Forest Ecology and Management 537 (2023) 120976

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Conditions affecting ant nesting in stumps in a temperate coniferous planted forest

Mii Tanaka [a], Seungyun Baek [b], Kahoko Tochigi [b], Tomoko Naganuma [c], Akino Inagaki [b], Bainah S. Dewi [d], Shinsuke Koike [c,*]

[a] Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan
[b] United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan
[c] Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan
[d] Tropical Biodiversity Research and Development Center, University of Lampung, Bandar, Lampung 35145, Indonesia

ARTICLE INFO

Keywords:
Ant nest
Conifer plantation
Dead tree
Formicidae
Thinning

ABSTRACT

Dead trees are an important component of forest ecosystems as they play various roles in these ecosystems and their biodiversity. The use of dead trees as a habitat and foraging resource by various organisms affects the decomposition of the trees. Ants use dead trees as nests and slow their decomposition by weakening the function of decomposers, such as fungi and termites, through interspecific interactions. However, our understanding of the characteristics of dead trees in which ants nest and the environmental conditions under which they exist is limited. In planted forests, stumps left after harvesting account for the largest biomass of deadwood. In the present study, the characteristics of such stumps, their location, and the relationship between these factors were determined in relation to ant nesting in a warm temperate conifer planted forest (a university forest with clear past history located in central Japan). In total, 85 stands consisting of *Cryptomeria japonica* or *Chamaecyparis obtusa* were surveyed, and various environmental conditions as well as the presence or absence of ant nests in stumps logged by forestry operations were recorded. In total, 1551 stumps were surveyed, of which 113 stumps contained ant nests with 16 different ant species. Modeling and Akaike information criterion evaluation results revealed that both large and small ant species tended to nest in old stumps located in areas with an open canopy, large species tended to nest in stumps with moss or lichen cover, and small species tended to nest in stumps with bark cover. Older stumps are typically softer owing to more decomposition, and solar heat can facilitate temperature control inside the nest, which may explain why ants tended to nest under the observed conditions. Based on these findings, long-term continuous thinning rather than clearcutting, which results in excessively large canopy openings and uniformly sized stumps, is the preferred management practice for promoting ant nesting in stumps in planted forests.

1. Introduction

The decomposition of dead trees can take decades to centuries; thus, such trees play various roles in forests over a long period. For example, dead trees serve as long-term storage sites and sources of organic matter in the carbon cycle of forest ecosystems (Gogoi et al., 2022). In addition, deadwood is a favorable site for the establishment and growth of seedlings, which promotes forest renewal by reducing interspecific competition with other plant species and fungi growing on the forest floor (Harmon and Franklin, 1989). Furthermore, dead trees have complex structures that provide microenvironments with various conditions that change over time, providing habitats for a range of taxonomic groups (Harmon et al., 1986). Thus, deadwood is an essential component of forest ecosystems, especially as its morphology and characteristics change during its decomposition.

Various organisms affect the decomposition rate of deadwood, with fungi and termites serving as two primary decomposers that use the wood as a habitat and foraging resource. The physicochemical properties of deadwood are altered within a short period by such organisms, which markedly reduce the decomposition time of deadwood (González et al., 2008). In contrast, ants are known to inhibit the decomposition of deadwood (Warren and Bradford, 2012) as they secrete chemicals that

* Corresponding author.
E-mail address: koikes@cc.tuat.ac.jp (S. Koike).

https://doi.org/10.1016/j.foreco.2023.120976
Received 15 January 2023; Received in revised form 22 March 2023; Accepted 26 March 2023
Available online 3 April 2023
0378-1127/

inhibit the growth of fungal mycelium and predate termites (Beattie et al. 1986, Tuma et al., 2020). Given that ants affect the decomposition of deadwood, quantifying the habitat conditions of ant-occupied deadwood will help inform forest management practices.

Ants nest in deadwood under several conditions depending on the ecological characteristics of the ants and the condition of the deadwood. For example, ants cannot drill into hard wood; therefore, they use physically soft wood formed by other invertebrates as a nesting site (Blüthgen and Feldhaar, 2009). In addition, a positive relationship exists between ant body size and the diameter of the deadwood used as a nesting site (Satoh et al., 2016). Furthermore, because ants nesting in deadwood tend to be thermophilic (Higgins, 2010), in colder regions they tend to nest in deadwood exposed to solar heat, thereby ensuring that temperature in the nest can be controlled (Higgins and Lindgren, 2012). However, there are little examples of ants using dead trees as nesting sites based on the characteristics and location of the trees themselves (e.g., Maziarz et al. 2021). Additionally, some studies analyzed stump colonization in clearcuts (e.g., Włodarczyk et al., 2009), but the environmental characteristics and location of these stumps (e.g., decay stage, size, and proximity to neighbors) were not quantified.

