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Conversion From Natural Broad-Leaved Forest to Conifer Plantation Increases Relative Detritus Dependency of Aculeata Communities

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ABSTRACT

Forest plantations can impact animal communities that depend on grazing and detritus food webs. In this study, we investigated this distinction by analyzing Aculeata bees and wasps that feed on different food resources in natural deciduous broadleaved forests and in two coniferous plantations, *Cryptomeria japonica* ("Sugi") and *Chamaecyparis obtusa* ("Hinoki"), in a mountainous region of southern Kyushu, Japan. Analysis of samples collected with yellow pan traps revealed that Aculeata abundance and species richness significantly declined in plantations, and that the communities exhibited greater reliance on detritus-based food chains. This suggests that detritus-dependent species are more resilient to the conversion of natural forests to plantations than grazing-dependent species. Moreover, species in plantations tended to have longer seasonal durations, indicating a lower seasonal segregation of food resources. They also tended to have larger body sizes, suggesting wider foraging ranges. We also observed differences between the Sugi and Hinoki plantations. Compared with Sugi plantations, Hinoki plantations were inhabited by only a few large species with wide feeding ranges. Overall, our findings highlight that land modification profoundly alters food web structure and aboveground Aculeata communities. Maintaining the detritus food web and enhancing the grazing food web could increase biodiversity in plantations.

1 | Introduction

Forest plantations are often referred to as "green deserts" because they are structurally less complex than natural forests (Koh and Gardner 2010). According to the resource heterogeneity hypothesis, the conversion of natural forests into plantations drastically reduces plant diversity, resulting in lower herbivore diversity due to a decrease in resource heterogeneity (Hutchinson 1959). These effects cascade through food webs, impacting consumers at higher trophic levels (Potapov et al. 2024). Therefore, to understand the mechanistic impacts of forest plantations on biodiversity, it is necessary to examine the dynamics of organisms across multiple trophic levels and different food chains.

Food webs are typically divided into grazing and detritus food chains, which are also referred to as the green and brown chains, respectively (Mittelbach and McGill 2019). The base of the grazing food chain consists of plant-derived resources produced within the current year (e.g., leaves, pollen, nectar), whereas in the detritus food chain, the plant-derived materials are from previous years (e.g., litter, deadwood, soil organic matter). Monoculture plantations support low species diversity (SD) of aboveground organisms dependent on the grazing food chain

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(Guo et al. 2021; Maeto et al. 2009; Wenninger et al. 2019), likely due to the low plant diversity and poor resource quality of plantation foliage (Bryant et al. 1983). In contrast, changes in SD among detritus-dependent aboveground species remain unclear (Bardgett and Wardle 2010; Tomita et al. 2025). The energy flux in detritus food chains is slower than that in grazing food chains (Ward et al. 2015), which contributes to greater food web stability (Moore et al. 2004; Rooney et al. 2006; Rooney and McCann 2012; Mittelbach and McGill 2019). This slower flux is consistent with the "green–brown imbalance hypothesis," which suggests that detritus-based food webs are more resistant than grazing-based food webs to environmental changes (Thakur 2020). The soil animal communities in coniferous plantations with sufficient litter and ground cover are typically comparable to those in natural broadleaved forests (Hasegawa et al. 2009; Minamiya et al. 2007; Salamon et al. 2008; Scheu et al. 2003). Although previous conversions of rainforests to rubber and oil palm plantations resulted in reduced aboveground energy flux, belowground energy flux did not necessarily decrease (Potapov et al. 2024). Thus, aboveground species that depend on detritus-based food chains may be more resilient to forest conversion than those that depend on grazing food chains.

Aculeata bees and wasps (suborder Aculeata, excluding Formicoidea), a distinctive taxonomic group comprising species that depend on grazing and detritus food chains, are excellent indicators for investigating food web structure (Duelli and Obrist 2003; Fabian et al. 2014; Guo et al. 2021). Species associated with the grazing food chain feed on pollen, nectar, butterflies, grasshoppers, leafhoppers, and herbivorous beetles (Tadauchi and Murao 2014; Terayama and Suda 2016), while species associated with the detritus food chain prey on flies, deadwood-feeding beetles, and spiders (Tadauchi and Murao 2014; Terayama and Suda 2016). These highly specialized species feed on very specific prey types (e.g., Pompilid wasps exclusively prey on spiders). Because species within the same genus or family tend to utilize similar food resources, dietary preferences of poorly studied species can often be inferred from those of well-known related species. Because members of Aculeata are less influenced by individual, seasonal, or geographic variation in resource use, they represent a practical model system.

In community ecology, trait-based approaches quantify species- and individual-level changes in characteristics that are caused by environmental conditions, enabling the assessment of community responses to environmental change (McGill et al. 2006; Moretti et al. 2017; de Bello et al. 2021). Such approaches have been effectively applied to Aculeata communities. For example, analysis of the proportion of individuals in a community that are dependent on detritus-based food chains has shown that the trophic levels and degree of detritus dependency vary with climatic conditions (Uemori et al. 2021, 2022). Changes in food web structure due to plantation forestry can, therefore, be inferred by monitoring changes in feeding-related traits. Combined with the analysis of traits unrelated to food web structure—e.g., body size or nesting location—a more comprehensive understanding of how Aculeata communities respond to plantations can be achieved.

