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Quantifying relative abundance of the lesser Japanese mole (*Mogera imaizumii*) in mountain forests: A comparison between natural broad-leaved forests and conifer plantations

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Abstract

Describing the population abundance of species remains a fundamental challenge in ecology, particularly in soil ecosystems. While the preferred habitats of moles—top predators in the soil food web—are well documented in open areas such as cultivated lands and grasslands, few studies have focused on mountain forests, where assessing mole abundance is complicated by thick layers of plant leaf litter and complex topography. Additionally, many monoculture conifer plantations in Japan are poorly managed, potentially resulting in compacted soil that is less suitable for moles compared to natural broad-leaved forests. Here, we aimed to quantify the relative abundance of the lesser Japanese mole (*Mogera imaizumii*) in the mountain forests of Yamagata, Japan, by carefully searching for mole tunnels along 29 census routes (unpaved mountain trails) over 7 months. Although tunnels were detected on most routes (75.9%) regardless of forest type, tunnel density (tunnels/km) was lower in cedar (*Cryptomeria japonica*) plantations than in natural oak forests. The variation in tunnel density was positively related to earthworm biomass, highlighting the importance of earthworms as a food source. Lower earthworm biomass was associated with either higher soil hardness or higher soil moisture; however, only soil moisture tended to be higher in plantations. As cedars are typically planted in moist environments, the reduced mole abundance in these plantations may be related to the specific soil conditions of cedar plantations. These results demonstrate that mole abundance varies significantly across forest sites in response to soil environments.

KEYWORDS

Cryptomeria japonica, earthworms, habitat preferences, mole tunnels, oak forests

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1 | INTRODUCTION

Population abundance estimates of species provide the foundational data for studying ecological niches (Waldock et al., 2022), tracking changes in abundance over time due to human impacts (Hankinson et al., 2023; Nagamitsu et al., 2023), and understanding the contribution to ecosystem functions (Gaston et al., 2018). However, describing population abundance remains one of the most basic challenges in ecology (Singer, 2016), particularly in soil ecosystems, where individuals of many animal species are difficult to locate and observe.

Talpid moles, excluding Desmanimi, Urotrichini (Talpinae), and Uropsilinae, are small mammals highly adapted to a subterranean lifestyle, living in tunnel systems made by themselves. Moles are known to be ecosystem engineers (Beca et al., 2022; Jones et al., 1994), with tunnels providing space underground for other small animals (e.g., Hartman et al., 2001) and molehills giving new habitats to some insects (e.g., Streitberger & Fartmann, 2013) and plants (e.g., Seifan et al., 2010). In addition, moles are top predators in soil ecosystems (Nesterkova et al., 2014) and thus can contribute to maintaining species diversity through the soil food web (Wallach et al., 2015). Given the important roles of moles in ecosystems, identifying preferred habitats is crucial for understanding their ecological functions and their interactions with other species and the surrounding environment.

The adaptation to a subterranean lifestyle has allowed moles to occupy a wide range of environments, from urban parks and cultivated lands to grasslands, forests, and mountains (Abe, 1968; Godfrey & Crowcroft, 1960; Gorman & Stone, 1990; Llorente et al., 2021). In open areas, such as cultivated lands and grasslands, moles are often regarded as pests, so many studies have attempted to understand their preferred habitats by quantifying their abundance through activity signs, such as molehills, or by capturing moles (Figure 1a). Previous studies have revealed that mole density is higher in habitats where earthworms, their primary food source, are more abundant (Arlton, 1936; Edwards et al., 1999; Funmilayo, 1977; García-López de Hierro et al., 2013; Gorman & Stone, 1990; Grendenning, 1957; Macdonald et al., 1997). Important environmental factors also include relatively high soil moisture (Arlton, 1936; Goszczyński, 1983; Ritchie & Nocera, 2010; Yokohata, 1998), moderately soft soils (Abe, 1968, 2001; Arlton, 1936; García-López de Hierro et al., 2013; Ritchie & Nocera, 2010), and grass cover (García-López de Hierro et al., 2013; Llorente et al., 2021).

