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Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants

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Abstract

1. The need to understand the mechanisms enhancing species coexistence and diversity is one of the central issues of community ecology. Theoretical work suggests that resource partitioning based on body size contributes to the coexistence of competing species, resulting in increased species diversity. Nevertheless, few empirical studies have investigated this. The species composition of wood-dwelling arthropods was surveyed to examine resource partitioning based on body size in the dead wood of the ubame oak (*Quercus phillyraeoides* A. Grey) trees.
2. Greater resource sizes (larger dead wood diameter) retained a lower overall density of wood-dwelling beetles per resource volume, greater total beetle biomass per resource volume and larger bodied individuals of the dominant species (Cerambycidae; *Anaglyptus nipponensis* Bates). A gradient in the species composition of arboreal ant assemblages along resource size and a positive correlation between resource size and ant body size was observed. These results suggest that the incidence of wood-boring beetles was limited by the size of the available resource, resulting in resource partitioning by the ants according to the sizes of galleries made by the beetles.
3. Our findings indicate that resource size leads both directly and indirectly to body size-dependent resource partitioning in beetle and ant assemblages, and contributes to the maintenance of species coexistence in the assemblages present in dead wood.

Keywords

harvester ant, intraspecific competition, mating partner

Introduction

One of the central goals of community ecology is to understand the mechanisms that enhance species coexistence and support species diversity (Agrawal *et al.*, 2007). The traditional ecological theory predicts that niche differentiation allows for the coexistence of potentially competitive species, resulting in increased species diversity (reviewed in Chesson, 2000; Chase & Leibold, 2003). Body size variation is one of the factors that allow competing species to avoid direct overlaps in resource use (Schoener, 1974; Werner & Gilliam, 1984). Differences in resource utilisation, that is, resource partitioning, between sympatric species depending on their body size promote the coexistence of different species living in the same habitat (MacArthur, 1972; Schoener, 1974; Bowers & Brown, 1982).

Dead wood provides a favourable habitat to various arthropods (Grove, 2002; Stokland *et al.*, 2012), and is a good system in which to study the mechanisms of species coexistence and diversity. The size (i.e. diameter) of dead wood is a determinant of the community structure of wood-dwelling arthropods. Past studies have shown that an increase in the size of dead wood leads to an increase in the average body size of the beetles (Hanks *et al.*, 2005) and their abundance (Banno & Yamagami, 1991), and to a change in the species compositions of their assemblages (Jonsell *et al.*, 2007; Foit, 2010). The increase in resource size provides a separate niche for primary colonisers such as beetles, which are the first to utilise the inside and surface of dead wood. The abandoned galleries and tunnels made by the primary colonisers subsequently have a positive effect on the species richness and abundances of secondary colonisers and their predators (Buse et al., 2008; Calderón-Cortés *et al.*, 2011). The primary colonisers, which create habitats for other organisms, are called ecosystem engineers (Jones *et al.*, 1994, 1997). This is recognised to be an important group, which constructs ‘indirect interaction webs’ (Ohgushi, 2005).

Wood-nesting ants are secondary colonisers, which utilise abandoned galleries and tunnels made by wood-boring beetles within dead wood (Tschinkel, 2002; Powell, 2008; Powell *et al.*, 2011). Among wood-dwelling ants, the occurrence of *Camponotus* was greater in dead wood with a larger diameter size than in that with the smallest (Torgersen & Bull, 1995). This means that the traits of wood-boring beetle assemblages (body size, abundance and species composition) affect the composition of wood-nesting ant assemblages through the configuration of their abandoned galleries and tunnels. Nevertheless, few studies have been conducted from this point of view.

In this study, we aim to elucidate the importance of body size-based resource partitioning by wood-dwelling arthropods as the mechanism of species coexistence and diversity. We have the following two hypotheses: (i) resource size (wood diameter) directly determines the body size of wood-boring beetles (primary colonisers); (ii) resource size indirectly promotes resource partitioning by wood-nesting ants (secondary colonisers) of different body sizes through the sizing of the abandoned beetle galleries and tunnels, resulting in species coexistence within each assemblage present in dead wood.