This study investigates the effects of converting deciduous broadleaved natural forests to conifer plantations on the food web structure by analyzing the distinctive feeding traits of Aculeata bees and wasps. Our aims were to test the following hypotheses:

1. Species that are dependent on grazing food chains decline in conifer plantations because of the reduction in plant diversity and resource availability.
2. Species that depend on detritus food chains are able to persist in plantations due to support from soil fauna.
3. As a result of (1) and (2), the relative detritus dependency of Aculeata communities increases in plantations.

Because factors other than food web structure also influence certain traits in Aculeata communities, we assessed the changes in body size, nesting position, seasonal duration, and the number of collected vegetation to gain a more holistic understanding of the effects of forest conversion on these communities.

2 | Materials and Methods

2.1 | Study Site

The study was conducted in the Shiiba Research Forest of Kyushu University, located in the central Kyushu Mountains in southwest Japan (32°21′ N 131°10′ E). The coniferous plantations are located in patches within old natural forests in this region, where Sugi (*Cryptomeria japonica*) plantations are prevalent, while Hinoki (*Chamaecyparis obtusa*) plantations are less common. These two tree species are important plantation species in Japan, covering 28% and 18% of Japan's forested land, respectively (Forestry Agency, Ministry of Agriculture, Forestry and Fisheries, Japan 2023). Litter generated by Sugi and Hinoki differs. On the one hand, Sugi litter tends to accumulate on the forest floor; therefore, protecting the soil; thus, the abundance and SR of soil animals in Sugi plantations are comparable to those in natural forests (Hasegawa et al. 2009). On the other hand, Hinoki litter fragments easily, resulting in outflow from the forest area (Oikawa 1977) and increased soil erosion due to poor ground cover (Onda 2007; Ide et al. 2009). Therefore, the SR of earthworms in natural deciduous forests is similar to that in Sugi plantations but higher than that in Hinoki plantations (Minamiya et al. 2007).

The characteristic natural vegetation at our study site consists of temperate mixed forests, with *Quercus crispula, Acer pictum, Ac. sieboldianum, Carpinus tschonoskii, Fagus crenata, Kalopanax septemlobus*, *Abies firma, Castanea crenata*, and *Magnolia obovata* dominating as the canopy (Uemori et al. 2021; Enoki et al. 2012; Akesaka et al. 2021). The forest floor in this area had been densely covered with dwarf bamboo, Sasa (*Sasa borealis*), before the 1990s, when its density began to decline (Murata et al. 2009; Cho et al. 2016). Overgrazing by deer in the 2000s has denuded the area of understory vegetation (Katayama et al. 2023). As of 2003, our study sites contained very few areas with healthy Sasa (Fujiyama et al. 2025); therefore, all plots had virtually no understory vegetation (including flowering herbs), regardless of elevation or forest age. The annual mean temperature was 11.4°C, and the mean annual precipitation was 3200 mm (according to the weather station in Hirono, near our plots, in 1100 m a. s. l.).

2.2 | Plot Selection

Plots within a 14 km^2 region were established in areas with the following three vegetation types: secondary deciduous broadleaved forests (four "natural" plots, N1–N4); Sugi plantations (five "Sugi" plots, S1–S5); and Hinoki plantations (three "Hinoki" plots, H1–H3) (Figure 1). Plots were demarcated within areas larger than 1 ha. Plots containing the same vegetation were set at least 600 m apart because the maximum foraging range of bees is 600 m (Gathmann and Tscharntke 2002). Aculeata species richness (SR) in forests declines rapidly during the early stages and levels off after stands have aged approximately 20–30 years (Taki et al. 2013; Makino et al. 2021). The impact of tree age on Aculeata communities is difficult to discern in stands that are less than 20 years old because of the effects of clear cutting on community assembly. Therefore, we selected plots containing a stand that was more than 20 years old (Table S1).

2.3 | Environmental Conditions

We measured five environmental conditions: slope, soil hardness, soil temperature, soil humidity, and leaf area index (LAI). The first four conditions were measured because of their impacts on the detritus food web, litter and soil animals, and the nesting sites of the belowground nesting species. We measured LAI as an indicator of the amount of leaf abundance, which forms the base of the living food web. Soil hardness, soil temperature, and soil humidity were measured at five points within each plot, and then the averages were calculated. Slope was evaluated using a clinometer. Soil hardness was evaluated using Yamanaka's soil hardness tester. Soil temperature and humidity were evaluated using a TDR soil moisture meter. The LAI, which represents leaf, branch, and stem area per unit ground area, was evaluated using an omnidirectional camera fitted with a fisheye lens (THETA SC, Ricoh Co. Ltd., Tokyo, Japan). The LAI was calculated from the images using a Gap Light Analyzer ver. 2.0 (Frazer et al. 1999). Soil temperature, soil humidity, and LAI were measured during each sampling season. All data for each plot is presented in Table S1.