The proportion of planted forests in Japan is one of the highest in the world, with 67 % of the country's land area covered by forests and about 40 % of its forest area covered by conifer plantations (Forestry Agency, Japan, 2021). Plantation forests differ from natural forests in terms of human management (i.e., thinning, pruning, and logging), which can result in little dead trees due to management compared with natural forests (Fridman and Walheim, 2000). However, harvested trees are removed from the forest for lumber production, and poorly grown timber as well as fallen and standing dead trees are also removed for power generation and pellet production (Bujoczek et al., 2021). Therefore, the only dead trees in planted forests tend to be stumps left during thinning and clear cutting, so these may be important for biodiversity conservation in planted forest ecosystems.

The purpose of the present study was to determine the conditions of stumps in which ants nest, including the characteristics and locations of the stumps as well as the relationships between these factors, with the aim of enhancing biodiversity in planted forest ecosystems. We divided ant species into large and small species as functional groups for verification because nest stump conditions differ depending on ant body size (Satoh et al., 2016). Heat gain from sunlight is an important factor in the ability of ants to control nest temperature (Higgins, 2010); therefore, we hypothesized that ants nest in stumps are frequently located on slopes with an open canopy and high solar radiation exposure (hypothesis 1). Additionally, the presence of bark or moss cover around stumps is advantageous for nesting in relation to temperature control, moisture retention, and mitigation of external environmental stimuli (Persson et al., 2013). Therefore, we hypothesized that ants nest in stumps are most frequently located in moist environments and covered with bark, moss, or lichen, which are byproducts of the wood decay (hypothesis 2). Finally, because differences in stump volume affect ant colony size (Mitrus, 2015) and colony size is correlated with ant body size (Kaspari and Vargo, 1995, Geraghty et al., 2007), we hypothesized that larger species prefer larger stumps because their colonies are larger (hypothesis 3). To test these three hypotheses, we investigated the number of stumps and ant nests in each forest segment and determined the factors influencing ant nesting in these stumps. Based on our results, we propose forest management practices considering the continuous presence of stumps for ant nests as a means to enhance the maintenance of biodiversity in conifer plantation ecosystems.

2. Materials and methods

2.1. Study area

This study was conducted at Kusaki University Forest, Tokyo University of Agriculture and Technology (36°32′N, 139°24′E, 650–1150 m a.s.l., 416 ha) in Gunma Prefecture, central Japan. The topography of the study area is characterized by steep slopes with many landslides. Annual rainfall is 1248.5 mm, and annual average temperature is 14.6 °C (2011–2020; Japan Meteorological Agency, 2022). The primary vegetation of the study area is deciduous forest dominated by *Quercus crispula* and *Quercus serrata*. However, 135 ha (32 %) of the forests are conifer plantations (*Cryptomeria japonica, Chamaecyparis obtusa*, and *Larix kaempferi*). In the study area, there are 54 deciduous forest stands [total area: 281 ha; mean area ± standard deviation (SD): 5.0 ± 8.4 ha] and 90 conifer plantation stands (total area: 135 ha; mean area ± SD: 1.5 ± 1.4 ha; age: 3–113 years). All of the conifer plantation stands have been properly managed (i.e., planted at a density of 3000 stems/ha, with grass establishment, weeding and brushing, improvement cutting, tree thinning, and precommercial thinning resulting in densities of around 1000 stems/ha in all stands). In the current study, stand or tree age refers to years after planting seedlings (usually-three years) (e.g., Kobashikawa and Koike, 2016).

We selected 85 conifer plantation stands (total area: 84.7 ha; mean area ± SD: 1.3 ± 1.1 ha) that were planted only in *Cryptomeria japonica* and *Chamaecyparis obtusa* study sites, given that these are the major species occurring in conifer plantations in Japan (Forestry Agency, Japan, 2021). These included stands with ages of 3–113 years: 11 stands of young forests (3–20 years old), 30 stands of younger forests (21–40 years old), 19 stands of mature forests (41–60 years old), and 25 stands of old forests (≥61 years old) as of 2021.