Although few such studies have been conducted in forests and mountainous areas, moles are originally considered forest-dwelling mammals (Stone & Gorman, 1991; Yokohata, 1998). For instance, some European and Japanese species have established symbiotic relationships with basidiomycete fungi, including *Hebeloma danicum* and *Hebeloma sagarae*, and their host trees in cool-temperate forests (Sagara et al., 2022). The fruit bodies of these fungi, which engage in mycorrhizal symbiosis with the tree roots, grow from mole excrement deposits. As the fungi decompose the excrement, they allow moles to use the same tunnel systems over extended periods (Sagara & Fukasawa, 2014)—a

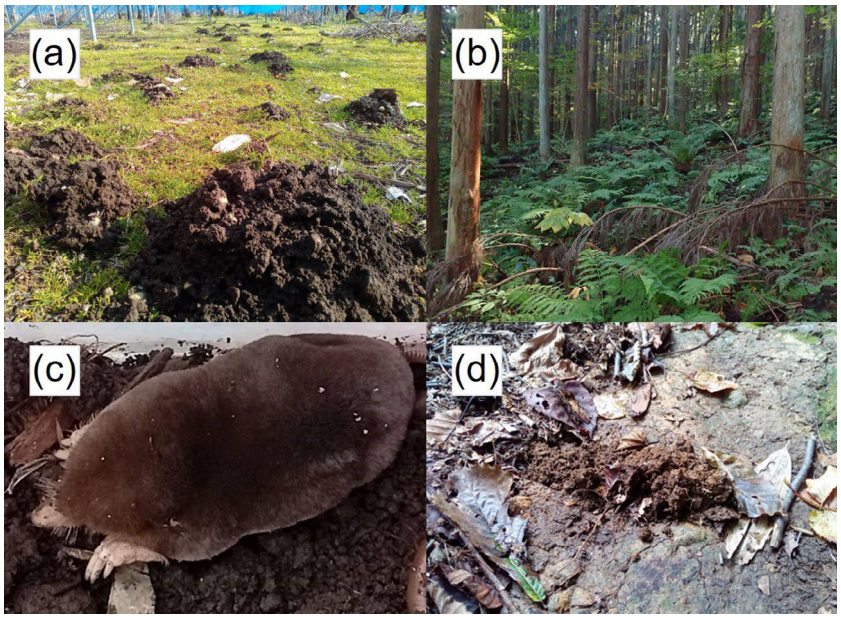


FIGURE 1 (a) Many studies on moles have been conducted in open areas by quantifying abundance through activity signs, such as molehills. However, (b) detecting mole activity signs or capturing moles in mountain forests is challenging. In this study, we quantified the relative abundance of (c) the lesser Japanese mole (*Mogera imaizumii*) along unpaved trails by counting (d) the "active" tunnels that had been restored after being filled with soil.

relationship hypothesized as "habitat-cleaning symbiosis" (Sagara, 1995). Moreover, field observations show that moles often use fallen leaves of deciduous broadleaf trees as nesting materials (e.g., Godfrey & Crowcroft, 1960; Yokohata, 1998). However, the thick litter layers and complex terrain of mountain forests make it challenging to detect mole activity signs or capture moles repeatedly (Figure 1b), which may explain the limited fundamental research on moles in these habitats.

In this study, we aim to evaluate the relative abundance of the lesser Japanese mole, *Mogera imaizumii* (Kuroda, 1957), in mountain forests in Yamagata Prefecture, Japan. Our preliminary year-long survey indicated that mole tunnels can be identified through careful observation and that their density tends to be lower in conifer plantations than in natural broad-leaved forests. Monoculture conifer plantations, which account for ca. 40% of Japan's total forest cover, can lead to the degradation of various ecosystem functions including the provisioning of wildlife habitat, if not properly managed (e.g., Seiwa et al., 2021; Taki et al., 2010). Thus, we compared the relative abundance of moles in Japanese cedar (*Cryptomeria japonica*) plantations to that in natural broad-leaved forests, based on the density of mole tunnels. Specifically, we asked (1) whether mole abundance differs between cedar plantations and natural broad-leaved forests, and (2) which environmental factors are responsible for differences in abundance.

2 | MATERIALS AND METHODS

2.1 | Study species and sites

The lesser Japanese mole (*M. imaizumii*; Figure 1c) is endemic to Japan, distributed in Honshu, Shikoku, and some surrounding islands (Abe et al., 2008). The species inhabits a wide range of habitats, from low, flat areas such as farmland and river banks to mountainous areas.