2.4 | Aculeata Sampling

We used yellow pan traps, which are least prone to researcher bias and are among the most efficient and cost-effective trapping methods (Westphal et al. 2008), to collect Aculeata bees and wasps. Compared to other colors, yellow has the highest collection efficiency (e.g., Leong and Thorp 1999; Buffington et al. 2020), likely because it is more easily perceived inside forests under low light intensity (Moreira et al. 2016). Nevertheless, it should be noted that different species may have different color biases (Leong and Thorp 1999).

Each yellow pan trap had a diameter of 15 cm, and each pan was filled with approximately 150 mL of water containing a few drops of dishwashing detergent as a surfactant. We placed 20 yellow pans on the ground surface per plot. Samples were collected 48 h after installation and preserved in bottles containing 80% ethanol. Samples were collected at the following times: early spring (before leafing), late spring (between leafing and the rainy seasons), early summer (after the rainy season), and late summer (before the typhoon season). Sampling was conducted

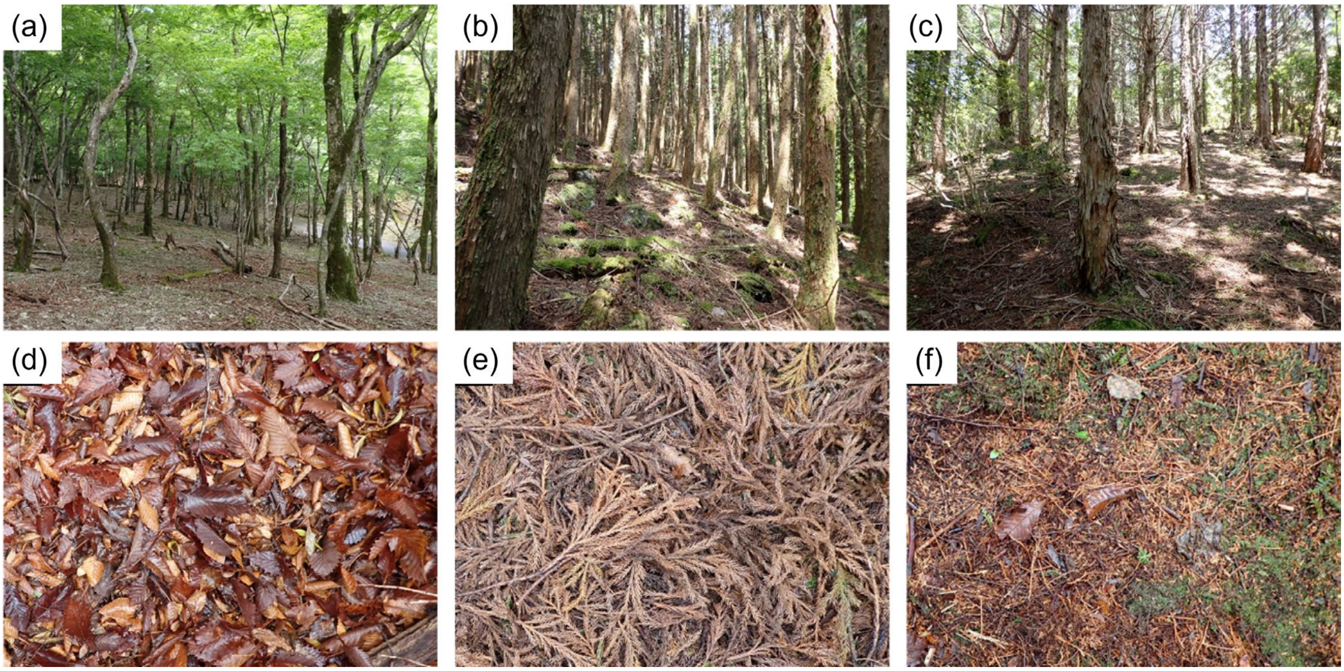

FIGURE 1 | Landscapes of study plots. (a, d) natural forest; (b, e) Sugi plantation; (c, f) Hinoki plantation. (a, b, c) the forests; (d, e, f) accumulated litter on the forest floor.

on the following dates in 2022: April 14–16 (early spring), May 16–18 (late spring), July 12–14 (early summer), and August 31–September 2 (late summer).

2.5 | Identification and Functional Trait Analysis

We identified all Aculeata specimens to the species level, except for members of Formicidae, because the sampling methodology used was unsuitable for this group. To identify bee and wasp species, we referred to Tadauchi and Murao (2014) and Terayama and Suda (2016), respectively; families were classified according to Aguiar et al. (2013). Voucher specimens were deposited in the Entomological Laboratory of Kyushu University, Fukuoka, Japan (ELKU Collection).

We quantified detritus dependency to analyze differences in food resources utilized by Aculeata among the different vegetation types (Table S2). To accomplish this, we classified specimens into two categories: (1) grazing-dependent species, which feed on material from the grazing food chain (e.g., pollen, pollinator bees, butterflies, grasshoppers, leafhoppers, and root-eater beetles); and (2) detritus-dependent species, which feed on material from the detritus food chain (e.g., flies, dead wood-eater beetles, and spiders) (Uemori, Mita, and Hishi 2022). Many of the spiders hunted by spider wasps in forests are ground-roaming species. Because they are presumed to feed primarily on soil animals, we treated them as part of the detritus chain. We expected detritus dependency to increase in plantations because of the reduced diversity and availability of aboveground resources in the grazing food web.