2.2. Method

A 0.04 ha circular plot was set up at the center of gravity of each target forest subgroup, and all stumps within the plot were targeted. The center of gravity of each subgroup was calculated in advance using GIS software, and the slope of the plot was estimated to determine a plot radius of 11.28 m in a horizontal distance All stumps included in the study were < 50 cm high, and the top surface of each stump had been cut by logging operations. All surveys were conducted between August and September 2021.

The recorded stump characteristics included the following: percentage of bark cover on the sides (visually determined in 10 % increments), percentage of moss and lichen cover on the exterior including the cut surface (visually determined in 10 % increments), volume (calculated from height and diameter), the presence or absence of perforations on the cut surface, and the number of years since felling (harvesting). The age of the stumps was calculated using the logging records. Tree species were excluded because almost all stumps were *Cryptomeria japonica*.

Stump location was determined according to two factors: the canopy openness of each stump and topography (ridge, slope, or valley). Canopy openness was determined by mounting a fisheye lens (FCON-T02 fisheye converter) on a camera (Tough TG-6) and taking pictures at 50 cm above ground level. We used CanopOn 2 (Takenaka 2009) to measure canopy openness.

After all characteristics and factors were measured, stumps were partly destroyed to the extent necessary to determine the presence of an ant nest. Following a previous study (Boucher et al., 2015), ants were considered to be nesting when larval and pupae care by adults was observed, regardless of the presence of a queen ant. If larvae or pupae of the same species were found in different parts of one stump, they were considered as the same colony. Ants from confirmed nests were preserved in 95 % ethanol and transported to the laboratory for species identification. In addition, species with worker body lengths of < 3.5 mm and ≥ 3.5 mm were classified as small and large species, respectively, referring to published illustrations (Japanese Ant Image Database, 2008).

2.3. Statistical analysis

We created a generalized linear mixed model with a binomial distribution to verify the relationship between environmental factors on and around the stump and the presence of an ant nest. Analysis was conducted separately for small and large ant species to determine differences in habitat selection according to ant body size. In the model, the presence or absence of an ant colony (1 or 0) was set as the response variable, and the explanatory variables were set as (1) bark cover, (2) cover of moss or lichen, (3) stump volume, (4) canopy openness, (5) terrain category (ridge, slope, or valley), (6) age of stumps (not age class), (7) number of years since felling (hereafter, "from felling"). We also used forest stands as a random effect. We used the glmmTMB (Brooks et al. 2017) for model fitting and the MuMIn package (Bartoń, 2022) for model selection. We used an AIC (Akaike information criterion) framework, using a balanced model design where we analyzed each variable and combinations of each pair of variables (Symonds & Moussalli, 2011). Top models were selected based on having ΔAIC values < 2 (Burnham & Anderson, 2002). The top variables were selected using their model-averaged weight and their effects were based on their standardized coefficients (Symonds & Moussalli, 2011). Additionally, we calculated the relative importance (RI) of variables by summing the Akaike weights for models in which they appear using the complete candidate set of models. Statistical analyses were conducted using R 4.3.1. (R Core Team, 2021).

3. Results

In the 1551 total stumps, we observed 113 ant nests in 43 stands [mean nesting rate in each stand (±SD): 6.8 % ± 10.2 %; range: 0 %–54.3 %)]. In five stumps, two different species were found nesting in the same stump. In addition, 61 and 57 stumps contained the ant nests of small and large species, according to our classification, respectively.

In the 16 total ant species were collected from stumps (7 large and 9 small species; Table S1). *Pheidole fervida*, the species most frequently observed, was found nesting in 46 stumps (44.0 %). Furthermore, the 4 species most frequently observed nesting in stumps accounted for 86.7 % of stumps, whereas the remaining 12 species were found in only 1–4 stumps.

