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Impacts of the invasive diatom Cymbella janischii on benthic macroinvertebrate communities in two Japanese rivers

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Abstract

The invasive stalk-forming diatom *Cymbella janischii* has recently spread in Japan and forms thick mats resembling those of *Didymosphenia geminata*, raising concerns about its effects on river ecosystems. We investigated the effects of *C. janischii* cover on benthic macroinvertebrate communities in two Japanese rivers differing in geographic location and sampling season: the Ohyama River (Ohyama; southern Japan in spring) and the Zako River (Zako: central Japan in autumn). Macroinvertebrates were collected from cobbles with high and low cover at Ohyama (≥ 95%, n = 6; ≤ 20%, n = 5) and with high and low-to-moderate cover at Zako (≥ 90%, n = 4; 0–60%, n = 9), and were assessed for Rényi diversity, community composition, taxonomic groups, and functional structure based on life types, dietary groups, and functional feeding groups, with Diptera excluded from functional structure analyses. Diversity was significantly lower at high cover at Ohyama and showed no significant relationship, although the slope was negative at Zako. Community composition differed significantly with cover in both rivers (PERMANOVA: Ohyama, R^2 = 0.693, p = 0.004; Zako, R^2 = 0.194, p = 0.006), and high-cover communities at Ohyama showed evidence of homogenization. These changes were driven mainly by increases in Diptera and decreases in ephemeropteran and trichopteran taxa, particularly taxa classified as Crawlers, Net-spinners, Detritus feeders, Predators/Parasites, and Collector-gatherers. Plecoptera and Swimmers showed no significant response in either river. These responses broadly resemble those reported for *D. geminata* and may represent common ecological effects of blooms by mat-forming stalked diatoms.

Introduction

Biological invasions disrupt local ecosystems and alter community structure, and their management has become an urgent global issue. Reducing the introduction and establishment of invasive alien species is one of the targets of the Kunming–Montreal Global Biodiversity Framework for 2030. Among invasive diatoms, *Didymosphenia geminata* (Didymo) is well known for causing serious impacts in New Zealand, and its thick mats have been reported to affect riverine benthic macroinvertebrate communities (Kilroy et al. 2009; Whitton et al. 2009). In Japan, the genetically closely related diatom *Cymbella janischii* has recently invaded and has raised concerns about its potential impacts on river ecosystems because it forms thick mats similar to those of Didymo (Suzawa et al. 2011; Kato-Unoki et al. 2022; Kato-Unoki et al. 2026). However, the impact of this species on benthic macroinvertebrates has not been fully investigated.

Cymbella janischii is a stalk-forming diatom endemic to the Pacific Northwest (Krammer 2002; Bahls 2007). However, it has recently been recorded outside its native range (Suzawa et al. 2011; Khan-Bureau et al. 2014; Medvedeva and Nikulina 2014). In Japan, *C. janischii* was first discovered in 2006 in the Chikugo River (Suzawa et al. 2011), and its distribution has since expanded (e.g., Suzawa et al. 2011; Kato-Unoki et al. 2022; Mugikura et al. 2022). Beyond impairing scenic value, these blooms raise ecological concerns, including reported adverse effects on *Plecoglossus altivelis*, an economically important algivorous fish in Japan (Ashizawa and Kaji 2019). The mats covering the riverbed are expected to have a particularly significant impact on benthic macroinvertebrates (Khan-Bureau et al.

2016). However, although attached *C. janischii* has been reported to impair the movement of aquatic insects (Hayashi 2023), its effects on community structure remain unknown.