In 2023, we established 29 survey routes using unpaved trails (ca. 0.5–1.5 m wide) of six mountains in Yamagata Prefecture (Figure 2; Supporting Information Table S1), where only a single mole species, the lesser Japanese mole, has been recorded (Kawada & Yokohata, 2015). The vegetation of each survey route was categorized as cedar plantations (monoculture of *C. japonica*), oak forests (dominated by *Quercus serrata*, *Quercus crispula* var. *crispula*, or *Quercus variabilis*), or beech forests (dominated by *Fagus crenata*). The route length ranged from 40 to 972 m, measured as surface distances that account for elevation, using ArcMap 10.8.2 (ESRI, Redlands, CA, USA). The total length of survey routes was 9214 m.

2.2 | Mole abundance

Every month from April to October 2023, we walked the census routes over two consecutive days to estimate the relative abundance of moles. The survey was not conducted in April for four routes of two sites (Shirataka and Obanazawa) due to snow cover. On the first day, we identified mole tunnels crossing the survey routes. Since the tunnels are hardly visible on the ground surface, we located them by carefully detecting slight ground depressions and probing the soil with a shovel. The portions of the detected tunnels were then filled with soil. On the following day, we counted any tunnels that were restored, even partially, as "active" tunnels (Nesterkova, 2014; Poche, 1997; Figure 1d). As an index of relative abundance, we calculated tunnel density by dividing the total number of active tunnels observed over the 7 months by the total distance walked on each route. No other mole species were recorded in Yamagata (Kawada & Yokohata, 2015), so all the tunnels found in this study were attributed to the lesser Japanese moles.

2.3 | Environmental variables

We measured environmental variables (soil macrofauna biomass, soil hardness, soil moisture, plant litter mass, and understory cover) for 18 out of 29 survey routes, where we were able to obtain permissions from landowners for soil sampling. Measurements were taken in 2023 at one or two locations per route (but six locations along the Obanazawa route), depending on the route length. When the environmental variables were measured at multiple locations, we used the mean values for analysis. We investigated soil animals three times, in May, August, and October, by excavating a 50 cm × 50 cm × 30 cm (depth) soil block from each location. Soil macrofauna within the blocks were hand-sorted into major taxa, following Aoki (1999), and their biomass (fresh weight) was measured. Ants (Formicidae) were excluded from the analysis because their distribution is localized and they do not constitute a significant food source for moles (Funmilayo, 1979). Earthworm biomass was measured after being kept in the refrigerator overnight in order to minimize the effect of gastrointestinal tract content by allowing it to be expelled. Soil hardness data (MPa) were collected at every 5 cm from the ground surface to a maximum depth of 60 cm and depicted on a chart with an intrusive proctor needle (DIK-5520, Daiki-rika-kogyo, Konosu, Japan). Mean values of three replicates, averaging from 5 to 30 cm depth, were used for analysis. Soil moisture was measured monthly as volumetric water content by using a

