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# Earwigs and woodlice as some of the world's smallest internal seed dispersal agents: Insights from the ecology of *Monotropastrum humile* (Ericaceae)

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**Societal Impact Statement**

This study illuminates the underappreciated role of invertebrates in seed dispersal, extending beyond the well-documented contributions of ants. Focusing on *Monotropastrum humile* (銀竜草 [silver dragon plant] or 水晶蘭 [crystal orchid]), a non-photosynthetic plant known for its minuscule, dust-like seeds, the present research uncovers their seed dispersal roles of woodlice and earwigs in Japan. Remarkably, these invertebrates include the smallest known endozoochorous seed dispersers.

**Summary**

- Endozoochory, or internal seed dispersal through the digestive tracts of animals, has been less studied in invertebrates compared with vertebrates. Nonetheless, endozoochory is plausible whenever seeds are small enough for ingestion by frugivorous animals, suggesting a potential role for invertebrates in seed dispersal, especially for plants with minute seeds.
- *Monotropastrum humile* (Ericaceae), characterized by its fleshy fruits and dust-like seeds, is known to utilize invertebrate agents such as camel crickets and cockroaches for seed dispersal. Here, we investigate this seed dispersal mechanism using time-lapse photography, feeding experiments, and seed coat anatomy analysis, particularly focusing on interactions among undocumented invertebrate internal seed dispersers.
- Field observations indicated that in the studied population, *M. humile* fruits were primarily consumed by camel crickets, woodlice, and earwigs. Their effectiveness as seed dispersers varied, with camel crickets primarily acting as dispersers, whereas earwigs and woodlice were more inclined toward seed predation. Nonetheless, some seeds defecated by earwigs and woodlice remained intact, suggesting that they could also function as dispersal agents.
- The woodlouse *Porcellio scaber* is now recognized as the world's smallest internal seed dispersal agent. Combined with earlier discoveries, such as seed dispersal by camel crickets, cockroaches, and ants, and the fact that *P. scaber* is an exotic species in the study site, *M. humile* likely depends on a broad spectrum of local

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invertebrates. The engagement of multiple invertebrate dispersers may enhance seed dispersal across diverse habitats.

**KEYWORDS**

camel cricket, endozoochory, fleshy fruits, frugivore, heterotrophic plant, mycoheterotrophic plant, seed dispersal, seed predation

## 1 | INTRODUCTION

Vertebrates, primarily birds and mammals, are recognized as the principal seed dispersers in most plant communities, facilitating seed movement either internally via endozoochory (seed dispersal through the digestive tracts of animals) or externally through epizoochory (seed dispersal by attachment to fur or feathers) (Corlett, 2002; Herrera, 1995; van der Pijl, 1982). On the other hand, aside from ants, acknowledged as key epizoochorous seed dispersers across diverse habitats (Rico-Gray & Oliveira, 2007; Wolff & Debussche, 1999), the role of invertebrates in seed dispersal has been relatively understudied (Andresen & Levey, 2004; de Vega et al., 2011; Duthie et al., 2006; Estrada & Coates-Estrada, 1991). Due to biophysical size-related constraints, invertebrates are often disregarded as likely endozoochorous seed dispersal agents (de Vega et al., 2011). New Zealand's large endemic flightless crickets known as Weta, which occupy ecological niches similar to those of small mammals in other regions, are established to be endozoochorous seed dispersers (Duthie et al., 2006). While Weta may represent an unusual case of endozoochorous seed dispersal by insects, endozoochory could be feasible whenever seeds are sufficiently small to be ingested by frugivorous animals and robust enough to survive consumption and subsequent defecation intact (Corlett, 2021; de Vega et al., 2011; Suetsugu, 2018a, 2018b). This suggests that certain invertebrates may play an underestimated role in seed dispersal, especially for plants with very small seeds (Suetsugu, 2020).

