EZ4D stereomicroscope (LEICA) to ensure that specimens were not overlooked. The collected specimens were counted, placed in glass vials to discriminate taxonomic groups, and dried.

Having extracted and sorted the invertebrates collected from the nests, we sought to identify the sources of the nest materials based on morphological characteristics of the leaves and branches. Material corresponding to each of the identified plant taxa was weighed using an electronic scale (± 0.05 g, EL600; SHIMADZU Corporation), and its relative mass in each layer was calculated. Residual material generated during decomposition and sorting was also weighed, although this material was too fragmented for species-level identification. Identification of the vegetation material was based on the morphological keys published by The Flora-Kanagawa Association (2018).

The different layers of Pallas's squirrel nests are often constructed of different materials, the nature of which can differ depending on the type of local vegetation (Chang 1976). In Japan, the outer layer generally consists of small branches from evergreen broadleaf trees, such as the hinoki cypress *Chamaecyparis obtusa* (Siebold & Zucc.) Endl., Itajii chinquapin *Castanopsis sieboldii* (Makino) Hatus., bamboo-leaved oak *Quercus myrsinifolia* Blume, and konara oak *Q. serrata* Murray (Okubo et al. 2005). The intermediate layer includes small branches and leaves from deciduous broadleaf trees, such as the Japanese cedar *Cryptomeria japonica* (L. f.) D. Don, konara oak, evergreen broadleaf trees, such as the Japanese laurel *Aucuba japonica*

Thunb., the wax-leaf privet *Ligustrum japonicum* Thunb., herbaceous leaves from the bamboo-leaved oak, Japanese silver grass *Miscanthus sinensis* Anderson, and the white-stripe bamboo *Pleioblastus chino* (Franch. & Sav.) Makino, and the outer bark of different coniferous trees. The inner layer primarily comprises the inner bark from both coniferous and broadleaf trees.

Identification of invertebrates

For the purposes of morphological analysis, specimens were examined using an SZX16 light microscope (OLYMPUS) and an EZ4D stereomicroscope (LEICA). Specimens were identified to the lowest taxonomic category possible based on morphological characters provided in the literature on Stylommatophora (Minato 2015), Acarina (Asanuma 1965; Sasa 1965a, b, c), Araneae (Ono 2009), Polyxenida (Shinohara et al. 2015), Collembola (Tanaka 1980; Ichisawa 2012), Blattaria (Roth 1968), Hemiptera (Tomokuni 2015), Psocoptera (Tomita and Haga 1991; Yoshizawa 2016), Hymenoptera (Terayama et al. 2014), Coleoptera (Sasaji et al. 2015), and Diptera (Hayashi and Shinonaga 1979; Tanaka 2000). However, numerous specimens had been severely damaged during sampling and sorting, had missing body parts, or were collected as eggs or larvae, so that taxonomic identification was possible only to the order level in some cases. Specimens that were difficult to identify, even at the family level, were subjected to genetic analysis to supplement morphological identification.

The target gene used for genetic identification was a partial sequence of the cytochrome *c* oxidase subunit I mitochondrial gene. For the extraction of DNA, a portion of the specimens was lysed in 20 µL of 0.02 mol/L NaOH at 94 °C for 1 h (Nakao et al. 2018). Polymerase chain reaction (PCR) amplification was conducted in a total volume of 25 µL, including 1 µL of each primer and 2 µL of the extracted template DNA, using the universal primers LCO1490 and HCO2198 (Folmer et al. 1994), with the program run for 35 cycles, consisting of an initial denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. Amplification of the target region was confirmed based on agarose gel electrophoresis. The PCR products were purified using a commercial kit (Wizard® SV Gel and PCR Clean-up System, Promega) prior to their submission to Eurofins Genomics for sequencing analysis. The nucleotide sequences thus obtained were aligned using MEGAX (Kumar et al. 2018) and compared with respective reference sequences available in the GenBank/EMBL/DDBJ databases using the basic local alignment search tool.

Statistical analysis

To assess similarities in compositions among the nest materials and associated organisms, we performed a hierarchical cluster analysis based on Ward's method, which groups objects by minimizing within-cluster dispersion.

The analysis was implemented using the *hclust* function of the *stats* package in R. Similarities were estimated as Euclidean distances, calculated from the weights of nest materials and the numbers of invertebrate individuals, which were conventionally expressed as unit-less numerical values. Due to limitations in species identification, order-level data were used as a tentative proxy. These analyses were performed using R version 4.4.1 (R Core Team 2024).