We also analyzed the following five functional traits, as they may be potentially affected by the conversion to forest plantations: trophic level, seasonal duration, mean body size, nesting position, and the number of collected vegetation (Table S2). The specimens were classified into four trophic levels: (1) pollinators, (2) predators and parasitoids feeding on herbivores, (3) predators and parasitoids feeding on detritivores, other predators, and parasitoids, and (4) parasitoids of predators (kleptoparasitoids of spider-hunting wasps, Pompilidae). Although trophic level tends to decrease under environmental stress (Uemori et al. 2021), it is expected to remain high in plantations due to the significant reduction in resources from the grazing food web. Seasonal duration refers to the total number of seasons in which a species is collected (ranging from one to four). It is expected to be higher in plantations due to reduced seasonality associated with lower plant diversity. The mean body sizes (mm) of our specimens were based on literature data (Tadauchi and Murao 2014 for bees; Terayama and Suda 2016 for wasps). Body size is an indicator of tolerance to temperature changes and foraging range (Gathmann and Tscharntke 2002; Greenleaf et al. 2007; Hoiss et al. 2012). Larger species with wider foraging ranges are expected to appear in plantations because of limited food availability. Nesting position was classified into two categories (above- and belowground), based on literature sources. The nesting position of parasitoids was defined based on the level(s) of their host(s). Extreme climatic conditions promote belowground nesting, which provides better protection from harsh environmental conditions (Hoiss et al. 2012). Conversely, high humidity favors aboveground nesting, because nesting in humid soil exposes Aculeata to fungal infections (Uemori, Mita, and Hishi 2022). The number of collected vegetation refers to the total number of vegetation types (natural forest, Sugi plantation, and Hinoki plantation) from which an Aculeata species was collected. If different Aculeata species are specifically associated with either natural forests or plantations, then this value is expected to decrease. However, generalist species can occur in both natural forests and plantations; therefore, generalists in plantations are expected to increase.

3 | Statistical Analysis

All samples collected within each plot were pooled prior to analysis. For each plot, we calculated the following parameters for each trait: abundance, SR, Chao1- estimated SR (ESR), Simpson's index of SD, phylogenetic diversity (PD), multiple functional diversity (mFD), functional diversity (FD) and community-weighted mean (CWM). FD is defined as the diversity within a single trait, while mFD is a diversity index that encompasses all traits used in the analysis.

The FD index was calculated based on Rao's quadratic entropy (Rao 1982), which reflects the sum of dissimilarity in trait space among all possible pairs of species, weighted by the product of the species' relative abundances. Higher FD values indicate a greater trait dissimilarity within a community. PD is also an indicator of dissimilarity within a hierarchical classification (Shimatani 2001; Warwick and Clarke 1995; see Table S2). The decline in SD and PD values in plantations indicates selective loss of particular phylogenetic groups, whereas stable PD values suggest random species loss. PD was calculated using the same approach as FD, with the “taxa2dist” function in the “vegan” package in R (Oksanen et al. 2018; Uemori et al. 2021). The CWM is weighted by the relative abundance of species with each trait value and is used to summarize shifts in mean trait values within communities along environmental gradients (Ricotta and Moretti 2011). All values were calculated using the R packages “vegan” (Oksanen et al. 2018) and “FD” (Laliberté and Legendre 2010; Laliberte et al. 2014) and are presented in Table S3.

We used a generalized linear model (GLM) in linear regression mode to examine the effect of each functional trait on SR, followed by a Gamma distribution, excluding vegetation types. Following GLM, a Tukey–Kramer test was performed to investigate the effect of vegetation type (natural broadleaved forest, Sugi plantation, and Hinoki plantation) on environmental conditions and community properties. Count data (environmental conditions, abundance, and SR) were fitted with a negative binomial distribution, while continuous data (ESR, SD, mFD, FDs, CWMs, and PD) were fitted with a gamma distribution. All statistical analyses were conducted using R version 4.2.2 for Windows (R Core Team 2022).

4 | Results

4.1 | Environmental Conditions

The slopes in natural forest plots were less steep than those in plantation plots ($p < 0.05$). The LAI values in natural plots during early spring (before leafing) were significantly lower than those in plantation plots ($p < 0.05$). No significant differences were found in other environmental conditions among the vegetation types ($p > 0.05$).