Angiosperms exhibit a wide range of seed sizes, spanning over ten orders of magnitude in weight (Harper et al., 1970). Heterotrophic plants that rely on fungi or other plants during at least part of their development, often produce dust-like seeds lacking endosperm and containing minimal energy reserves (Leake, 1994). Dust seeds have evolved independently in at least 12 families (Burmanniaceae, Corsiaceae, Orchidaceae, Triuridaceae, Petrosaviaceae, Ericaceae, Gentianaceae, Polygalaceae, Orobanchaceae, Rubiaceae, Buddlejaceae, and Gesneriaceae) (Eriksson & Kainulainen, 2011; Leake, 1994). Given that fleshy and non-splitting fruits are adaptations for endozoochory (Jordano, 1995), plants possessing both dust seeds and fleshy indehiscent fruits are potential candidates for invertebrate-mediated endozoochorous dispersal. The genus *Monotropastrum* (Monotropoideae, Ericaceae) is one of the mycoheterotrophic plants with fleshy fruits and dust-like seeds (Matsuda et al., 2011; Yamada et al., 2008). *Monotropastrum* contains two species (Suetsugu et al., 2023), and *Monotropastrum humile* has a broad distribution across East Asia, extending from the Himalayas to Japan (Matsuda et al., 2011; Suetsugu et al., 2023; Tsukaya, 1998). While most mycoheterotrophic plants are notable for their rarity, this species is relatively common in Japan (Tsukaya, 1998; Uehara & Sugiura, 2017). Despite its prevalence and wide distribution, its seed dispersal mechanism remains somewhat elusive.

Uehara and Sugiura (2017) identified the forest cockroach *Blattella nipponica* as a legitimate seed disperser for *M. humile*. They highlighted several traits indicative of cockroach-mediated seed dispersal in *M. humile*: (1) the inconspicuous fruit display (subdued color and lack of flavor) likely deters vertebrate consumption; (2) the fruit ripening period aligns with the eclosion period (emergence) of the forest cockroach, which follows a univoltine life cycle (May and June) (Tsuji, 1985); (3) fruits are presented at ground level, where forest cockroaches reside; (4) the small seed size allows seeds to be ingested whole; and (5) the durable seed coat (hard testa) ensures the viability of ingested seeds. Based on these observations, Uehara and Sugiura (2017) suggested that *M. humile*, with its fleshy fruits, is highly adapted for seed dispersal specifically by adult cockroaches.

However, despite the identification of the forest cockroach *B. nipponica* as a potential seed disperser for *M. humile*, the geographic range of this insect does not align with that of *M. humile*. While *M. humile* is primarily found in cool-temperate and occasionally subalpine forests, *B. nipponica*, and similar forest-dwelling cockroaches are absent from cooler, higher-elevation forests in central and northern Japan (Asahina, 1991). Given the infrequency of specialized coevolutionary relationships between fruits and frugivores (Herrera, 1985; Jordano et al., 2007), it is plausible that *M. humile* relies on other invertebrates that are more prevalent in its habitat. Suetsugu (2018b) highlighted that in cool-temperate environments devoid of forest-inhabiting cockroaches, camel crickets could act as primary seed dispersers. Additionally, Yamada et al. (2021) noted that a small number of seeds with fleshy pulp were transported by *Nylanderia flavipes* ants. The present research explores the seed dispersal strategies of *M. humile* in Sapporo City, Hokkaido, Japan, focusing on its interactions with previously undocumented invertebrate seed dispersers.

## 2 | MATERIAL AND METHODS

### 2.1 | Assemblages of fruit consumer

Field studies were conducted during the fruiting season of *M. humile* (late July to early August 2013) in Shinei, Kiyota, Sapporo City, Hokkaido, located in a cool temperate region of northern Japan. The area, characterized by a dense deciduous broad-leaved forest with dominance of *Acer pictum* subsp. *dissectum* (Sapindaceae), *Quercus serrata* (Fagaceae), and *Q. crispula* (Fagaceae), hosted numerous fruiting *M. humile* individuals within a study site measuring approximately 10 m by 10 m. To investigate fruit consumer assemblages, we utilized the interval-programming function of a waterproof digital camera (Optio W80, Pentax, Japan), a method increasingly recognized for effectively substituting direct observations of pollination and seed dispersal activities. The camera, affixed to a flexible tripod (Gorillapod, Joby, San Francisco), was positioned about 30 cm from the fruiting *M. humile* individuals to ensure a clear focus on the fruits. Manual focus was employed to conserve battery life, as the automatic mode largely reduced it. Pre-set to capture images at intervals ranging from 30 s to 8 min, the camera used an internal flash and batteries (D-LI78 Pentax, Japan), with JPEG-format images recorded onto an 8 GB SD card. Preliminary findings suggested nocturnal fruit consumption, prompting the majority of observations to occur from sunset to sunrise. Over this period, 9291 photographs were taken across 276.75 h of monitoring. Fruit consumers were identified solely from instances of observed fruit consumption, with the total number of frames featuring each species feeding on the fruits tallied. Our focus was solely on animals that fed on *M. humile* fruits, and we took care to consider visitors of the same species that were captured in consecutive frames as the same individual.