Results

Nest materials

The initial weights of the examined nests prior to sorting ranged from 178 to 360 g, with a mean $\pm$ standard deviation (SD) of 280.67 ± 65.68 g. Of the nine nests, three had a single layer, five were two-layered with an outer and inner layer, and the remaining one had three layers with an additional intermediate layer (Supplementary material Table S1). Furthermore, the outer layer of the three-layered nests showed evidence of repair, as indicated by the presence of both old and new leaves. The remaining nests consisted exclusively of older materials, although it was not possible to ascertain whether any of these had been abandoned.

The inner layer of nests consisted of fibers from *C. japonica* and the chusan palm *Trachycarpus fortunei* (Hook.) H. Wendl., the latter of which is becoming established as an exotic species, as well as the leaves of the *C. sieboldii* (Table S1). The outer layer primarily comprised the branches of cherry *Padus* sp., branches and leaves of *C. sieboldii*, branches of *Q. serrata*, and leaves of *Q. myrsinifolia*. The intermediate layer consisted predominantly of the leaves of the Japanese bird cherry *Prunus buergeriana* (Miq.) T. T. Yu & T. C. Ku, and the ring-cupped oak *Q. glauca* Thunb.

Invertebrates

All nests harbored a range of invertebrate organisms, with a total of 1,467 specimens classified within 14 orders (Table S2). The average $\pm$ SD (and range) numbers of orders and individuals per nest were 8.2 ± 1.79 (5–11) and 163.0 ± 106.44 (36–314), respectively. The taxon with the highest overall abundance was the order Diptera ($n = 355$, 21.20%), followed by the orders Collembola, Acarina and Psocoptera, to which we assigned 261 (17.79%), 235 (16.02%), and 226 (15.41%) specimens, respectively.

Genetic analyses were conducted on specimens for which morphological identification was limited to the order level, resulting in sequence data from 12 individuals in eight orders (Table S2, accession numbers LC874838–LC874850). Among the genetic sequences analyzed for taxonomic identification, specimens corresponding to potential urban pest species included cockroaches belonging to the families Blattidae and Blattellidae and flies belonging to the families Phoridae, Muscidae, Drosophilidae, and