The likelihood of an ant nest presence in a stump tended to increase with the amount of bark or moss cover on the stump, canopy openness, and the number of years since tree felling, but the effects were insignificant in all cases (Fig. A1). The following six variables were included in our top 14 GLMMs for the presence of a nest of small and large ants: bark cover, canopy openness, years from felling, cover of moss or lichen, age of stump, and stump volume (Fig. 1 and Table 1). For small ants, the top variable across all models was canopy openness (RI = 1.00), which was nearly-two times more likely to appear in a top model than the next two best variables (years from felling and bark cover; Table 2). Model averaging revealed that the likelihood of a small ant nest presence in a stump significantly increased with canopy openness (β = 3.064; 95 % confidence interval [CI] = 0.849–5.279; Fig. 1a; Table 2). Furthermore, the likelihood of an ant nest presence tended to increase with year from felling (β = 0.314; 95 %CI = − 0.529–1.156) and bark cover (β = 0.215; 95 %CI = − 0.372–0.802), but the 95 % CI of the averaged coefficients of these variables overlapped zero (Fig. 1; Table 2). For large and small ants, the top variable across all models was canopy openness (RI = 1.00; Table 2). Years from felling (RI = 0.89) and cover of moss or lichen (RI = 0.77) were also more frequently included in top models (Tables 1 and 2). The likelihood of a large ant nest presence significantly increased with canopy openness (β = 2.744; 95 %CI = 0.684–4.805; Fig. 1b; Table 2). In addition, the likelihood of an ant nest presence tended to increase with years from felling (β = 0.890; 95 %CI = − 0.374–2.154) and cover of moss or lichen (β = 0.536; 95 %CI = − 0.371–1.442), but the 95 % CI of averaged coefficients of these two variables overlapped zero (Fig. 1; Table 2).

The environmental variables for (a) small ants and (b) large ants are shown on the x-axis. The standardized mean (dots) and 95% confidence intervals (error bars) of model-averaged coefficients of variables (GLMM) are shown on the y-axis. The environmental variables for (a) small ants and (b) large ants are shown on the x-axis. The standardized mean (dots) and 95 % confidence intervals (error bars) of model-averaged coefficients of variables (GLMM) are shown on the y-axis.

4. Discussion

Our results support hypothesis 1, as high canopy openness was found to be an important condition for the nesting of both small and large ants in stumps. Ants are thermophilic organisms (Higgins, 2010) that prefer warm habitats. Because many ant species are unable to generate heat, they regulate the temperature by moving their larvae or pupae to places with suitable thermal conditions (Jones and Oldroyd, 2006). Previous studies also show experimentally that the presence of heat can attract ants rearing their broods (Maziarz et al., 2020). Moreover, ants are known to expend energy maintaining internal nest temperature, especially in humid nests (Frouz, 2000), and sunlight increases internal stump temperature (Higgins and Lindgren, 2012); therefore, ants may choose to nest in stumps with an open canopy. The presence of sunlight, which strongly influences nest temperature, may be generally important for ant nesting in tree stumps because Risch et al. (2005) also found that

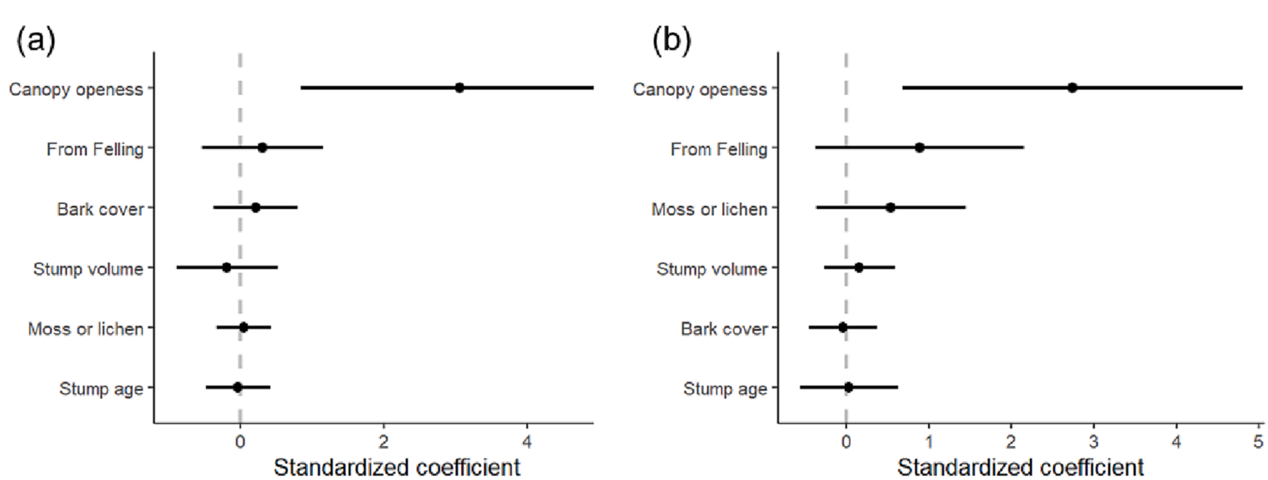

Fig. 1. Effects of environmental factors on the presence of ant nests in stumps. The environmental variables for (a) small ants and (b) large ants are shown on the x-axis. The standardized mean (dots) and 95% confidence intervals (error bars) of model-averaged coefficients of variables (GLMM) are shown on the y-axis.