Riverine macroinvertebrate assemblages vary seasonally with life histories and emergence periods and also vary among rivers and among habitats within a river (Vinson and Hawkins 1998; Townsend 2003; Allan et al. 2021). Macroinvertebrates can be further classified into functional categories based on functional traits related to their habitats and modes of life (life types), diets (dietary groups), and modes of food acquisition (functional feeding groups [FFGs]) (Merritt and Cummins 1996; Ohta and Takahashi 1999; Takemon 2005). Analyses of these categories can reveal the functional traits of benthic macroinvertebrates that respond to invasive diatom blooms and help elucidate the mechanisms underlying their responses. Studies of Didymo blooms have accumulated worldwide. Although individual findings differ, probably because of variation in river environments and sampling times, many studies have reported that blooms are associated with changes in community composition, including decreases in Ephemeroptera or in the proportion of EPT (Ephemeroptera, Plecoptera, and Trichoptera), and increases in small invertebrates such as chironomids, oligochaetes, and nematodes (e.g., Larned et al. 2007; Brand and Grech 2020; Bray et al. 2020). However, few studies have jointly evaluated functional structure –such as life types, dietary groups, and FFGs–, and the reported responses are not fully consistent (Larned and Kilroy 2014; Ladrera et al. 2018; Brand and Grech 2020). Consequently, knowledge of which functional categories of benthic macroinvertebrate communities are affected by stalk-forming diatom blooms remains limited.

In this study, we investigated the effects of *C. janischii* cover on benthic macroinvertebrates in two rivers differing in geographic location and season: the Ohyama River in spring and the Zako River in autumn (Fig. 1). Within each river, we selected nearby cobbles with high and low *C. janischii* cover to limit environmental variation unrelated to the bloom. We then evaluated macroinvertebrate diversity, taxonomic community composition, and functional structure based on life types, dietary groups, and FFGs. This study elucidates the effects of *C. janischii* cover on benthic macroinvertebrates in the two rivers and provides a case study of the effects of an invasive, mat-forming stalked diatom other than Didymo on these communities.

Materials and methods

Study sites and macroinvertebrate sampling

Surveys were conducted downstream of Matsubara Dam in the Ohyama River, part of the Chikugo River system (Ohyama: 33.195789° N, 130.994871° E), and in the Zako River, part of the Shinano River system (Zako: 36.766050° N, 138.536624° E) (Fig. 1a). Blooms of *C. janischii* have been observed in the Ohyama and Zako rivers since 2010 and 2022, respectively (Suzawa et al. 2011; Takeuchi et al. 2024). Samples were collected from April to May 2024 at Ohyama and in October 2024 at Zako. At Ohyama, six cobbles with visually estimated *C. janischii* cover of ≥ 95% (high-cover group, H) and five cobbles with cover of ≤ 20% (low-cover group, L) were selected in high- and low-cover areas, respectively (11 samples in total;

Fig. 1b). At Zako, because *C. janischii* cover was spatially variable, four cobbles with cover ≥ 90% (H) and nine cobbles with varying levels of cover ranging from 0 to 60% (L) were selected at two locations approximately 50 m apart (13 samples in total; Fig. 1b, c). Cobbles were selected for 15–25 cm along their longest axis. Detailed information on the samples is provided in Table S1. Macroinvertebrates living on each cobble surface and on the riverbed immediately beneath it were collected with a D-frame net (30 cm width, 0.5 mm mesh size) held downstream.

The collected material was spread in a tray, and macroinvertebrates were hand-picked with forceps and preserved in 99.5% ethanol. When the residue contained large numbers of chironomids, the tray was photographed, the residue was recollected in the net, drained, transferred to a zipper bag, and preserved in 99.5% ethanol. Samples were transported at 4°C and subsequently stored at − 20°C.

Environmental variables

To evaluate whether differences in community exist between habitats due to environmental factors other than *C. janischii* cover, in addition to visually estimating *C. janischii* cover on the exposed surface of each cobble (%), we measured water temperature (°C), water depth (cm), and current velocity (cm/s) (Table S1). These were used as environmental variables in the analysis of community composition. Water temperature was measured using an APERA PC60-Z meter (Apera Instruments, Tokyo, Japan). Current velocity was measured as the 10-s mean using a VR-301 propeller-type current meter (KENEK, Tokyo, Japan).