Materials and Methods

Study area

The research was conducted in a coastal forest (34°39′47″N, 138°56′15″E; about 200 × 100 m) at Shimoda, Shizuoka Pref., at the southern end of the Izu Peninsula in Japan. This area is in a warm temperate region under the influence of the Asia monsoon climate. The mean annual rainfall and the annual mean air temperature were 1780 mm and 16.6 °C, respectively, at the nearest weather station [1981–2010, Japan Meteorological Agency (JMA), 2015]. The forest was dominated by the evergreen broad-leaved ubame oak (*Quercus phillyraeoides* A. Grey), which is distributed along the Pacific coast of south to central Japan, Korea and China. The ubame oak reaches a height of 5–7 m and a diameter of 20 cm, and is characterised by the growth of several trunks stemming out from the root. Dead trunks are abundant in the forest, likely due to damage caused by seawater and strong salty winds blown in from the sea (Ito & Gyokusen, 1996), especially during the typhoon season. In addition, light competition within the clump of multiple trunks (self-thinning), generally observed among sprouting species, might affect mortality rates (O'Hara & Berrill, 2010). High levels of exposure to salt deposition potentially have a negative effect on ground-dwelling insects (Kaspari *et al.*, 2008). Nevertheless, this would not seriously affect resource utilisation by the wood-dwelling arthropods studied here, because these groups mainly utilise tree trunks or the space under bark. In addition, because seawater deposition by a typhoon is a short-term event, the seawater would be flushed from standing tree trunks by heavy rainfall.

Collection of dead wood

The collection of dead trunks was performed in mid-March, 1986, when the insects inhabiting the trees had not yet emerged. Twelve dead trunks *c*. 2–3 m in height were cut down at their base, stripped of their side branches and transported to the laboratory. The dead trunks were harvested from different individuals, and were either main or sub-trunks, depending on the trees. In the laboratory, the dead trunks were each cut into sections of length of 40 cm, and their diameter was measured at the centre with vernier callipers. The pieces of dead wood were sorted into eight thickness categories according to diameter (Table 1: small to large; A–H). All bottom pieces were classified as the thickest group (H), and used to breed arthropods in a bucket (see below). For other wood thickness groups (A–G), the pieces of dead wood in each thickness category were selected to prevent sampling bias, because of the limitation of the buckets' volume. The average diameters ranged from 5.4 mm (A) to 78.4 mm (H). The total volume of dead wood was c. 0.12 m^3, and the trunk section diameters ranged from 1 to 95 mm (overall average: 18.2 mm).

Rearing of arthropods in dead wood

The pieces of dead wood were placed into each ‘breeding bucket’ and kept at room temperature. The breeding buckets were each comprised of a stainless steel basket of 5-mm mesh placed in a 70-L bucket (Fig. S1). A packing sponge was inserted between the glass lid and the bucket to prevent any insects from escaping, while still allowing for air permeability. The moisture was supplied occasionally within the buckets by spraying water mist to prevent dry our completely, especially for smaller dead wood groups. We checked the buckets every week. When we found emergent beetles or dwelling ants, we identified them to the species level. Furthermore, once every 2 weeks we sifted the woody debris in the bucket with a 0.5-mm mesh sieve and identified any arthropods remaining on the sieve. The study continued for 6 months, until September 1986, when we surveyed all beetles and ants remaining inside the dead wood. Insect carcasses found in the wood were also identified to the order or family level.

Measurement of body weight and size

Emergent beetles were completely dried in the desiccator for more than 1 month. The body weights of the beetles were measured individually using a balance (0.01 mg scale), and from these measurements the average body weight and first to third quartile values were calculated for each species. The head widths of the worker ants (minor workers for dimorphic species) were measured with an ocular micrometre (0.01 mm scale), from which mean and SD were calculated for each species. The samples were randomly selected from the collected specimens.

Data analysis

The species number and diversity of wood-dwelling arthropods were not compared among the wood thickness groups, because the total weight and volume of dead wood were different among them (Table 1). Abundance data were carefully interpreted when being compared among the thickness groups. For all arthropods collected, the Spearman's rank correlation between the diameter of dead wood and (i) total individual density and (ii) total biomass per dead wood volume was calculated. The differences in the mean body weight of individuals among the dead wood groups were analysed using analysis of variance (anova). Tukey's honest significant difference test was used for multiple comparisons. Similarities in ant species composition between groups were calculated using Odum's similarity index (Odum, 1950), and cluster analysis was performed using group average methods.