Table 1
Generalized linear mixed models (GLMM) used for model averaging describing the effect of environmental factors on the presence of ant nests in stumps.

	Model	LogLik	k	AIC	ΔAIC	w
Small size						
	Canopy openess	−109.359	3	224.7	0.00	0.066
	Bark cover + Canopy openness + From felling + Stump volume	−106.360	6	224.7	0.00	0.066
	Canopy openness + From felling	−108.463	4	224.9	0.21	0.060
	Bark cover + Canopy openness	−108.545	4	225.1	0.37	0.055
	Bark cover + Canopy openness + From felling	−107.749	5	225.5	0.78	0.045
	Canopy openness + From felling + Stump volume	−107.790	5	225.6	0.86	0.043
	Canopy openness + Moss or lichen	−109.054	4	226.1	1.39	0.033
	Bark cover + Canopy openness + Moss or lichen	−108.066	5	226.1	1.41	0.033
	Bark cover + Canopy openness + Stump volume	−108.092	5	226.2	1.47	0.032
	Bark cover + Canopy openness + From felling + Moss or lichen + Stump volume	−106.186	7	226.4	1.65	0.029
	Canopy openness + Stump age	−109.212	4	226.4	1.71	0.028
	Canopy openness + Stump volume	−109.240	4	226.5	1.76	0.027
	Bark cover + Canopy openness + From felling + Stump age + Stump volume	−106.315	7	226.6	1.91	0.025
	Canopy openness + From felling + Moss or lichen	−108.342	5	226.7	1.96	0.025
Large size						
	Canopy openness + From felling + Moss or lichen	−87.277	5	184.6	0.00	0.096
	Canopy openness + From felling + Moss or lichen + Stump volume	−86.363	6	184.7	0.17	0.088
	Canopy openness + From felling	−88.753	4	185.5	0.95	0.059
	Canopy openness + Moss or lichen + Stump volume	−87.884	5	185.8	1.21	0.052
	Canopy openness + From felling + Stump volume	−88.022	5	186.0	1.49	0.045
	Bark cover + Canopy openness + From felling + Moss or lichen	−87.142	6	186.3	1.73	0.040
	Bark cover + Canopy openness + From felling + Moss or lichen + Stump volume	−86.185	7	186.4	1.81	0.039
	Canopy openness + From felling + Moss or lichen + Stump age	−87.198	6	186.4	1.84	0.038

All models included the random effect of forest stand ID. logLik means the log–likelihood values and k indicates the number of parameters in each model. ΔAIC indicates the difference in the Akaike information criterion (AIC) values between a model and the model with the lowest AIC. w indicates the Akaike weight.

ants tend to nest in areas with an open canopy. In natural forests, there are other suitable structures for ant nests (e.g., bird nests) (Maziarz et al., 2021), so ants may nest in places other than stumps, but in well-managed conifer plantations, stumps may be the preferred nesting structure for ants, as there are no other structures made of dead wood or the presence of other animals.

Table 2
Summary of averaged generalized linear model (GLMM) to investigate the effect of environmental factors on the presence of ant nests in stumps.

	Variable	β	SE	RI
Small size				
	Bark cover	**0.215**	**0.299**	**0.50**
	Canopy openess	**3.064**	**1.127**	**1.00**
	From felling	**0.314**	**0.429**	**0.52**
	Moss or lichen	0.054	0.195	0.21
	Stump age	−0.027	0.228	0.09
	Stump volume	−0.185	0.360	0.39
Large size				
	Bark cover	−0.042	0.212	0.17
	Canopy openness	**2.744**	**1.049**	**1.00**
	From felling	**0.890**	**0.644**	**0.89**
	Moss or lichen	**0.536**	**0.462**	**0.77**
	Stump age	0.032	0.304	0.08
	Stump volume	0.154	0.219	0.49

β indicates model-averaged standardized coefficient and SE shows unconditional standard error for each variable of the top models (ΔAIC < 2). Relative importance (RI) refers to the summed Akaike weights across all of the top models in which the variables were present. The top three variables with high RI are shown in bold.