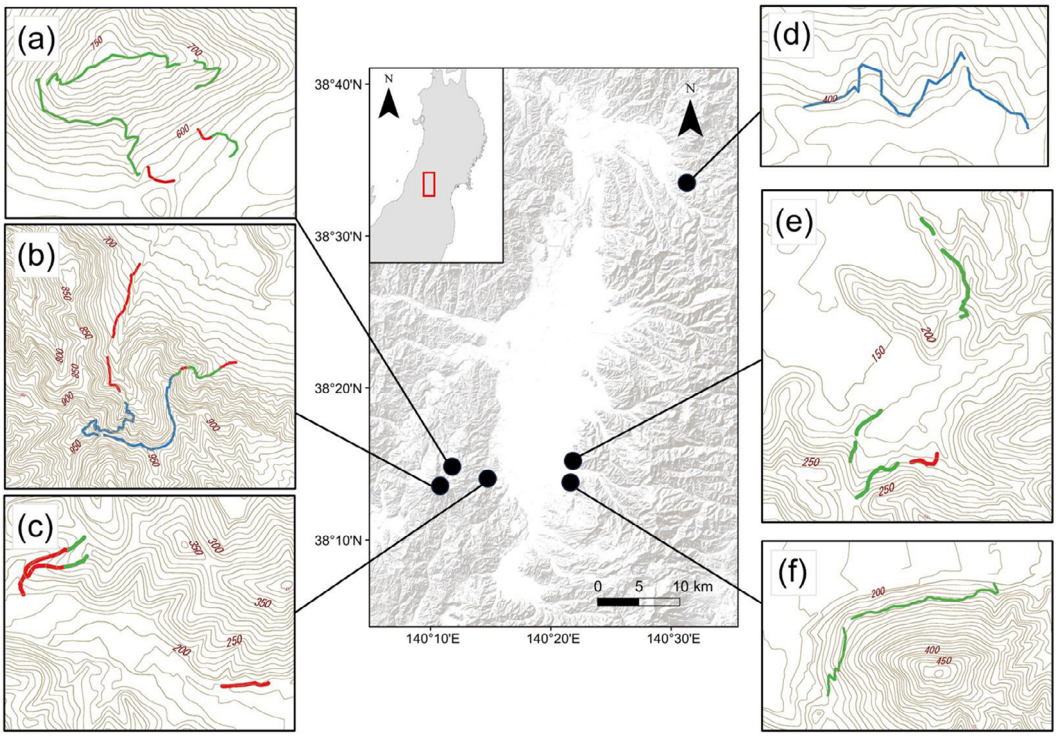


FIGURE 2 Map of the study area and site locations in Yamagata Prefecture, Japan. Black points are site locations. Sites (a: Kuromori, b: Shirataka, c: Tokami, d: Obanazawa, e: Sakazuki, f: Chitose) and forest types (red: Cedar plantation, blue: Beech forest, green: Oak forest) are distinguished by symbols and colors, respectively. Altitudes are shown as small values on each site map.

HydroSense II handheld soil moisture sensor (Campbell Scientific, Logan, UT, USA) to a depth of 12 cm. When the measurement using the sensor was difficult due to tree roots and rocks, the sieved soil was dried in an oven at 105°C for 24 h and weighed. We took the measurements at least 2 days after rainfall, with three replicates. To measure plant litter mass, we harvested the litter from a 20 cm × 20 cm area in late August and sifted it through a 2 mm sieve. The dry mass of the litter was measured after oven-drying the sieved material at 70°C for 72 h. The understory cover was measured by photographing a 1 m × 1 m area from a height of 1 m in August. The images were divided into 400 cells (20 × 20), and the proportion of cells containing plant leaves was calculated as understory cover. Typical locations were selected for measuring plant litter mass and understory cover.

2.4 | Statistical analysis

Earthworm biomass, soil macrofauna biomass, and soil hardness were log-transformed (or log +0.01 transformed for data containing zeros) for analysis to improve normality and homogeneity of variance. To analyze the difference in tunnel density among the three forest types, we used a generalized linear mixed model (GLMM), which included forest type (cedar plantation, beech forest, oak forest) as a fixed effect and site as a random effect, assuming a Poisson error distribution. The total number of active tunnels was used as a response variable, and the total route length walked was used as an offset term in the model. Because only four routes were categorized as beech forests, we also conducted an analysis by merging beech and oak forests under the category of "natural forests."

The effects of environmental variables on mole tunnel density were analyzed as follows. We first analyzed the direct effects of earthworm biomass, other macrofauna biomass, and soil hardness using a GLMM assuming a Poisson error distribution. The final model was obtained by sequentially removing nonsignificant terms ($p > 0.05$) as long as the Akaike information criterion (AIC) declined. Because only the significant effect of earthworm biomass on tunnel density was detected, we then explored which environmental factors explain the difference in earthworm biomass by fitting a GLMM with a gamma error distribution and a log-link function. Soil hardness, soil moisture, plant litter mass, and understory cover were included as predictor variables, and again, we removed non-significant terms ($p > 0.05$) to obtain the final model. Variance inflation factors (VIF) suggest low levels of multicollinearity in these models (VIF <2). Due

to the limited access to soil sampling on only 18 survey routes, the direct and indirect effects of environmental variables on mole abundance were not analyzed using structural equation modeling but instead analyzed as described above. We also tested whether each environmental variable differs among the forest types using GLMMs with forest type as a predictor variable.

We conducted all statistical analyses using R 4.3.2 (R Core Team, 2023). The GLMM analyses were performed using the "lme4" (Bates et al., 2023) and "lmerTest" packages (Kuznetsova et al., 2022).