Results

Arthropod fauna

In total, three classes (Arachnida, Diplopoda and Insecta) and 12 orders of arthropods were reared from dead ubame oak wood (Table 2). In Insecta, species of the order Hymenoptera, including ants and wasps, were the most abundant, followed by species of Coleoptera, Lepidoptera and Psocoptera. In addition to Insecta, Polyxenida (class: Diplopoda) was also abundant. Species of Hymenoptera, Coleoptera, Psocoptera and Polyxenida appeared in all thickness groups, whereas species of Psocoptera and Polyxenida appeared mainly in the small to medium thickness groups (B–D). Lepidopterans appeared in the medium to large thickness groups (D–H), especially in the largest group (H).

Wood-boring beetles

In total, 16 families, 28 genera and 29 species of Coleoptera were found in the dead wood (Table 3). The density of individual beetles was higher in the small to medium thickness groups (A–E) than in the trunks with larger diameters, although lager thickness groups included a larger volume and dry weight of dead wood. The total number of individual beetles per wood volume was negatively correlated with the diameter of the dead wood (Fig. 1a; $r_s = -0.881$, d.f. = 6, $P < 0.01$), whereas the total biomass per volume of dead wood was positively correlated with the diameter of the dead wood (Fig. 1b; $r_s = 0.690$, d.f. = 6, $P < 0.05$).The dominant species were *Gastrallus affinis* Sakai (Anobiidae) and *Anaglyptus nipponensis* Bates (Cerambycidae), of which 322 and 138 were observed in total respectively (Table S1). *Gastrallus affinis* was abundant in the small to medium thickness groups (B–E), whereas *A. nipponensis* was abundant in the medium to large dead wood groups (B–H). *Anaglyptus nipponensis* individuals from the smaller dead wood (B) were significantly smaller than those that emerged from the larger dead wood (C–E) (Fig. 2; anova, $F = 3.64$, $P < 0.005$).

Arboreal ants

In total, three subfamilies, four genera and seven species of arboreal ants were found in the dead wood (Table 4; Table S2). Although *Tapinoma* sp. (Dolichoderinae), *Camponotus nipponicus* Wheeler (Formicinae) and *Camponotus nawai* Ito were collected from almost all dead wood groups (Fig. 3; Table S2), they dominated different size groups. *Tapinoma* sp. dominated the first and second smallest dead wood groups (A and B), whereas *C. nipponicus* dominated the third smallest group (C), and *C. nawai* dominated the larger groups (D–G). *Camponotus devestivus* Wheeler emerged and dominated only the largest group (H). Cluster analysis of the similarities in ant community species composition revealed three major clusters corresponding to the diameter of dead wood (Fig. 4). The first cluster, corresponding to small dead wood groups (A–C), was characterised by the dominance of *Tapinoma* sp. and *C. nipponicus*. The second cluster, corresponding to the medium to large groups (D–G), was characterised by the dominance of *C. nawai*, and the third cluster, corresponding to group H, was characterised by the dominance of *C. devestivus*.

Correspondence of body size between wood-boring beetles and arboreal ants

The body sizes of wood-boring beetles and arboreal ants increased with the diameter of the dead wood they inhabited (Fig. 5). The smallest beetle, *Xylosandrus* sp. (Scolytidae), and the second smallest, *G. affinis*, emerged mainly from trunks in the small dead wood groups and the smallest ants, *Tapinoma* sp., and relatively small *C. nipponicus* dominated the arthropod communities in small dead wood. The mid-sized beetle *A. nipponensis* emerged mainly from medium to large dead wood, and the mid-sized ant *C. nawai* dominated the ants in those thickness groups. The largest beetle, *Mesosa longipennis* Bates (Cerambycidae), emerged mainly from trunks in the largest thickness groups, and the largest ant, *C. devestivus*, also dominated in those thickness groups.

Discussion

We showed that larger resource sizes (thicker dead wood) supported a lower total number of individual wood-dwelling beetles per resource volume, and more total beetle biomass per resource volume. This means that the biomass of wood-dwelling beetles per individual increased with increasing resource size. Smaller resource sizes supported smaller beetle species, and the smaller individuals of the dominant species (*A. nipponensis*). These results support our first hypothesis, and agree with the results of previous studies that have reported a positive correlation between dead wood size and the body sizes of wood-boring beetles (Hanks *et al*., 2005).