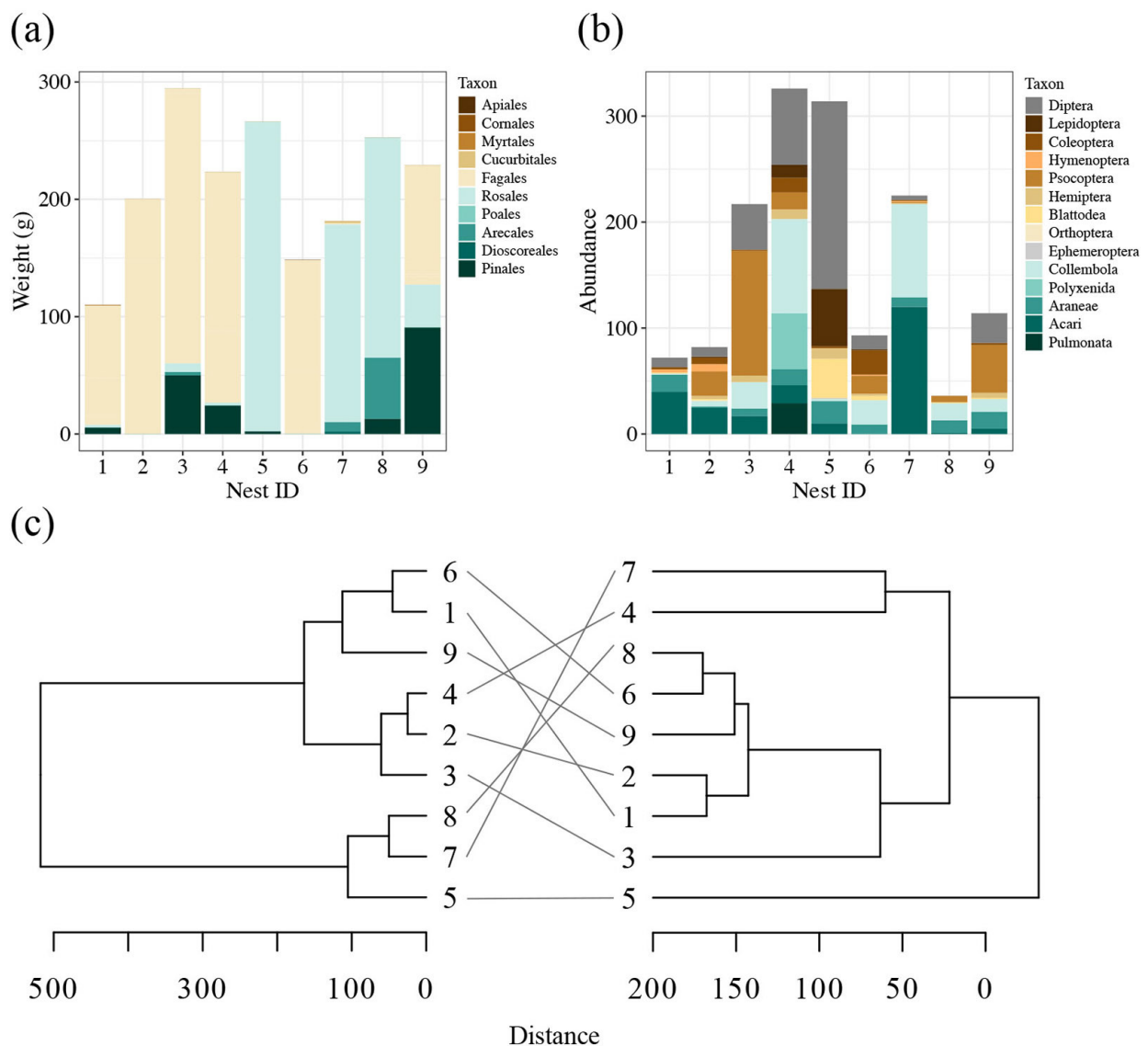


Figure 2. . Composition of nest materials and co-habiting organisms. (a) Weights of the nest materials classified according to plant order. (b) Numbers of co-habiting invertebrates according to taxonomic order. (c) Cluster dendrograms, with the results of the nest materials shown on the left and those of the cohabiting invertebrates on the right. The provided numbers correspond to the nest ID (see Tables S1, S2). Scales represent unit-less similarities expressed as Euclidean distances calculated using Ward's method.

Calliphoridae. The examined blattarian larvae showed the highest homology to *Sorineuchora nigra* (Shiraki, 1908) in the family Ectobiidae. The dipteran specimens exhibited highest matches with an unidentified species in the family Phoridae, *Leucophenga* sp. and *Drosophila tsigana* Burla & Gloor, 1952 in the family Drosophilidae, and *Triceratopyga calliphoroides* in the family Calliphoridae. In addition, among the Lepidoptera, one taxon was identified as *Simplicia cornicalis* (Fabricius, 1794) in the family Noctuidae, a non-native species in Kanagawa Prefecture.

Comparisons of nest material with invertebrate compositions

At the order level, no clear pattern emerged for either nest material or cohabiting fauna, with respect to the number of nest layers (Figure 2a, b). On the basis of the cluster analysis, we were able to roughly divide nesting

materials into two or three clusters and the collected organisms into two, three, or five clusters (Figure 2c). However, with the exception of a single nest (ID5), we were unable to detect any clear parallel patterns between the clusters of nest materials and those of organisms.

Discussion

Our findings demonstrate that the nests of invasive Pallas's squirrels can serve as microhabitats for a variety of invertebrates, including several urban pest species such as nuisance flies, cockroaches, and pyralid moths. Although we did not assess the extent to which these effects extend beyond the nest scale, a valuable next step would be to examine whether squirrel nests, providing small-scale structural changes in their spatial distribution, potentially contribute to autogenic engineering in a broader ecological context (Jones et al. 1994; Hastings et al. 2007).

More importantly, however, the present results help to highlight an overlooked indirect pathway via which invasive species may influence urban ecosystems. The study site is located at a heavily modified urban area in which native squirrels are entirely absent. In such settings, the nests constructed by invasive squirrels may unintentionally provide novel or additional niches for pest species and potentially for other non-native organisms, such as the moth *Simplicia cornicalis* identified in this study. Evaluating the population- or ecosystem-level consequences of this nest-associated facilitation in future studies would contribute to establishing the extent and ecological significance of these indirect effects, and it would be prudent to reassess the detrimental effects of invasive squirrels, not only as consumers and pathogen reservoirs but also as inadvertent habitat providers and potential invasion facilitators in urban environments (Simberloff and Von Holle 1999; Rodriguez 2006).

The co-habiting species in the nests of Pallas's squirrels included several common taxa of urban pests, particularly phorid flies, muscid houseflies, and drosophilid fruit flies. These groups are well known to cause household nuisance, contribute to food contamination, and act as mechanical vectors of bacterial pathogens associated with food poisoning (Bahrndorff et al. 2013, 2017). In addition, the cockroach egg sheaths recovered in this study may be those of species in the genus *Periplaneta* or a related group, which are major household pests; however, considering the small sample size, further confirmation is required.