Regarding hypothesis 2, the presence of moss and/or lichen affected the nesting of large ants but not small ants. In contrast, the presence of bark had a positive effect on nesting in small ants. Moss and lichen cover protects ants from predators (Li et al., 2011), and the water and heat retention properties of moss and lichen reduce microclimate fluctuations (Moore et al., 2018). Additionally, Marchal et al. (2013) found that bark cover on dead trees provides a stable habitat for ants owing to its moisture retention properties. Furthermore, the space between the bark and wood is known to function as a habitat (Dossa et al., 2018), and ants are more likely to nest in the bark, gaps between the bark and wood, and under the bark than in the wood of the stump itself (Marchal et al., 2013). However, the presence of bark did not affect the nesting of large ant species in our results. The reason why large ants and small ants have different influences in this result can be considered as follows. First, because moss and lichen cover increases with the decomposition of deadwood (Hovemeyer and Schauermann, 2003) and small ants may prefer to nest in stumps in earlier stages of decomposition, moss and lichen did not affect the nesting of small ant species in the present study. Second, the reason that the presence of bark did not affect large ant nesting was probably due to the presence of bark on many of the target stumps (including those without ant nests). In the present study, nests including *Camponotus* were frequently observed in the gaps between the bark and wood, indicating that the bark cover provides nesting sites for ants. None of the nests observed in the present study were exposed on the outer surface of the stump, and ants were observed in the bark, under moss and lichen, and inside the wood, suggesting that some type of protective cover is a prerequisite for ant nesting. Bark is known to decompose faster than sapwood or heartwood (Chang et al., 2020); thus, bark may function as an ant habitat in the early stages of decomposition, whereas moss may replace bark as a habitat when the stump is considered in terms of long-term ant nesting.

Hypothesis 3 was not supported by our results as large species did not prefer large stumps. Stumps with a large volume have many advantages in ant nesting, including increased space, which helps stabilize the internal microclimate and reduce competition for habitat (Bobiec et al., 2005). A positive correlation is known to exist between the diameter of dead trees and the body size of the inhabiting ants, which is attributed to the sizes of holes produced by primary nesters (Satoh et al., 2016). In the present study, ant nesting was observed even in relatively small stumps, i.e., with both a height and diameter of 10 cm, suggesting that conditions such as temperature and humidity are more important than stump size in terms of influencing the stump nesting sites of ants.

5. Management implications

Given that bark cover was degraded over 20 years after logging in our study site, moss and lichen cover should be promoted to create a continuous habitat for large ant species. Moderate humidity is necessary for moss and lichen cover (Oldén et al., 2019); therefore, excessive increases in canopy openings associated with logging should be avoided. Furthermore, because a positive relationship exists between ant species body size and the diameter of dead trees in which they nest (Satoh et al., 2016), stumps with various diameters should be produced to encourage the presence of many species. In addition, the number of years since felling was also an important factor for both small ants and large ants. Therefore, continuous thinning rather than clearcutting, which results in excessively large canopy openings and uniformly sized stumps, will provide stumps of various sizes covered by mosses and lichens, and it will encourage ant nesting in stumps.

Additionally, dead wood can be common nesting sites for ants, as well as for other groups of invertebrates; it is colonized by many species of fungi. Moreover, the invertebrates that live in dead wood are common food for vertebrates, such as bears (Yamazaki et al., 2012, Koike et al., 2012). Thus, management practices should focus on maintaining dead wood in forest habitats in plantation in the world. We assume that it takes a long time for stumps to start decomposing and for ants or other invertebrates to colonize them; thus, perhaps there more attention should be paid to leaving dead wood laying before (and after) tree logging (thinning stands). Many of the forests in Japan planted after World War II are 50–60 years old and in the main cutting stage. Therefore, to ensure that these planted forests continue to produce wood and source of biodiversity in planted forest ecosystems, thinning must be continued under a long-term plan.

Funding

This work was partly supported by the Institute of Global Innovation Research in TUAT.