## 2.2 | Seed viability

Feeding experiments were performed to assess the proportion of seeds that remained intact after passing through the digestive systems of the primary fruit consumers in the studied population: the camel cricket *Diestrammena brunneri*, the woodlouse *Porcellio scaber*, and the earwig *Anechura harmandi*. Adults of *D. brunneri* and *P. scaber* were collected near *M. humile* fruit patches, while *A. harmandi* adults were collected in another forest (Ebetsu City, Hokkaido) approximately 5 km away from the *M. humile* population. Ground beetles from the genus *Synuchus*, despite being one of the major consumers, were not included in the feeding experiments due to prior studies showing that *Synuchus* spp. did not expel any intact *M. humile* seeds (Suetsugu, 2018b). Moreover, while intraspecific variations in seed dispersal effectiveness might exist based on developmental stage (King et al., 2011; Larsen & Burns, 2012), our investigation was limited solely to adults of a standard body length (∼19–23 mm in *D. brunneri*, ∼8–11 mm in *P. scaber*, and ∼11–16 mm in *A. harmandi*). *P. scaber* is an introduced species but has become one of the common crustaceans in the northern parts of Japan (Tanaka & Udagawa, 1993).

To accurately determine the number of seeds consumed by camel crickets, earwigs, and woodlice, seeds were extracted from field-collected *M. humile* fruits and mixed with the fruit's fleshy parts without seeds, totaling 50 seeds per mixture. This mixture was then placed on moist filter paper within enclosures for each species ($n = 10$ per each fruit feeding species). While camel crickets consumed all seeds in most cases, any remaining seeds were forcibly fed to them if not consumed within 12 h. In contrast, because some seeds remained unconsumed by all woodlice and earwigs after 12 h, these were counted, removed, and noted. Fecal pellets from camel crickets, earwigs, and woodlice were collected every 6 h up to 48 h post-consumption to count intact seeds under a dissection microscope.

The differences in the proportion of intact seeds among those consumed by camel crickets, woodlice, and earwigs were analyzed using ANOVA, followed by a post hoc Tukey–Kramer test. Additionally, the intact seeds were subjected to 2,3,5-triphenyl tetrazolium chloride (TTC) viability staining, a technique previously applied to dust-like seeds (de Vega et al., 2011; Suetsugu, 2018b). In this method, TTC, initially a white salt, transforms into pink/red formazan within living cells, signifying seed viability (Copeland & McDonald, 1995). The viability of the seeds excreted by the consumers was then compared with the viability of 50 seeds directly collected from the same fruits using ANOVA, followed by a post hoc Tukey–Kramer test.

## 2.3 | Seed coat anatomy

The seed coat anatomy of *M. humile* was examined and compared with its wind-dispersed mycoheterotrophic species *Monotropa uniflora*, *Monotropa hypopithys*, and *Pyrola subaphylla* within the family Ericaceae (Merckx, 2013). Seed samples from each species were initially fixed in a formalin-acetic acid-alcohol (FAA) solution, followed by dehydration through a graded series of ethanol. Subsequently, the samples were embedded in Technovit 7100 resin (Kulzer, Wertheim, Germany) to prepare them for microtome sectioning. Serial sections of the resin-embedded seeds were cut to a thickness of 4–5 μm and stained with Safranin O to highlight structural details. These sections were then mounted in Entellan mounting medium (Merck, Darmstadt, Germany) for examination. Observations were conducted using an Olympus BX-51 microscope (Olympus, Tokyo, Japan).