These pest organisms are assumed to use leaf litter, decaying wood, and other decomposing plant materials as food resources and developmental substrates (Bell et al. 2007; Mlynarek et al. 2018; Ulyshen 2018). Such substrates support fungal decomposers that, in turn, provide resources for flies and cockroaches (Nehring et al. 2016; Zuev et al. 2019). Moreover, they provide sheltered microclimates with relatively stable temperatures

and humidity (Schal et al. 1984; Parisi et al. 2018). In managed urban green spaces, structures such as wood piles may serve as potential ground-level refuges for these pests. Considering that invertebrate assemblages similar to those identified in this study have previously been recorded from bird nests (Hicks 1959; Tomioka and Nakamura 2000; Krivosheina et al. 2018; Hamao and Nasu 2022), the arboreal nests of Pallas's squirrels may likewise function as tree-borne counterparts of wood piles, providing comparable microhabitats for pest taxa. In any case, an increase in squirrel nests in the vicinity of residential areas could provide additional habitat opportunities for these organisms, and thereby heighten concerns regarding urban public health.

Not only native species, but also certain non-native invasive pests appear to benefit from colonizing the nests of Pallas's squirrel. For example, the noctuid moth *S. cornicalis* was originally distributed in southern Japan, including Okinawa Prefecture and the surrounding islands (Sugi 1965). However, in 1971, this species was reported in Ibusuki City, Kagoshima Prefecture (Yamamoto and Yoshimoto 1973) and was subsequently detected at Narita Airport in 1998 (Tokihiko 1998), probably introduced via imported plants. Although the origin and invasive route of the *S. cornicalis* specimen recovered in the present study require further assessment, it is plausible that squirrel nests are used as breeding habitats by established populations.

Among the examined nests, we noted considerable differences in the composition of co-habiting fauna. Psocids and collembolans, typically soil- and tree surface-dwelling organisms that feed on fallen leaves and lichens (Takeda 1982), were abundant in several nests, suggesting that they become incorporated into the nest along with plant materials that collected by squirrels during construction. Together with free-living mites, these organisms can serve as prey for predators such as jumping spiders, leading to the development of predator-prey interactions that may be unique to the composition of individual nests. Furthermore, three of the collected nests, one with a single layer and two with two layers, were damaged and appeared to be old and already abandoned at the time of sampling, yet they still supported diverse invertebrate assemblages. Thus, similar to nesting birds that provide novel habitats for insects (Hamao and Nasu 2022), Pallas's squirrels may provide arboreal niches for soil-dwelling arthropods, fostering small patchy ecosystems whose characteristics depend on the materials used to construct each nest. Further investigation of these community patterns is warranted, considering potential factors shaping the initial conditions of each nest. These include the number of layers, material composition, successional changes during nest development, and variation associated with the builder's age, sex, and access to available tree resources.

In recent years, there has been a notable increase in the size of the Pallas's squirrel population distributed in Kanagawa Prefecture, with current estimates indicating that the numbers of these squirrels may exceed 100,000 (Tamura and Yasuda 2023). Although no systematic studies have

quantified the number of nests constructed per individual, and little is known about their nesting behavior, the increasing population size suggests that there are currently a substantial number of nests across the distribution range. Multiplying the number of organisms recovered per nest by the size of the squirrel population thus serves to highlight the potential impact on the associated communities. Furthermore, this co-habiting phenomenon appear to be applicable to both new and old nests. This accordingly indicates that, as part of ongoing eradication programs, all such nests should be removed as soon as they are detected. As a broader consequence of squirrel invasion, these nests have long been overlooked, thereby highlighting the need for further investigations into nest-centered interactions among organisms inhabiting them.

Authors' contribution

Yuya Eguchi: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, writing – original draft. Kaito Tsumori: investigation and data collection. Takumi Tsujino: investigation and data collection. Hiroki Yajima: investigation and data collection. Yumi Funakoshi: data analysis and interpretation. Tatsuki Shimamoto: data analysis and interpretation, writing-review and editing. Kozue Nitta: investigation and data collection, data analysis and interpretation, writing – review and editing. Hirotaka Katahira: research conceptualization, sample design and methodology, writing – review and editing.

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Ethics statement

This study was conducted with permission from Yokohama City (Yokohama City Environmental and Creative Bureau, Northern Park Open Space Office Directive No. 1302, permission day: December 15, 2021).

Data availability statement

All data obtained are presented in the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Composition of the nest materials recovered from the nine nests of Pallas's squirrel collected in an urban green space of Kanagawa Prefecture, Japan, on January 6 and 14, 2022.

Table S2. Composition of the invertebrates recovered from the nine nests of Pallas's squirrel collected in an urban green space of Kanagawa Prefecture, Japan, on January 6 and 14, 2022.

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