3 | RESULTS

3.1 | Differences in mole abundance among forest types

We detected a total of 137 active mole tunnels across 75.9% of the survey routes (22 out of 29), regardless of forest type. Tunnel density (tunnels/km) was, on average, highest in oak forests (3.00), followed by beech forests (1.66) and cedar plantations (0.87; Figure 3). The GLMM analysis showed that the density in cedar plantations was significantly lower than in oak forests ($z = 3.665$, $p < 0.001$), but there was no significant difference compared to beech forests ($z = 1.432$, $p = 0.15$; Table 1). Due to the small sample size, we also analyzed the data by combining oak and beech forests into a single category of "natural forests," and found that the tunnel density was still significantly lower in cedar plantations compared to natural forests ($z = -3.189$, $p < 0.01$).

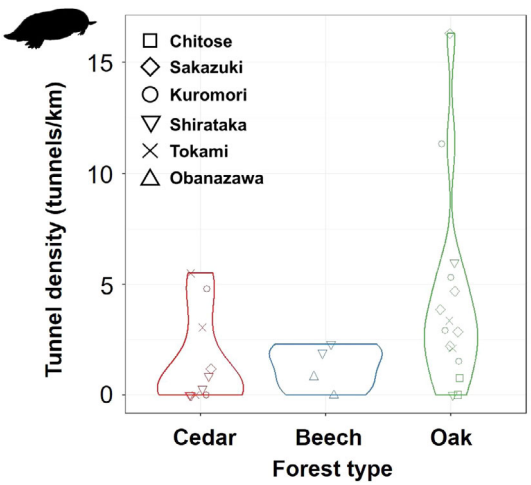


FIGURE 3 Tunnel density of the lesser Japanese mole for three forest types ($n = 29$). Symbols and colors correspond to those in Figure 2.

Seasonal variations in tunnel density were also observed (Figure S1). Tunnel density tended to increase from May to June in all forest types, but in oak forests, the density continued to rise until July and remained higher than the other forest types until the end of the survey.

3.2 | Environmental factors affecting mole abundance

The GLMM analysis showed that mole tunnel density significantly increased with earthworm biomass ($z = 2.997$, $p < 0.01$; Table 2; Figure 4). Although earthworm biomass was positively correlated with the biomass of other soil macrofauna (Pearson's $r = 0.534$, $p < 0.05$), the effect of other soil macrofauna on mole tunnel density was not significant ($z = -1.132$, $p = 0.258$). Earthworm biomass was negatively affected by both soil hardness and soil moisture (Table 3; Figure 5), even though soil hardness and soil moisture were negatively correlated ($r = -0.635$, $p < 0.01$). Figure 6 summarizes these direct and indirect effects of environmental variables on mole tunnel density. While no environmental variables differed significantly among the forest types, earthworm biomass and

TABLE 1 Differences in tunnel density of the lesser Japanese mole (*Mogera imaizumii*) among forest types, analyzed using a generalized linear mixed model.

	Estimate	SE	z	p
Intercept (Cedar)	−0.134	0.439	−0.305	0.761
Beech	0.509	0.355	1.432	0.152
Oak	1.100	0.300	3.665	**<0.001**

Note: Note that since a log link function was employed in the model, exponential transformation is necessary to convert the estimates back to their original units. Cedar: Cedar plantation, Beech: Beech forest, Oak: Oak forest. Bold numbers of *p*-values indicate significant differences from zero (<0.05).

TABLE 2 A direct factor significantly affecting the tunnel density of the lesser Japanese moles was earthworm biomass.

	Estimate	SE	z	p
Intercept	0.820	0.405	2.024	**<0.05**
Earthworm biomass	0.215	0.072	2.997	**<0.01**

Note: The final model was obtained by excluding non-significant variables ($p > 0.05$) from the generalized linear mixed model, which originally included three predictor variables: earthworm biomass, other soil macrofauna biomass, and soil hardness. Note that since a log link function was employed in the model, exponential transformation is necessary to convert the estimates back to their original units. Bold numbers of *p*-values indicate significant differences from zero (<0.05).