4.2 | Aculeata Communities

We collected a total of 1128 Aculeata individuals and 94 species (including five morphological species) (Table S4). The mean numbers of individuals collected in natural, Sugi, and Hinoki plots were 222, 34.2, and 23, respectively. The SR values in natural, Sugi, and Hinoki plots were 75, 45, and 24, respectively, and Chao 1's estimated SR values are 118, 75, and 42, respectively (Figure S1). We collected 365 individuals and 27 species in early spring; 160 individuals and 23 species in late spring; 189 individuals and 43 species in early summer; and 292 individuals and 34 species in late summer. No Aculeata were collected in S4, S5, H2, or H3 plots in early spring. The most abundant species was *Fiorianteon junonium* (148 individuals), which was observed only in early spring. Traps in Sugi plots mainly collected a few *Andrena* spp. (pollinators), *Anteon* spp. (parasitoids of leafhoppers), Bethylidae spp. (parasitoids of beetle larvae), and several Pompilidae spp. (predators of spiders) (Table S4). Traps in Hinoki plots captured species such as *Bischoffitilla ardescens* and *Nomada hakonensis* (parasitoids of pollinator bees), *Tiphia* spp. (parasitoids of beetle larvae), and Pompilidae spp. (Table S4). None of the species were captured exclusively in either Sugi or Hinoki plantations.

4.3 | Relationship Between SR and Functional Traits

SR increased as the CWMs of trophic level, detritus dependency, body size, and the number of collected vegetation decreased ($p < 0.05$; Figure 2, Table 1). SR also increased as the FDs of detritus dependency decreased, and as the seasonal duration time and the number of collected vegetation increased ($p < 0.05$; Table 1). No significant relationships were found between SR and the other traits ($p > 0.05$; Table 1).

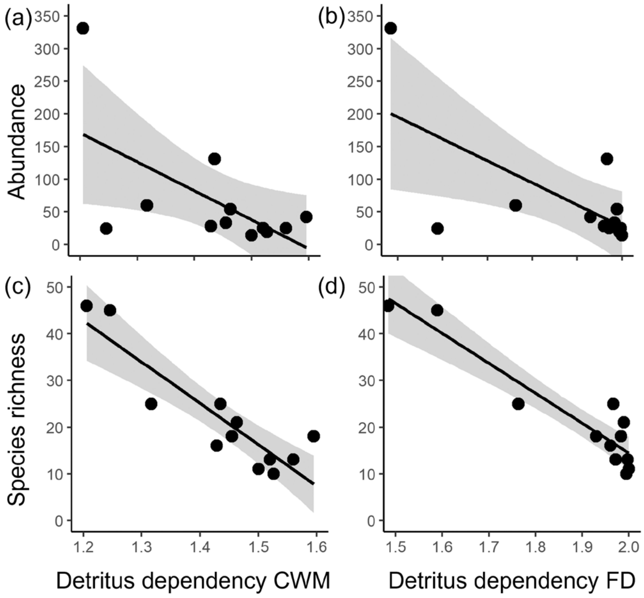

FIGURE 2 | The relationship between abundance, species richness, and functional diversity (FD) and community weighted mean (CWM) of detritus dependency. Solid lines represent linear regression, and shaded areas show 95% confidence interval.

TABLE 1 | The relationship between each functional trait and species richness, using a generalized linear model (GLM).

	Species richness				
	Estimate	**df**	**R^2**	***p***	**Model**
CWMs					
Trophic level	0.09	10	**0.62**	**0.0040**	Linear
Detritus dependency	0.15	10	**0.81**	**< 0.001**	Linear
Body size	0.02	10	**0.50**	**0.014**	Linear
Seasonal duration	0.07	10	0.15	> 0.05	Linear
Nesting position	0.10	10	0.03	> 0.05	Linear
Distribution index	0.00	10	0.00	> 0.05	Linear
Appearance vegetation	0.05	10	**0.43**	**0.024**	Linear
FDs					
Trophic level	0.01	10	0.00	> 0.05	Linear
Detritus dependency	0.09	10	**0.76**	**< 0.001**	Linear
Body size	−0.09	10	0.01	> 0.05	Linear
Seasonal duration	−0.15	10	**0.47**	**0.023**	Linear
Nesting position	0.05	10	0.04	> 0.05	Linear
Distribution index	0.07	10	0.22	> 0.05	Linear
Appearance vegetation	−0.08	10	**0.65**	**0.00261**	Linear

Note: The significant values are shown bold.
Abbreviations: CWM, community weighted mean; FD, functional trait.

The abundance and SR of both grazing- and detritus-dependent species were lower in the plantations than in natural forests ($p < 0.05$; Figure 3). The abundance and SR of grazing-dependent species declined more severely than those of detritus-dependent species.

4.4 | Effects of Forest Plantation

Abundance and SR were higher in natural plots than in plantation plots ($p < 0.05$; Figure 4). However, ESR and SD values did not differ significantly between natural and plantation plots ($p > 0.05$; Figure 4). PD and mFD values were higher in natural and Sugi plots than in Hinoki plots ($p < 0.05$; Figure 4).

FD values and the CWM of detritus dependency were higher in plantation plots than in natural plots ($p < 0.05$; Figure 5).