# 3 | RESULTS

## 3.1 | Observation of fruit visitors

*M. humile* is an achlorophyllous plant with one-loculed ovaries with parietal placentation and fleshy fruits (Qin & Wallace, 2005; Wallace, 1987). As highlighted in prior research (Uehara & Sugiura, 2017), upon ripening, the entire plant frequently fell down, positioning the fruit at ground level where it becomes easily accessible and readily consumed by terrestrial frugivores (Figure 1).

Time-lapse photography revealed that the fruits of *M. humile* were consumed by a diverse array of invertebrates, including camel crickets, ants, ground beetles, and woodlice (Table 1). Among these invertebrates, camel crickets, specifically *D. brunneri* and *Diestrammena japanica*, were the most voracious (Figure 2), consuming a

**FIGURE 1** *Monotropastrum humile*, a mycoheterotrophic plant from East Asia with seeds that are dispersed by invertebrates. (a) Flowering plant. (b) Fruiting plant. Scale bars: 2 cm. Photographs: Osamu Kimura-Yokoyama.

**TABLE 1** Taxa of invertebrates found to consume the fruit of *Monotropastrum humile* in the investigated population.

| Animal taxa | | Frames captured | Times visited | Body length (mm) |
|---|---|---|---|---|
| Orthoptera | *Diestrammena brunneri* | 587 | 133 | 19–23 |
| | *Diestrammena japonica* | 81 | 36 | 24–33 |
| Hymenoptera | *Paratrechina flavipes* | >500 | >100 | 2–2.5 |
| | *Formica* sp. | >300 | >100 | 4–7 |
| | *Myrmica* sp. | >300 | >100 | 3.5–5.5 |
| Dermaptera | *Anechura harmandi* | 526 | 89 | 11–16 |
| | *Eparchus yezoensis* | 293 | 107 | 12–16 |
| Coleoptera | *Synuchus* spp. | 305 | 44 | 12–15 |
| | *Leptocarabus arboreus* | 6 | 4 | 26–30 |
| | *Pterostichus* spp. | 6 | 3 | 11–12 |
| | Histeridae sp. | 4 | 1 | 7–9 |
| | *Plesiophthalmus nigrocyaneus* | 1 | 1 | 16–20 |
| | Nitidulidae sp. | 1 | 1 | 5 |
| Diptera | *Drosophila* spp. | >300 | >50 | 2–3 |
| | Heleomyzidae sp. | 109 | 9 | 2–3 |
| | *Phelotrupes laevistriatus* | 3 | 1 | 12–22 |
| Isopoda | *Porcellio scaber* | >800 | >100 | 8–11 |

*Note*: The numbers represent total frames showing each species consuming fruits and the number of individuals feeding on the fruits. Animals captured in consecutive frames were considered the same individual.

significant portion (likely more than 50%) of the fruits in the studied populations. Instances of multiple camel crickets feeding on the same fruit were noted, as well as individual camel crickets feeding on several fruits. The earwig species *A. harmandi* and *Eparchus yezoensis* also frequently visited the fruits and, despite individual earwigs consuming only small quantities, collectively emerged as major fruit consumers. Similarly, the woodlouse *P. scaber*, often feeding on the fruits in groups (Figure 2), was identified as a primary fruit feeder, even though individual woodlice consumed only minimal portions. Ant species, such as *Nylanderia avipes*, fed mainly on the fleshy parts of the fruit, acting more as pulp thieves than seed dispersers. However, because the dust-like seeds were embedded within the fleshy pulp, ants might still contribute to seed dispersal by dispersing both seeds and pulp. No vertebrate fruit consumption was observed during the study.

## 3.2 | Seed passage through the digestive tract

The feeding experiments demonstrated that a significantly higher proportion of seeds remained intact after being passed by camel crickets