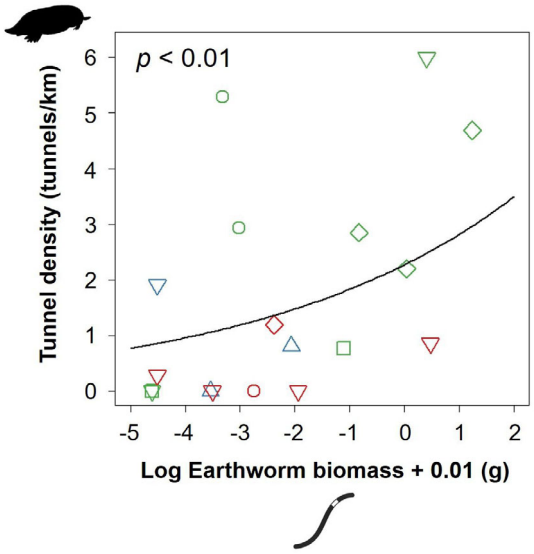


FIGURE 4 Relationship between tunnel density and earthworm biomass ($n = 18$). Symbols and colors correspond to those in Figure 2. Earthworm biomass was log +0.01 transformed before analysis.

TABLE 3 Factors significantly affecting earthworm biomass.

	Estimate	SE	*t*	*p*
Intercept	2.161	2.282	0.970	0.332
Log (soil hardness)	−4.622	1.059	−4.365	**<0.001**
Soil moisture	−20.653	7.408	−2.788	**<0.01**

Note: The final model was obtained by excluding non-significant variables ($p > 0.05$) from the generalized linear mixed-effects model containing four predictor variables; soil hardness, soil moisture, plant litter mass, and understory cover. Note that since a log link function was employed in the model, exponential transformation is necessary to convert the estimates back to their original units. Bold numbers of *p*-values indicate significant differences from zero (<0.05).

soil hardness tended to be lower in cedar plantations than in oak forests (Figure 7a,b; Table S2). Conversely, soil moisture tended to be higher in cedar plantations than in oak forests (Figure 7c).

4 | DISCUSSION

Most previous studies on moles have focused on open areas such as cultivated fields and grasslands (e.g., Edwards et al., 1999; Funmilayo, 1977; Goszczyński, 1983; but see Llorente et al., 2021). Consequently, the distribution of moles in mountain forests, which are likely their original habitats (Stone & Gorman, 1991; Yokohata, 1998), has remained unclear. Despite the challenges of assessing mole population abundance in mountain forests due to thick litter layers and complex topography, we successfully detected active tunnels of the lesser Japanese mole on most survey routes (75.9%), indicating that the species broadly inhabits mountain forests regardless of vegetation type. However, moles do not distribute uniformly across these forests; tunnel density differed significantly among the forest types. As initially expected, we found that the tunnel density was lower in cedar plantations than in natural broad-leaved forests (Table 1; Figure 3). The seasonal variation in tunnel density (Figure S1) could be attributed to reproductive needs. Generally, during the breeding season (spring to summer; Kawada & Yokohata, 2015), males expand their home ranges compared to the nonbreeding season to increase opportunities for contact with potential mates (Loy et al., 1994).

The variation in tunnel density among census routes was explained by the differences in earthworm biomass (Table 2; Figure 4). Although moles also consume larvae of Coleoptera, Araneae, and Chilopoda (Funmilayo, 1979;

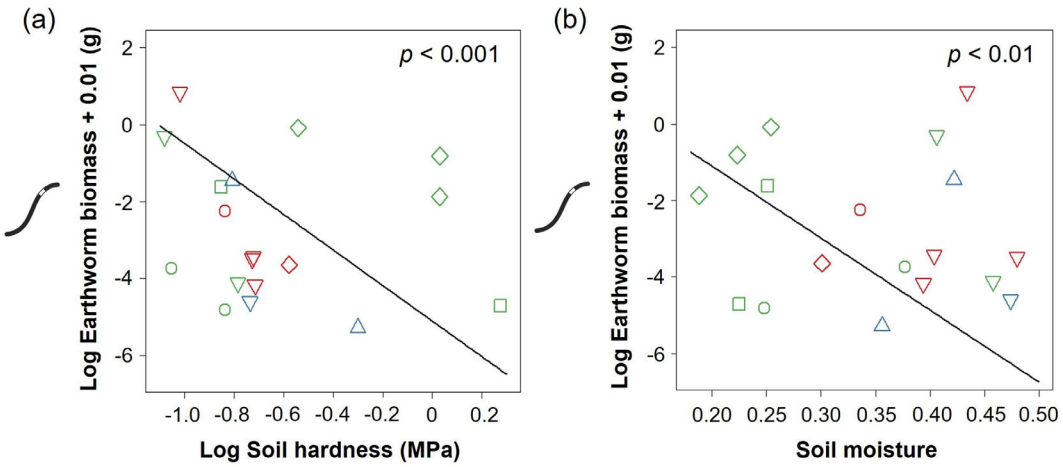


FIGURE 5 Partial residual plots showing the relationships of earthworm biomass to (a) soil hardness and (b) soil moisture. Soil moisture was measured as volumetric water content. Symbols and colors correspond to those in Figure 2. Earthworm biomass was log +0.01 transformed before analysis.