The FD values of trophic level in natural and Sugi plots were higher than those in Hinoki plots ($p < 0.05$; Figure 5). The FD of seasonal duration time in natural plots was higher than that in Hinoki plots ($p < 0.05$; Figure 5). The FD of the number of collected vegetation was highest in natural plots, followed by values in Sugi and Hinoki plots ($p < 0.05$; Figure 5). The CWM of trophic level in Hinoki plots was higher than that in natural plots ($p < 0.05$; Figure 6). The CWM of seasonal duration time in Sugi plots was higher than that in natural plots ($p < 0.05$; Figure 6). The CWM of mean body size in Hinoki plots was higher than that in natural plots ($p < 0.05$; Figure 6). The CWM value of the number of collected vegetation in Hinoki plots was higher than those in natural and Sugi plots ($p < 0.05$; Figure 6).

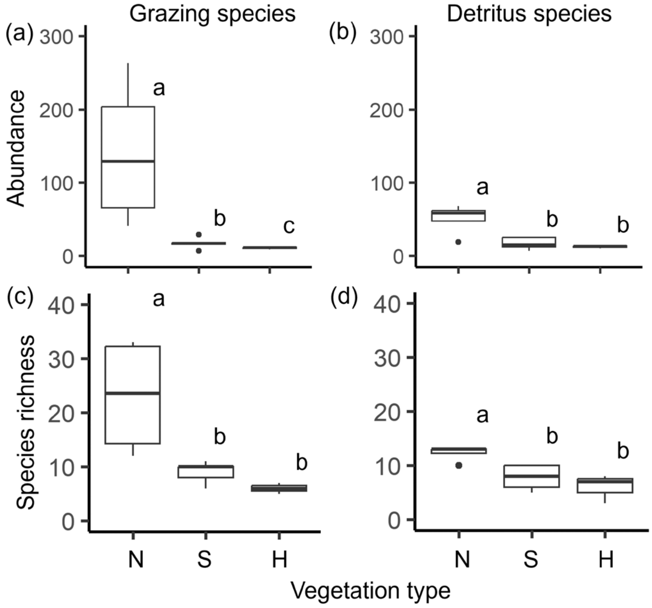

FIGURE 3 | Comparisons of abundance and species richness among vegetation types. (a, c) Grazing species; (b, d) Detritus species. N: Natural forests; S: Sugi plantations; H: Hinoki plantations. Boxes with the different lowercase letters differ at $p < 0.05$.

5 | Discussion

We found that the detritus dependency in Aculeata communities was higher in plantation forests than in natural forests. Although both grazing- and detritus-dependent species declined in abundance and richness in plantations, declines were more pronounced among grazing-dependent species, resulting in increased detritus dependency in plantations. These results are consistent with the "green–brown imbalance" hypothesis (Thakur 2020).

The relationships between SR and the community-weighted mean (CWM) of each trait suggest that reduced plant diversity and limited food availability constrain low-trophic-level and grazing-dependent species, as well as species with low foraging ability, resulting in reduced SR in plantations. In contrast, the relationships between SR and FDs of traits indicate that the coexistence of species with different food chains and seasonal activity periods contributes to maintaining SR. Overall, our findings suggest that the Aculeata community's response to forest conversion depends on how the diversity of feeding guilds, foraging strategies, and seasonality affect diversity. This is the first study to quantitatively elucidate the mechanisms

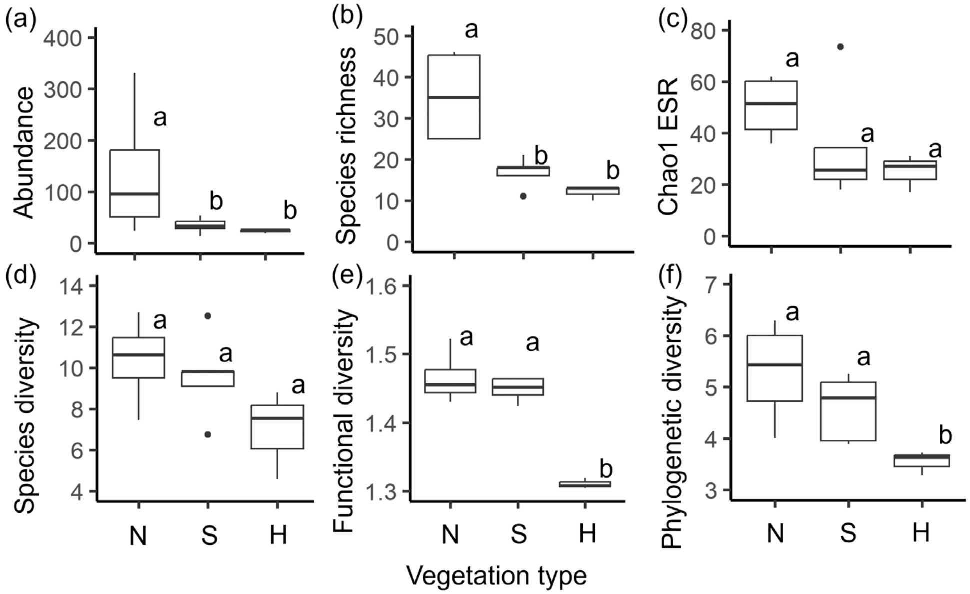

FIGURE 4 | Comparisons of Aculeata communities among vegetation types. (a) Abundance; (b) species richness; (c) Chao1-estimated species richness (ESR); (d) Simpson's species diversity; (e) multi-functional diversity; (f) Phylogenetic diversity. N: Natural forests; S: Sugi plantations; H: Hinoki plantations. Boxes with the different lowercase letters differ at $p < 0.05$.