Some parameters of dead wood, which correlate with wood diameter, affect the growth and survival of wood-dwelling arthropods. The differences in wood diameter provide different heterogeneous habitats and allow for different colonisation processes (Grove, 2002; Heilmann-Clausen & Christensen, 2004). The proportions of wood components, such as bark, cambium, phloem and sapwood, to volume are partially dictated by the diameter of the dead wood (Grove & Forster, 2011). Past studies showed positive correlations between wood diameter and phloem thickness, and between phloem thickness and the gallery construction rate of bark beetles (Scolytidae) (Amman, 1977; Haack *et al*., 1984). Smaller diameter dead wood provides a more variable microclimate owing to its larger amount of surface area per volume and to smaller quantities of substrates that are well-buffered from the external environment (Schiegg, 2001). Zhang *et al.* (1993) demonstrated a positive correlation between trunk diameter and bark thickness, and between bark thickness and the emergence density of a long-horned beetle species. Nevertheless, the smaller diameter dead wood is made up of many more individual wood pieces per volume than the larger diameter wood, resulting in higher microhabitat diversity per volume (Schiegg, 2001). This causes the colonisation processes by wood-dwelling organisms to be more stochastic (Heilmann-Clausen & Christensen, 2004). Therefore, smaller diameter wood provides higher colonisation opportunity for wood-dwelling organisms, but lower survival condition due to drought. In our study, higher emergent beetle density in smaller diameter wood would be attributed to moderate moisture condition by spraying water within rearing containers.

We identified a gradient in the species composition of arboreal ants along their resource size, and a positive correlation between the diameter of the dead wood and the body size of the ants. Positive correlations between resource size and the sizes of wood-dwelling beetles and ants support our second hypothesis, which suggested that the different sizes of wood-boring beetles (primary colonisers), as dictated by their resource size, leads to the production of different sizes of galleries and tunnels, ultimately leading to resource partitioning by arboreal ants (secondary colonisers). Pratt and Pierce (2001) examined three geometric parameters of hollow acorn nests associated with nest site selection by cavity-dwelling ant species (*Leptothorax curvispinosus*): entrance hole area, cavity volume and cavity shape. They clarified that this ant species preferred the cavities that had small entrance holes, larger volumes, and compact, high-ceilinged shapes. The wood-dwelling ants in our study were also influenced by these gallery and tunnel parameters.

The entrance hole area of ant nests affects the ants' ability to defend their nests against predators and other ants (Powell, 2009). In some cavity-dwelling ant species, whose nest entrances are blocked by the heads of one or more major workers (Hölldobler & Wilson, 1990; Powell, 2008), the optimal entrance area is equal to the head area of the major workers of that species (Powell, 2009). Because the optimal entrance area differs among cavity-dwelling ant species, cavity-entrance diversity promotes the niche differentiation of the species (Powell *et al*., 2011). Cavity-dwelling ant species often reduce the size of the entrance area by adding rims of mud and debris (Herbers & Banschbach, 1995; Pratt & Pierce, 2001). Among the arboreal *Camponotus* species, the subgenera *Colobopsis*, *Myrmamblys* and *Paramyrmamblys* are known to exhibit behavioural and morphological adaptations relating to the blocking of nest entrances (Klimes & McArthur, 2014). The *Camponotus nipponicus*, *C. nawai*, and *C. kiusiuensis* collected in our study belong to these three subgenera, and *C. nipponicus* were observed to exhibit the behaviour of plugging nest entrances holes with their heads (Hasegawa, 1993). *C. nipponicus* and *C. nawai* exhibit both entrance-blocking and entrance-reduction behaviours (T. Satoh, pers. obs.). They could utilise a relatively wide range of dead wood sizes because of these behaviours. Therefore, the variability in nest entrance areas with the body sizes of wood-boring beetles account for the presence different ant species and their ability to coexist in dead wood.

The volume and shape of the beetles' galleries and tunnels also affect the colonisation of dead wood by arboreal ants. In some ant-plants (myrmecophytes), a positive correlation between domatia volume and ant body size causes each domatium to be occupied by a different ant species, resulting in the coexistence of multiple ant species on individual plants (Fonseca, 1999; Campbell *et al*., 2013). The volume and shape of beetles' galleries and tunnels vary with tree species, beetle species and their colonisation density (e.g. Connor & Wilkinson, 1983; Zhong & Schowalter, 1989;

Schowalter *et al*., 1998). Cerambycid larvae have been known to excavate bark beetle mines to feed on bark beetle larvae (Coulson *et al*., 1980; Dodds *et al*., 2001; Schowalter, 2006). Such interactions might increase the complexity of the gallery and tunnel structures, providing a wider range of suitable habitats to secondary colonisers. Therefore, this variability in wood volume and shape also plays an important role in the determination of the species composition of wood-dwelling ant communities in dead wood.