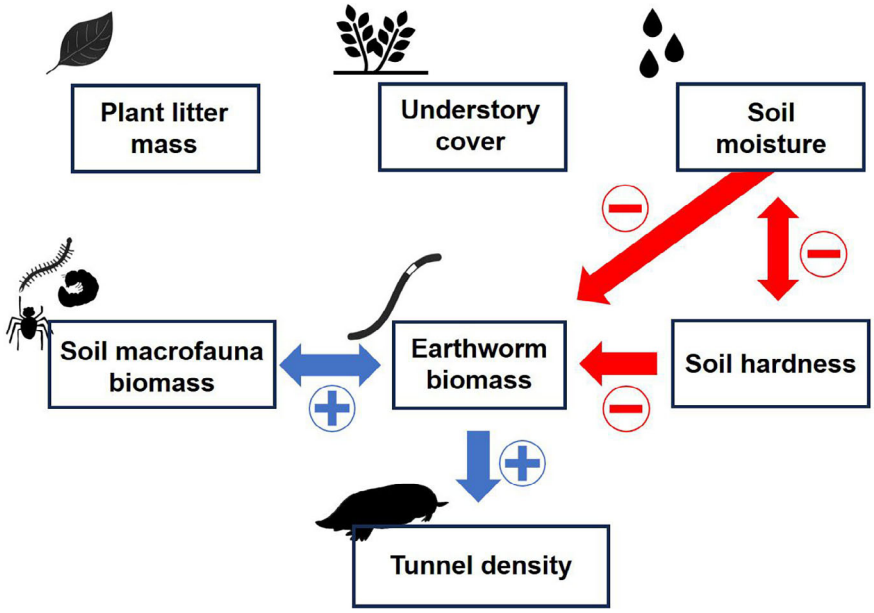


FIGURE 6 Relationships among mole tunnel density and environmental variables. One-way arrows show the effects of environmental variables, while two-way arrows indicate the correlation relationships. Blue and red arrows represent positive and negative relationships, respectively.

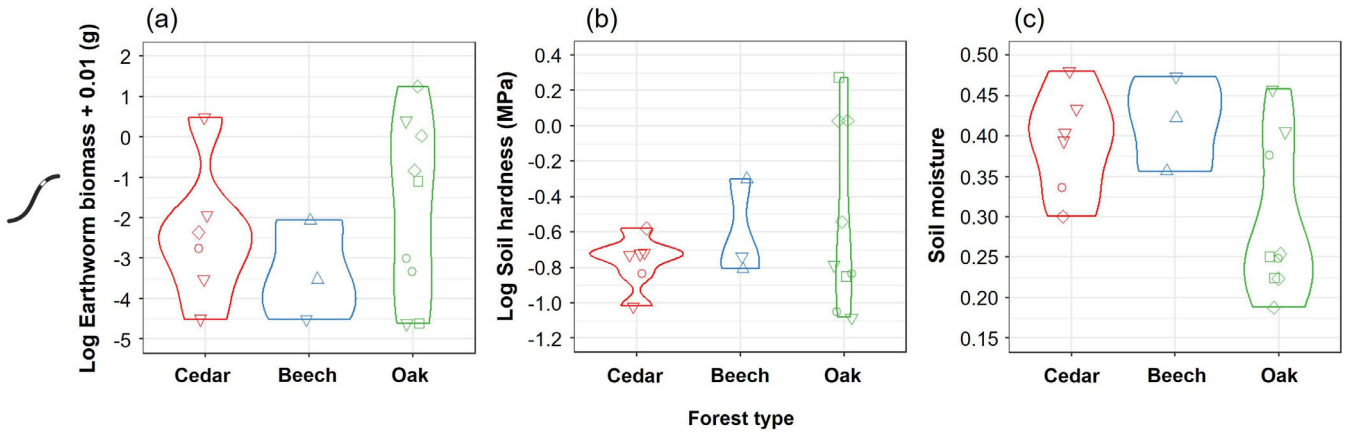


FIGURE 7 Variation among the forest types in three variables with direct or indirect effects on the tunnel density ($n = 18$): (a) earthworm biomass, (b) soil hardness, and (c) soil moisture. There was no significant difference among forest types for any of the variables. Symbols and colors correspond to those in Figure 2.