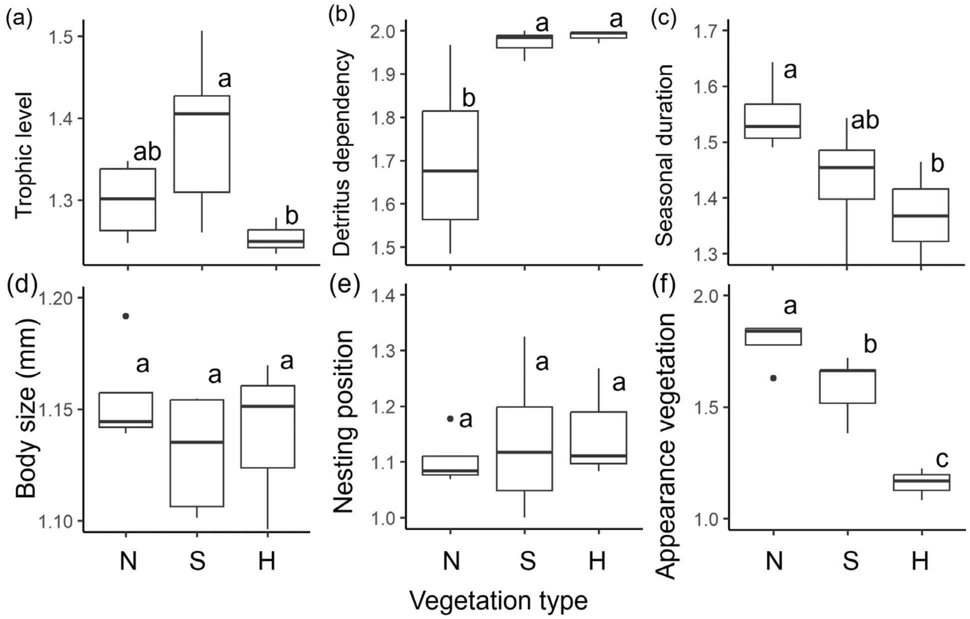

FIGURE 5 | Comparisons of functional diversity (FD) among vegetation types. (a) Trophic level; (b) Detritus dependency; (c) Seasonal duration; (d) Body size; (e) Nesting position; (f) The number of vegetation types collected. N: Natural forests; S: Sugi plantations; H: Hinoki plantations. Boxes with the different lowercase letters differ at $p < 0.05$.

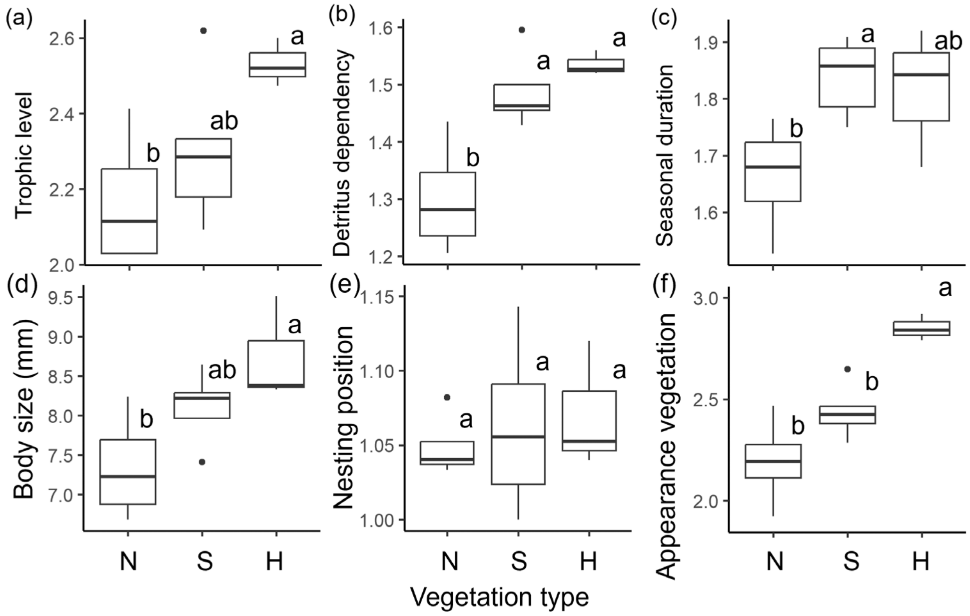

FIGURE 6 | Comparisons of community weighted means (CWMs) among vegetation types. (a) Trophic level; (b) Detritus dependency; (c) Seasonal duration; (d) Body size; (e) Nesting position; (f) Number of collected vegetation. N: Natural forests; S: Sugi plantations; H: Hinoki plantations. Boxes with the different lowercase letters differ at $p < 0.05$.

underlying SR decline in plantations using Aculeata communities with multiple functional traits.