CRediT authorship contribution statement

Mii Tanaka: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing original draft. **Seungyun Baek:** Methodology, Software, Writing review & editing. **Kahoko Tochigi:** Formal analysis, Software. **Tomoko Naganuma:** Software, Validation, Visualization, Writing review & editing. **Akino Inagaki:** Validation, Visualization, Writing review & editing. **Bainah S. Dewi:** Writing review & editing. **Shinsuke Koike:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We thank the many people who helped us conduct field work. We also thank M. Akasaka and N. Iwai for their valuable comments and discussions during the planning of our study. Additionally, we thank T. Yoshida, K. Kinoshita, M. Kaneko, and T. Iwamoto, who gave useful advice about field data collection at Kusaki University Forest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120976.

References

Bartoń, K., 2022. MuMIn: Multi-model inference, software. Available from https://CRAN.R-project.org/package=MuMIn.
Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical information—theoretical approach. Springer-Verlag, New York.
Beattie, A.J., Turnbull, C.L., Hough, T., Knox, B., 1986. Antibiotic production: a possible function for the metapleural gland of ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 79, 448–450.
Blüthgen, N., Feldhaar, H., 2009. Food and Shelter: How Resources Influence Ant Ecology. In: Lach, L., Parr, C.L., Abbott, K.L. (Eds.), Ant Ecology. Oxford University Press, Oxford, pp. 115–136.
Bobiec, A., Gutowski, J.M., Zub, K., Pawlaczyk, P., Laudenslayer, W.F., 2005. The afterlife of a tree. WWF Poland, Warszawa-Hajnówka.
Boucher, P., Hébert, C., Francoeur, A., Sirois, L., 2015. Postfire succession of ants (Hymenoptera: Formicidae) nesting in dead wood of northern boreal forest. Environ. Entomol. 44, 1316–1327.
Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9 (2), 378–400.
Bujoczek, L., Bujoczek, M., Zięba, S., 2021. How much, why and where? Deadwood in forest ecosystems: The case of Poland. Ecol. Ind. 121, 107027.
Chang, C., van Logtestijn, R.S.P., Goudzwaard, L., van Hal, J., Zuo, J., Hefting, M., Sass-Klaassen, U., Yang, S., Sterck, F.J., Poorter, L., Cornelissen, J.H.C., 2020. Methodology matters for comparing coarse wood and bark decay rates across tree species. Methods Ecol. Evol. 11, 828–838.
Dossa, G.O.G., Schaefer, D., Zhang, J., Tao, J., Cao, K., Corlett, R.T., Cunningham, A.B., Xu, J., Cornelissen, J.H.C., Harrison, R.D., 2018. The cover uncovered: Bark control over wood decomposition. J. Ecol. 25, 2147–2160.
Forestry Agency, Japan, 2021. Annual Report on Trends in Forest and Forestry, Japan. Association of Agriculture and Forestry Statistics, Tokyo (In Japanese).
Fridman, J., Walheim, M., 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. For. Ecol. Manage. 131, 23–36.
Frouz, J., 2000. The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena* wood ants. Insect. Soc. 47, 229–235.
Geraghty, M.J., Dunn, R.R., Sanders, N.J., 2007. Body size, colony size, and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's Rule? Myrmecological News 10, 51–58.
Gogoi, A., Ahirwal, J., Sahoo, U.K., 2022. Evaluation of ecosystem carbon storage in major forest types of Eastern Himalaya: Implications for carbon sink management. J. Environ. Manage. 302, 113972.
González, G., Gould, W.A., Hudak, A.T., Hollingsworth, T.N., 2008. Decay of Aspen (*Populus tremuloides* Michx.) wood in Moist and Dry Boreal, Temperate, and Tropical Forest Fragments. AMBIO: J. Human Environ. 37, 588–597.
Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S., Lattin, J., Anderson, N., Cline, S., Aumen, N., Sedell, J., Lienkaemper, G., Cromack Jr., K., Cummins, K., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.
Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70, 48–59.
Higgins, R.J., 2010. The ant (Hymenoptera: Formicidae) communities of the central interior of British Columbia: Adaptations to a temperature-constrained environment. University of Northern British Columbia, Prince George, BC, Canada. PhD thesis.
Higgins, R.J., Lindgren, B.S., 2012. The effect of manipulated shading on the colony abundance of two species of ants, *Formica aserva* and *Leptothorax muscorum*, in dead wood. Entomol. Exp. Appl. 143, 292–300.
Hovemeyer, K., Schauermann, J., 2003. Succession of Diptera on dead beech wood: A 10-year study. Pedobiologia 47, 61–75.
Japan Meteorological Agency, 2022. Past weather data research. Japan Meteorological Agency, Tokyo. http://www.jma.go.jp (accessed September 5, 2022) (In Japanese).
Japanese Ant Image Database (2008). http://ant.edb.miyakyo-u.ac.jp/ (accessed November 17, 2022) (In Japanese).
Jones, J.C., Oldroyd, B.P., 2006. Nest thermoregulation in social insects. Advances in insect physiology 33, 153–191.
Kaspari, M., Vargo, E.L., 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. Am. Nat. 145, 610–632.
Kobashikawa, S., Koike, S., 2016. Spatiotemporal factors affecting bark stripping of conifer trees by Asiatic black bears (*Ursus thibetanus*) in Japan. For. Ecol. Manage. 380, 100–106.
Koike, S., Morimoto, H., Goto, Y., Kozakai, C., Yamazaki, K., 2012. Insectivory by sympatric five carnivores in cool-temperate deciduous forests. Mammal Study 37, 73–83.
Li, X.R., Jiaa, R.L., Chenb, Y.W., Huanga, L., Zhanga, P., 2011. Association of ant nests with successional stages of biological soil crusts in the Tengger Desert, Northern China. Appl. Soil Ecol. 47, 59–66.
Marchal, L., Paillet, Y., Guilbert, E., 2013. Habitat characteristics of Aradidae (Insecta: Heteroptera) in two French deciduous forests. J. Insect Conserv. 17, 269–278.