Grendenning, 1957; Raw, 1966), earthworms are considered their primary food source (Funmilayo, 1979; Godfrey & Crowcroft, 1960; Mellanby, 1967) and thus a critical factor explaining their density and abundance in cultivated fields and grasslands (Arlton, 1936; Edwards et al., 1999; Funmilayo, 1977; García-López de Hierro et al., 2013; Gorman & Stone, 1990; Grendenning, 1957; Macdonald et al., 1997). In contrast, in mountain forests, maintaining extensive territories to access sufficient food might be energetically costly due to physical barriers for burrowing, such as rocks and extensive tree root systems, potentially making a more varied diet advantageous. However, in our study, only the effect of earthworm biomass was detected, despite a positive correlation between earthworm biomass and other soil macrofauna biomass. This finding emphasizes the critical role of earthworms in determining mole abundance in mountain forests. For fossorial mammals, maintaining their basal metabolic rates demands considerable energy (Gorman & Stone, 1990; McNab, 1979). Consequently, feeding on earthworms may provide an especially efficient way for moles to meet their nutritional requirements.

Lower earthworm biomass was associated with both higher soil hardness and higher soil moisture (Figure 5). Since these two environmental variables were negatively correlated, either high soil hardness or high soil moisture may explain the relatively small earthworm biomass observed in cedar plantations (Figure 6a). It could be assumed that the lack of or delayed thinning in conifer plantations may result in a significant loss of understory

vegetation and subsequently compacted soils (Ishii et al., 2008; Yukawa & Onda, 1995), making the environment less suitable for moles. However, in this study, high soil hardness was observed in some oak forests (Figure 7b), whereas soil moisture was generally higher in cedar plantations (Figure 7c). Cedar trees have high water requirements (Nagakura et al., 2004) and are typically planted in moist soil environments. Therefore, although no environmental variables differed significantly among forest types, the lower abundance of lesser Japanese moles in cedar plantations may be more a consequence of the soil environment where the cedar trees were planted, rather than the plantations themselves. While understory cover exceeded 80% in most cedar plantations in this study, inadequate management could still potentially lead to a significant loss of understory vegetation, rendering the soil environment unsuitable for moles. Our study shows that the abundance of the lesser Japanese mole—the top predator of soil ecosystems—differs significantly across forest sites in response to soil environments, with implications for the structure of the food web in soil ecosystems.

Soil moisture is a key factor in earthworm ecology (Curry, 2004; Lee, 1985). One study shows that earthworm density decreases in soils with over 40% moisture in temperate deciduous forests (Hopfensperger & Hamilton, 2015), while another study reported that the highest growth rates of earthworms occur at 25% soil moisture at 15 and 20°C (Wever et al., 2001). These suggest that earthworms prefer soils with moderate moisture levels, as excessively wet soils may not be preferable. Notably, no direct effect of soil hardness on mole tunnel density was observed, even though both earthworms and moles generally prefer soft soils that are easy to dig (García-López de Hierro et al., 2013). In mountain forests, mole abundance may not be simply explained by soil hardness due to the influence of extensive tree root systems on burrowing behavior. Plant litter mass did not have a significant effect on earthworm biomass (Table 3). While the litter mass tended to be greater in cedar plantations (Table S1), the preference of earthworms for litter varies by plant species (Curry & Schmidt, 2007), and coniferous leaves, such as those of Japanese cedars, may not be preferred.

In conclusion, we were able to quantify the relative abundance of moles in mountain forests by carefully searching for active mole tunnels along unpaved trails. The significant positive relationship between our tunnel density estimates and the biomass of earthworms was consistent with previous studies in open areas and supports the reliability of our estimates. Although further studies are needed to understand the effect of forest vegetation on mole abundance, our method can help identify areas with high (or low) densities and track changes in abundance over time, thereby providing fundamental insights into the ecology of moles.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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