Our results show that Sugi and Hinoki plantations negatively impact the abundance and richness of Aculeata species in the study area. These findings align with earlier studies of Aculeata in conifer plantations (Taki et al. 2013; Makino et al. 2021), as well as non-Aculeata parasitoids such as Ichneumonidae and Braconidae in monoculture plantations (Fraser et al. 2007; Maeto et al. 2009). Overall, these results indicate that the coniferous composition and monoculture conditions in plantations make them less suitable for Aculeata inhabitation.

The results of ESR and SD analyses suggest that no particular Aculeata species dominates in plantations; rather, several species occur in very low numbers. Meanwhile, lower FD and PD values in Hinoki plantations compared to Sugi plantations indicate biased assembly of both functions and taxa in the community. Most species detected in Hinoki plantations were spider-hunting wasps or parasitoid wasps (Table S4), although it is unclear whether these species were actively nesting or foraging, or merely passing through. We found no significant structural differences between the forests in Sugi and Hinoki plantations; therefore, other factors such as the fragmentation of Hinoki litter or the greater susceptibility of Hinoki soils to degradation may make these forests less hospitable to Aculeata.

Functional trait analyses also revealed notable differences among forest types. Trophic level and detritus dependency analyses suggest a shift in energy pathways after converting natural forests to plantations. Aculeata communities in plantations rely more heavily on the detritus food chain and occupy higher trophic levels than those in natural forests. This supports the idea that forest conversion alters energy flow to Aculeata communities, consistent with findings of Potapov et al. (2024), who reported that forest conversion reduces aboveground (grazing) more than belowground (detritus) energy flux. The decline of grazing-dependent species following plantation establishment is likely due to reduced plant diversity and food availability (Bryant et al. 1983; Wenninger et al. 2019), consistent with past research (Fraser et al. 2007; Maeto et al. 2009; Taki et al. 2013). Our results suggest that Aculeata community structure in plantations is shaped by both the loss of grazing-derived food resources and increased reliance on detritus-based resources.

Analysis of other functional traits also indicates key differences between natural and plantation forests. Seasonal activity duration was higher in natural forests, and this high seasonality promotes species segregation and diversity (Uemori et al. 2021). Seasonal turnover in resource availability likely supports the diversity of grazing-dependent Aculeata species. In contrast, the seasonal activity of Aculeata species in Sugi plantations tended to be longer, implying more constant food availability. Unlike grazing resources, detritus resources are consumed slowly and are available year-round (Mittelbach and McGill 2019), allowing detritus-dependent species to persist in plantations.

Hinoki plantations were dominated by large-bodied Aculeata species, which likely have broader foraging ranges (Gathmann and Tscharntke 2002; Greenleaf et al. 2007). In addition, the species we detected in the Hinoki plantations were also found in natural forests and Sugi forests, suggesting that the former consist of generalist species with wide foraging ranges and were able to persist in plantations after forest conversion. These species may either nest within the plantation or wander in from surrounding areas. For instance, kleptoparasitic species such as *Nomada* and *Bischoffitilla*, which lack nests and parasitize other pollinators, likely represent transient visitors. Thus, only species capable of foraging across wide areas or those adapted to a low local food availability can survive in these habitats.

In summary, our results demonstrate that conversion from natural deciduous broadleaved forests to coniferous plantations increases the relative detritus dependency of aboveground Aculeata communities, suggesting that forest conversion alters food web structure and energy flows in terrestrial ecosystems. Grazing resources that are rapidly depleted and highly seasonal support Aculeata SR in natural forests, and these resources are lost in plantations. In contrast, detritus-based resources, which are consumed more slowly and are available year-round, serve as a fallback resource for Aculeata communities in plantations. Our results confirm that the conversion of natural forests to Sugi and Hinoki plantations significantly degrades Aculeata diversity in the central Kyushu Mountains of Japan. Despite reduced understory vegetation due to deer damage, Aculeata diversity in this region remains high compared to evergreen lowland and boreal forests in Japan (Uemori et al. 2020, 2021, 2022, 2022, 2023; Uemori and Hishi 2025). Forest conversion in such a species-rich area is not consistent with the principles of biodiversity-oriented forestry. Measures to enhance biodiversity in plantations may include promoting the development of understory vegetation through thinning (Seiwa et al. 2012; Maleque et al. 2007a, 2007b), creating structurally complex canopies (Ishii et al. 2004), and mitigating deer damage (Tamura and Yamane 2017) and soil erosion (Ide et al. 2016). Such measures can potentially restore grazing food web support. To increase biodiversity in artificial forests, it is necessary to maintain the detritus food web and enhance the grazing food web.

Author Contributions

K.U. compiled and analyzed the data and wrote the manuscript; K.U. and T.H. sampled Aculeata and conceived of the study; K.U. identified Aculeata; K.U. and T.H. interpreted the results.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study is available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Species accumulation curves for species richness in natural forests, Sugi, and Hinoki plantations, using vegan package (Oksanen et al. 2018). The vertical lines represent standard deviations for the rarefaction procedure. The observed (OR) and estimated (Chao 1) species richness are shown inside each graphic. **Data S1:** Supporting Information.