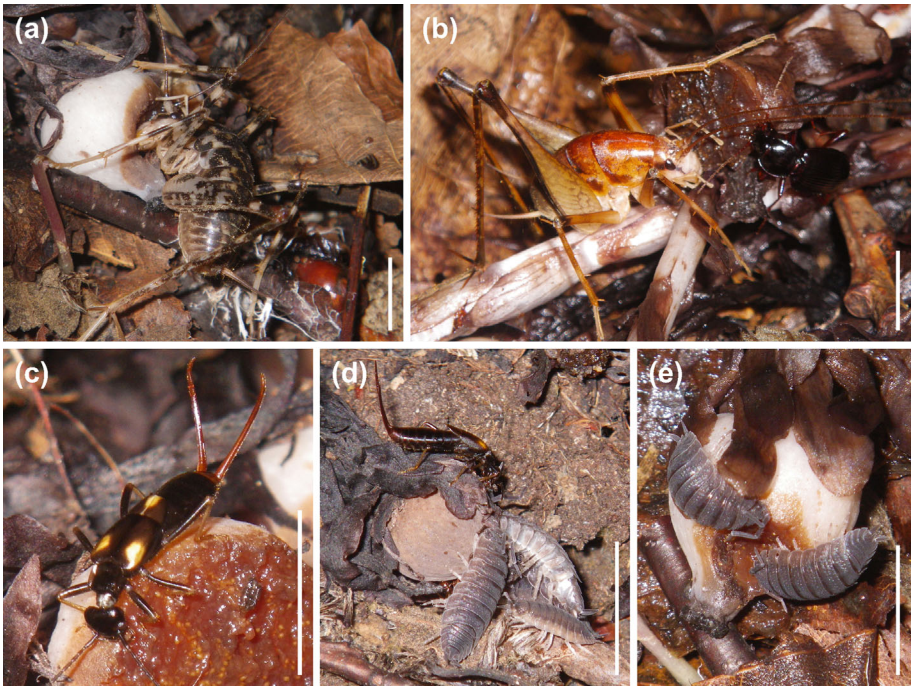

**FIGURE 2** Fruit consumers of *Monotropastrum humile*. (a) *Diestrammena japonica*. (b) *Diestrammena brunneri* and *Synuchus* sp. (c) *Eparchus yezoensis*. (d) *E. yezoensis* and *Porcellio scaber*. (e) *P. scaber*. Scale bars: 1 cm. Photographs: Osamu Kimura-Yokoyama.

(83.8 ± 5.7%; mean ± SD %; $n = 10$) than those found in the feces of woodlice (31.2 ± 12.5%; $n = 10$; $p < .001$) and earwigs (33.5 ± 11.8%; $n = 10$; $p < .001$; Dataset S1). Microscopic examination showed that seeds from camel cricket feces were intact, with normal embryos, similar to those from uningested fruits (Figure 3). Conversely, broken seeds were often observed in the feces of woodlice and earwigs. In contrast, TTC staining revealed no significant differences in viability among seeds excreted by camel crickets (48.4 ± 9.1%), woodlice (42.5 ± 13.6%), and earwigs (46.8 ± 11.3%) compared with those from intact fruits (50.8 ± 10.4%; $p > .3$ in all combinations).

Additionally, Safranin O staining indicated that the seed coat of *M. humile* is thicker than that of its wind-dispersed relatives *M. uniflora*, *M. hypopithys*, and *P. subaphylla* (Figure 4). This thicker seed coat may serve as an adaptation to protect seeds from digestive damage by fruit consumers such as camel crickets.

## 4 | DISCUSSION

Our field observations revealed that *M. humile* fruits in the studied population were primarily consumed by camel crickets, woodlice, and earwigs, with varying degrees of seed dispersal effectiveness. This study underscores the role of the camel cricket *Diestrammena* spp. in feeding on the fleshy fruits of *M. humile* and defecating viable seeds without causing seed destruction. Therefore, the present study provides further evidence that camel crickets function as *M. humile* seed dispersal agents (Suetsugu, 2018b). Considering the prevalence of camel crickets as a major part of the ground insect fauna in Japan and their substantial impact on local ecosystems (Sato et al., 2011; Suetsugu, 2018a, 2018b), their effectiveness as seed dispersal agents is a logical extension of their ecological role. While the weta in New Zealand has been recognized for occupying ecological niches similar to those of small mammals in other regions (Burns, 2006; Duthie et al., 2006), the identification of seed dispersal by camel crickets suggests that orthopteran insects may have adapted to serve as seed dispersal agents not only in regions lacking small mammals, such as New Zealand, but also in areas where small mammals are present.