In conclusion, we have demonstrated that variation in resource size leads both directly and indirectly to size-dependent resource partitioning by wood-dwelling beetles and ants, and thus contributes to the maintenance of species coexistence in insect communities within dead wood. We can consider this beetle–ant relationship with be a ‘nest web’. In cavity-nesting bird communities, several authors proposed and used this concept, which consists of primary cavity nesters (e.g. woodpeckers) and secondary cavity-nesting species that depend entirely on the production of cavities by primary cavity nesters (Martin & Eadie, 1999; Cockle *et al*., 2012). Shelter building by wood-boring beetles might have additional linkages around dead wood. Nakamura and Ohgushi (2003) described an ‘indirect interaction web’ (Ohgushi, 2005) in which leaf shelters made by leaf rolling caterpillars increased the abundance of aphids on willow shoots, which in turn increased the abundance of aphid honeydew-harvesting ants, indirectly reducing the larval survival of the leaf beetles due to ant predation pressure. Similarly, arboreal ants act as important predators in arboreal food webs (Floren *et al*., 2002), where the species composition and abundance of arboreal arthropod communities depend on the presence or absence of ant nesting and ant community composition in dead wood. Further empirical research relating to the above concepts is needed in order to elucidate the mechanisms behind species coexistence in dead wood.

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Competing interest

We have no competing interests.

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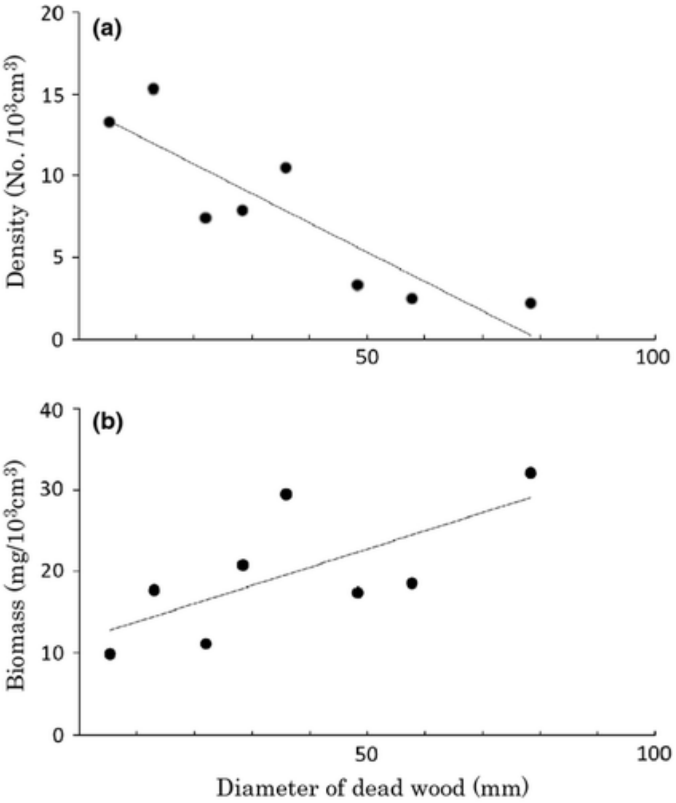


Figure 1. The relationships between diameter of dead wood and (a) population density, and (b) biomass (dry weight) of beetles respectively.