Maziarz, M., Broughton, R.K., Casacci, L.P., Dubiec, A., Maák, I., Witek, M., 2020. Thermal ecosystem engineering by songbirds promotes a symbiotic relationship with ants. Sci. Rep. 10, 20330.
Maziarz, M., Broughton, R.K., Casacci, L.P., Hebda, G., Maak, I., Trigos-Peral, G., Witek, M., 2021. Interspecific attraction between ground-nesting songbirds and ants: the role of nest-site selection. Front. Zool. 18, 43.
Mitrus, S., 2015. The cavity-nest ant *Temnothorax crassispinus* prefers larger nests. Insect. Soc. 62, 43–49.
Moore, P.A., Smolarz, A.G., Markle, C.E., Waddington, J.E., 2018. Hydrological and thermal properties of moss and lichen species on rock barrens: Implications for turtle nesting habitat. Ecohydrology 12, e2057.
Oldén, A., Peura, M., Saine, S., Kotiaho, S.J., Halme, P., 2019. The effect of buffer strip width and selective logging on riparian forest microclimate. For. Ecol. Manage. 453, 117623.
Persson, T., Lenoir, L., Vegerfors, B., 2013. Which macroarthropods prefer tree stumps over soil and litter substrates? For. Ecol. Manage. 290, 30–39.
R Core Team, 2021. R: A Language and Environment for Statistical Computing. R. Foundation for Statistical Computing, Vienna.
Risch, A.C., Jurgensen, M.F., Schütz, M., Page-Dumroese, D.S., 2005. The contribution of red wood ants to soil C and N pools and CO_2 emissions in subalpine forests. Ecology 86, 419–430.
Satoh, T., Yoshida, T., Koyama, S., Yamagami, A., Takata, M., Doi, H., Kurachi, T., Hayashi, S., Hirobe, T., Hata, Y., 2016. Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants. Insect Conservation and Diversity 9, 4–12.
Symonds, M.R., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65, 13–21.
Takenaka, A., 2009. CanopOn 2. Available at http://takenaka-akio.org/etc/canopon2/ (accessed on 5 June 2022).
Tuma, J., Eggleton, P., Fayle, T.M., 2020. Ant-termite interactions: an important but under-explored ecological linkage. Biol. Rev. 95, 555–572.
Warren, R.J., Bradford, M.A., 2012. Ant colonization and coarse woody debris decomposition in temperate forests. Insect. Soc. 59, 215–221.
Włodarczyk, T., Zmihorski, M., Olczyk, A., 2009. Ants inhabiting stumps on clearcuts in managed forest in western Poland. Entomologica Fennica 20, 121–128.
Yamazaki, K., Kozakai, C., Koike, S., Morimoto, H., Goto, Y., Furubayashi, K., 2012. Myrmecophagy of Japanese black bear in the grasslands of the Ashio area, Nikko National Park, Japan. Ursus 23, 52–64.