Our research has identified the earwigs *A. harmandi* and *E. yezoensis* as frequent visitors and one of the major consumers of *M. humile* fruits. Although earwigs and woodlice are widely recognized for their role in seed consumption, they have traditionally been considered seed predators (Lott et al., 1995; Sanguankeo & León, 2011; Saska, 2008). Thus, their contribution to seed dispersal has never been demonstrated. However, our findings indicate that some seeds passed through the digestive systems of both earwigs and woodlice remain intact, suggesting their potential as seed dispersers for *M. humile*, albeit less efficiently than camel crickets. Apart from ants, the role of invertebrates in seed dispersal has been relatively overlooked (Duthie et al., 2006; Midgley et al., 2015; Suetsugu, 2018b).

Notably, among small invertebrates acting as internal seed dispersers, which include camel crickets (approximately 19–33 mm in body length) associated with genera such as *Apostasia* (Orchidaceae), *Monotropastrum* (Ericaceae), *Yoania* (Orchidaceae), and *Phacellanthus* (Orobancheaceae), as well as tenebrionid beetles (approximately 20 mm in body length) within the genus *Cytinus* (Cytinaceae), *B. nipponica* stands out for its notably small size (approximately 11–13 mm in length and 5 mm in width), likely representing the smallest internal seed dispersal agent recorded (Asahina, 1991; Machida et al., 2016). Surpassing this, *P. scaber* (approximately 8–11 mm in length and 5 mm in width) establishes a new record as the world's smallest internal seed dispersal agent. Additionally, although

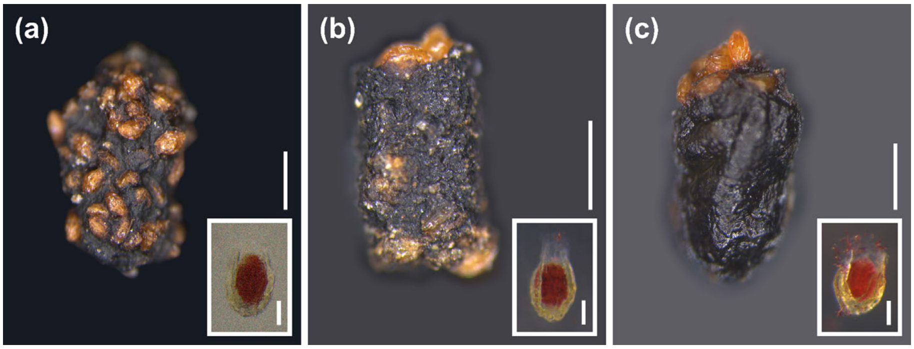

**FIGURE 3** Feces containing *Monotropastrum humile* seeds defecated by the camel cricket *Diestrammena brunneri* (a), the woodlouse *Porcellio scaber* (b), and the earwig *Anechura harmandi* (c). Inset: Viable seeds isolated from feces of each fruit consumer and stained with TTC. Scale bars: 500 and 100 μm (inset). Photographs: Kenji Suetsugu.

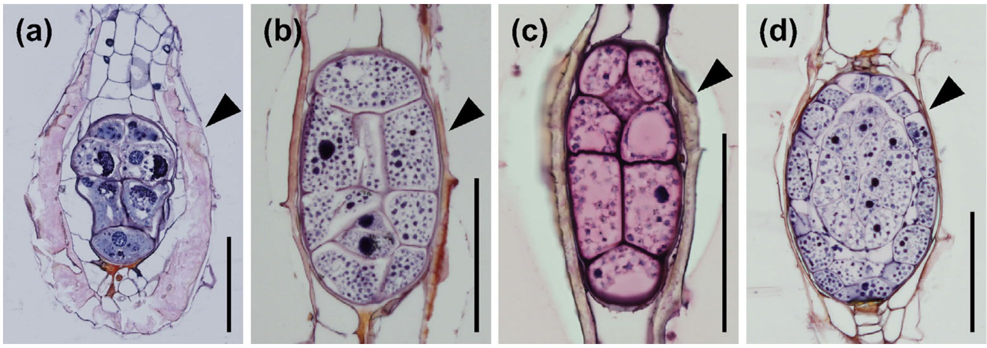

**FIGURE 4** Cross-section of *Monotropastrum humile* seed (a), *Monotropa uniflora* seed (b), *Monotropa hypopithys* seed (c), and *Pyrola subaphylla* seed (d). Seed coats are indicated by arrows. Scale bars: 100 μm. Photographs: Kenji Suetsugu.