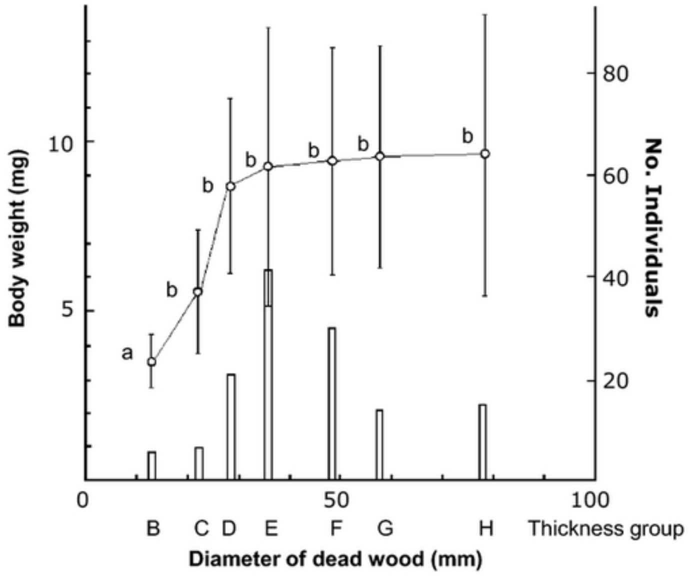


Figure 2. Body weight (open circle) and the number of individuals (histogram) of *Anaglyptus niponensis* according to the average diameter of each thickness group of dead wood (B–H; absent in group A, see Table S1). Values of the body weight represent means ± SD. Different lower case letters indicate significant difference at $P < 0.05$.

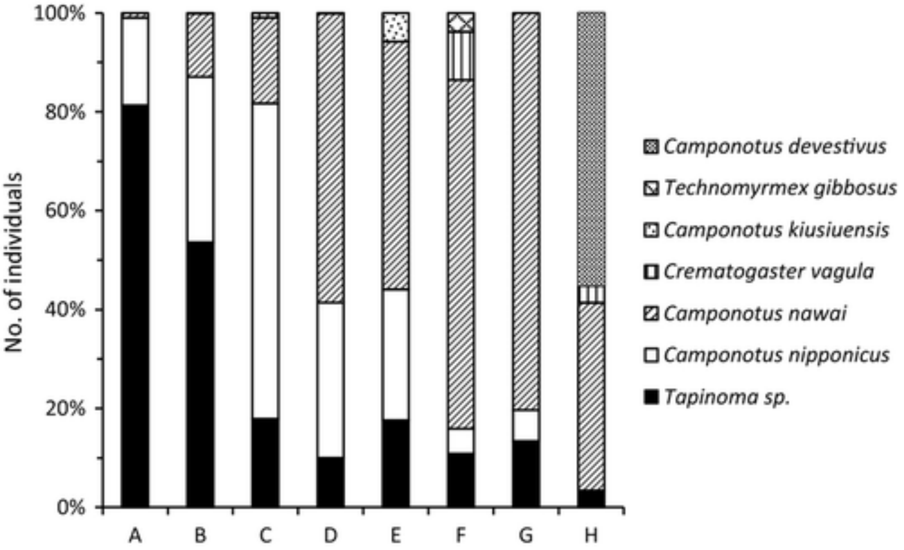


Figure 3. Species composition of arboreal ants in each thickness group of dead wood of ubame oak (*Quercus phillyraeoides*).

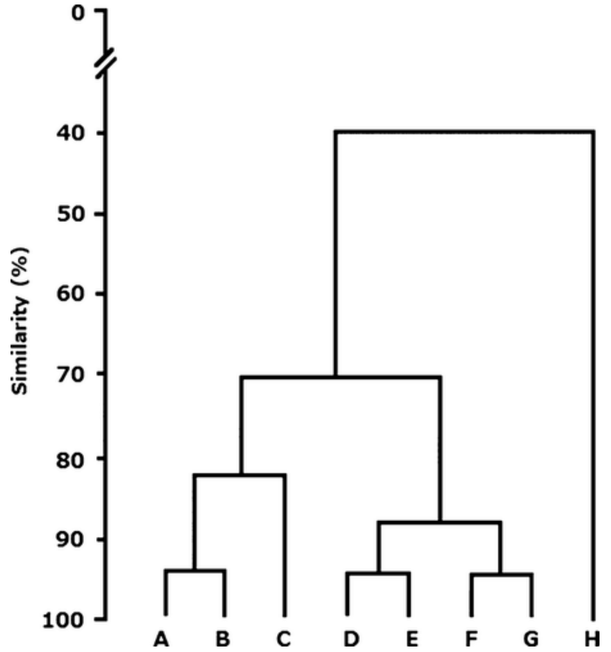


Figure 4. Similarity of ant species composition between thickness groups of dead wood of ubame oak (*Quercus phillyraeoides*). Similarity between groups was calculated by Odum's per cent similarity index, and group average method was employed.

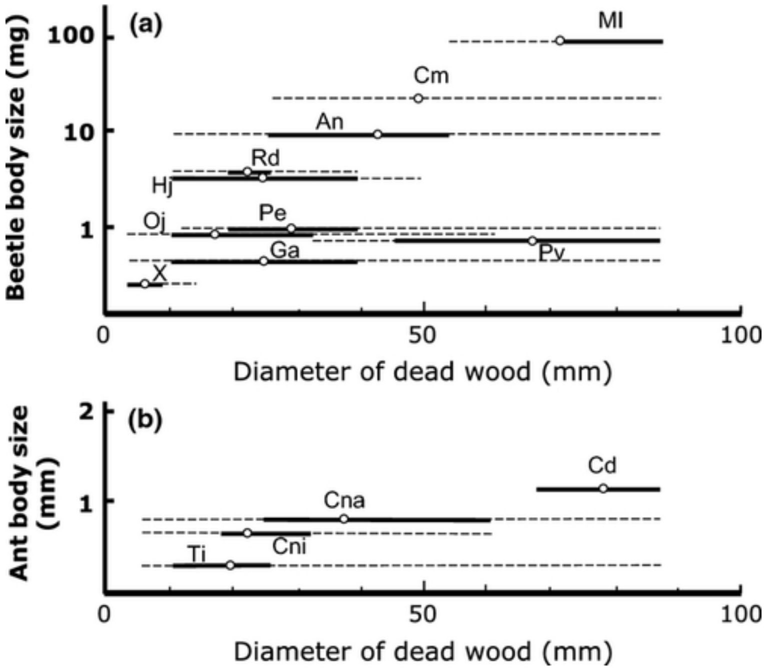
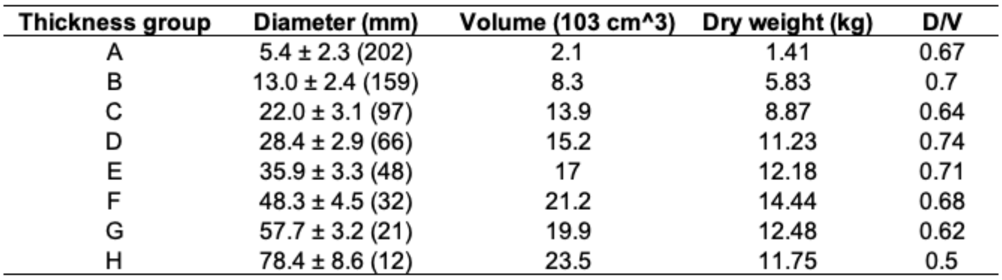


Figure 5. (a) Body size of wood-boring beetles (average body weight) and (b) ants (average head width of workers) in relation to wood thickness: mean (open circle), first to third quartile (solid line) and range (dashed line) were shown. Beetles (mean ± SD): *Mesosa longipennis* (Ml: 94.53 ± 25.32 mg, $n = 7$), *Chlorophorus muscosus* (Cm: 21.93 ± 7.31 mg, $n = 6$), *Anaglyptus niponensis* (An: 8.94 ± 3.18 mg, $n = 20$), *Rhaphuma diminuta* (Rd: 2.92 mg, $n = 2$), *Holcobius japonicas* (Hj: 2.51 ± 0.73 mg, $n = 20$), *Ptinomorphus exilis* (Pe: 0.89 ± 0.26 mg, $n = 20$), *Oligomerus japonicas* (Oj: 0.76 ± 0.26 mg, $n = 18$), *Penthelispa vilis* (Pv: 0.68 ± 0.18 mg, $n = 20$), *Gastrallus affinis* (Ga: 0.42 ± 0.12 mg, $n = 20$) and *Xylosandrus* sp. (X: 0.19 ± 0.03 mg, $n = 19$). Ants (mean ± SD): *Tapinoma* sp. (Ti: 0.41 ± 0.01 mm, $n = 30$), *Camponotus nipponicus* (Cni: 0.77 ± 0.03 mm, $n = 30$), *Camponotus nawai* (Cna: 0.99 ± 0.03 mm, $n = 100$) and *Camponotus devestivus* (Cd: 1.51 ± 0.10 mm, $n = 3$).