*A. harmandi* (approximately 11–16 mm in length) is marginally larger than both *B. nipponica* and *P. scaber*, its remarkably slender width (about 3 mm) potentially makes it the lightest endozoochorous seed disperser known. The recognition of these diminutive invertebrates as endozoochorous seed dispersers challenges traditional perceptions of internal seed dispersal mechanisms.

While woodlice and earwigs exhibit tendencies toward seed predation, this behavior does not exclude the possibility of mutualistic relationships (King et al., 2011; Larsen & Burns, 2012). Although fleshy fruits are commonly consumed by small mammals, which often destroy the seeds, these mammals can also form mutualistic associations as seed dispersers (Amico & Aizen, 2000; Williams et al., 2000). In addition, many small mammal species hoard seeds, particularly during winter, and while most of these seeds are later retrieved and consumed, a proportion is forgotten and effectively dispersed (Jansen et al., 2008). The plants associated with scatter-hoarding animals may “sacrifice” some seeds to ensure the dispersal of others (King et al., 2011). Thus, organisms known primarily as seed predators can also engage in mutualistic associations with plants as seed dispersers (Janzen, 1984; King et al., 2011; Suetsugu & Hashiwaki, 2023). Therefore, the behavior of earwigs and woodlice in destroying some seeds during ingestion does not necessarily render them antagonists. It is also noteworthy that the woodlouse *P. scaber* is an introduced species in Japan. Yet, it is recognized that widespread non-native species can contribute to ecosystem functions (Hobbs et al., 2006, 2009; Kiers et al., 2010; Pattemore & Wilcove, 2012).

Additionally, although the distances traveled by woodlice are likely shorter than those covered by flying earwigs and the more mobile camel crickets, shorter dispersal distances might effectively contribute to reducing seedling aggregation, thus benefiting plant recruitment (Higashi et al., 1989). For instance, Higashi et al. (1989) demonstrated that an average dispersal distance of 64 cm by ants was sufficient to decrease seedling mortality in *Trillium tschonoskii* (Melanthiaceae). For mycoheterotrophic plants such as *M. humile*, efficient seed dispersal involves not only the transport of seeds but also their placement near appropriate hosts (Bidartondo & Bruns, 2005). This requirement is crucial given the minute size of their seeds and limited energy reserves, necessitating germination close to suitable hosts (Bidartondo, 2005). The diversity in dispersal agents, including woodlice, can therefore be beneficial, increasing the likelihood of seeds reaching a variety of suitable habitats. This diversity is probably important for *M. humile*, which depends on specific ecological conditions for germination and growth.

Overall, the present study underscores the importance of diverse seed dispersal agents including camel crickets, earwigs, and woodlice for *M. humile* in the investigated population. Notably, *P. scaber* is the world's smallest internal seed dispersal agent recorded so far. Taken together with previous findings such as seed dispersal by camel crickets, cockroaches, and ants (Suetsugu, 2018a, 2018b; Uehara & Sugiura, 2017; Yamada et al., 2021), *M. humile* may rely more on locally available invertebrates rather than birds or mammals for seed dispersal, without being specialized to a narrow group of invertebrates. The small size of *M. humile* seeds is a critical factor in allowing invertebrates like camel crickets, earwigs, and woodlice to ingest the seeds whole. Similar mechanisms have been observed in other plants with small seeds; for instance, beetle endozoochory in the holoparasitic plant *Cytinus* (Cytinaceae), and slug seed dispersal in plants previously considered to be primarily dispersed by ants (Calvino-Cancela &

Rubido-Bará, 2012; de Vega et al., 2011; Türke et al., 2010, 2012). These findings suggest that novel seed dispersal systems involving unconventional or unexpected taxa may be more common than previously assumed, particularly among plants with small seeds.

## AUTHOR CONTRIBUTIONS

Kenji Suetsugu and Shumpei Kitamura designed the project. Osamu Kimura-Yokoyama conducted time-lapse photography. Kenji Suetsugu reviewed the images captured by time-lapse photography, conducted the feeding experiments, and examined the seed coat anatomy. Kenji Suetsugu wrote the initial draft. All authors revised the manuscript and approved the final version.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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