Table 1. Diameter and weight of each thickness group (A–H) of dead wood of ubame oak (*Quercus phillyraeoides*)



Thickness group	Diameter (mm)	Volume (103 cm^3)	Dry weight (kg)	D/V
A	5.4 ± 2.3 (202)	2.1	1.41	0.67
B	13.0 ± 2.4 (159)	8.3	5.83	0.7
C	22.0 ± 3.1 (97)	13.9	8.87	0.64
D	28.4 ± 2.9 (66)	15.2	11.23	0.74
E	35.9 ± 3.3 (48)	17	12.18	0.71
F	48.3 ± 4.5 (32)	21.2	14.44	0.68
G	57.7 ± 3.2 (21)	19.9	12.48	0.62
H	78.4 ± 8.6 (12)	23.5	11.75	0.5

Mean diameter ± SD (number of pieces of dead wood), volume, dry weight and dry weight per volume (D/V) are presented.

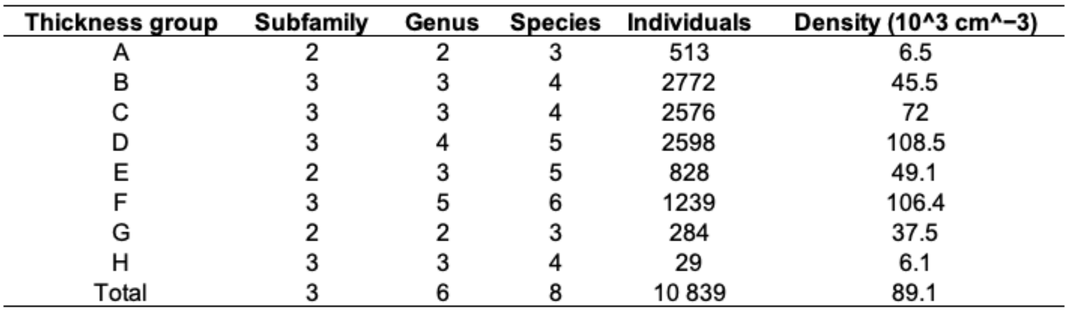
Table 2. Number of individuals of arthropods fauna in each thickness group (A–H) of dead wood of ubame oak (*Quercus phillyraeoides*)

Thickness group	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**Total**
Insecta									
Orthoptera	–	–	–	1	–	–	–	–	1
Psocoptera	5	16	29	25	6	17	5	1	104
Thysanoptera	–	2	–	–	2	–	–	–	4
Hemiptera	–	–	–	–	–	–	3	–	3
Lepidoptera	–	–	–	2	12	25	48	144	231
Coleoptera	28	127	103	120	178	70	49	52	727
Diptera	–	–	–	–	–	1	–	1	2
Hymenoptera (wasps)	5	3	55	222	238	175	78	55	831
Hymenoptera (ants)	513	2772	2576	2598	828	1239	284	29	10839
Other arthropods									
Geophilomorpha	–	–	4	–	–	–	–	–	4
Polyxenida	18	112	188	86	17	8	1	1	431
Pseudoscorpiones	9	2	–	–	2	1	–	–	14
Acarina	2	4	8	–	–	–	–	1	15
Araneida	1	3	3	4	4	3	1	–	19
Collembola	–	11	35	2	–	–	–	–	48
Total	581	3052	3001	3060	1287	1555	469	284	13289

Table 3. Number of families, genus, species, individuals and density of beetles emerged from each thickness group (A–H) of dead wood of ubame oak (*Quercus phillyraeoides*)

Thickness group	Family	Genus	Species	Individuals	Density (10^3 cm^−3)
A	3	4	4	28	13.3
B	3	7	7	127	15.3
C	5	9	9	103	7.4
D	5	11	11	120	7.9
E	6	11	11	178	10.5
F	7	11	11	70	3.3
G	9	13	13	49	2.5
H	9	13	14	52	2.2
Total	16	28	29	727	5.9

Table 4. Number of subfamilies, genus, species individuals and density of arboreal ants emerged from each thickness group (A–H) of dead wood of ubame oak (*Quercus phillyraeoides*)



Thickness group	Subfamily	Genus	Species	Individuals	Density (10^3 cm^−3)
A	2	2	3	513	6.5
B	3	3	4	2772	45.5
C	3	3	4	2576	72
D	3	4	5	2598	108.5
E	2	3	5	828	49.1
F	3	5	6	1239	106.4
G	2	2	3	284	37.5
H	3	3	4	29	6.1
Total	3	6	8	10 839	89.1