Identification and functional classification

Macroinvertebrates were identified by a specialist at CTI Lead Co., Ltd. (Saitama, Japan). Identification followed the 2016 Manual for the National Survey for River and Riparian Environments (River Edition) and the latest Biological Species List for the National Survey for River and Riparian Environments available on 26 November 2025 (https://www.nilim.go.jp/lab/fbg/ksnkankyo/mizukokuweb/system/seibutsuListfile.htm). For each cobble, the number of individuals was standardized per 100 cm² based on the projected area estimated from the cobble's long and short axes. Individuals ≤ 3 mm in body length were excluded because newly hatched larvae sometimes occurred in very large numbers. Dipterans retained with the residue at Ohyama were not identified individually; when their abundance exceeded 40 per 100 cm² of projected area, it was recorded as > 40.

Functional categories within three classification schemes (life types [Swimmers, Crawlers, Burrowers, Net-spinners, Clingers, Case-bearers, Surface dwellers, Parasites], dietary groups [Algal feeder, Detritus feeder, Predator/Parasite, Omnivore, Herbivore], and FFGs [Filter-feeder, Collector-gatherer, Grazer (Scraper), Predator, Shredder, Piercer, Parasite]) were assigned based primarily on the following references: Merritt and Cummins (1996); Ohta and Takahashi (1999); Takemon (2005), and

supplemented by ecological observations (Tables S2 and S3). For species with unknown functional category assignments, assignments at the genus or family level were used. Taxa whose functional category assignments remained unknown—or that were assigned three or more functional traits at the family or genus level—were excluded from the functional analyses. Accordingly, Diptera were excluded from all functional structure analyses in both rivers. The functional assignments were summarized as classification scores, with each individual contributing one point to every applicable category. Thus, an individual assigned to multiple dietary groups or FFGs contributed one point to each applicable group. The scores summed for each cobble were then standardized per 100 cm² of projected area, as for taxon abundance.

Statistical analyses

Changes in diversity, community composition, taxonomic groups, and functional structure (life types, dietary groups, and FFGs) for H and L were analyzed using the analysis software R (Ver. 4.4.3) and its packages vegan (ver. 2.6-8), tidyverse (ver. 2.0.0), ggrepel (ver. 0.9.6), and grid (ver. 4.4.3; R Core Team, 2025) as follows. Statistical significance was set at $p < 0.05$. Exploratory interpretations were provided for nonsignificant correlations with $|r|$ or $|\rho| \geq 0.4$ and for comparisons yielding $|t| \geq 2.0$.

Community composition was visualized by non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarities, with a maximum of 100 random starts. Differences between the H and L groups within each river were tested by permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities. To aid interpretation of PERMANOVA, homogeneity of multivariate dispersion was evaluated using PERMDISP. PERMDISP used distances from samples to the spatial median of each group and applied a small-sample bias adjustment. Significance of PERMANOVA and PERMDISP was evaluated with 999 permutations. Species and environmental variables (*C. janischii* coverage, water depth, current velocity, and water temperature) were fitted to the ordinations using 999 permutations, and significant vectors ($p < 0.05$) were displayed.

Diversity was assessed using Rényi diversity profiles. In the analyses of taxonomic (order) and functional structure, categories detected in two or fewer samples (cobbles) were excluded from the analyses. Diptera were excluded from functional structure analysis as described above. At Ohyama, diversity metrics and measures of taxonomic and functional structure were displayed as boxplots for the H and L groups and compared using Welch's t-tests. Contrasts were calculated as H minus L; thus, negative *t*-values indicated lower values in H than in L. At Zako, associations between these response variables and *C. janischii* coverage were evaluated using correlation analyses, with coverage treated as the explanatory variable because it varied continuously. Variables underwent log-transformation to improve normality where necessary; Pearson's product-moment correlation was used when both explanatory and response variables were normally distributed; otherwise, Spearman's rank correlation was used. For functional categories showing significant responses, the same analyses were repeated separately by taxonomic order in those categories to identify the organisms responsible for the response.

Results

Diversity and community composition

A total of 9 orders, 14 families, and 27 taxa (including 19 species) were identified from 11 cobbles at Ohyama (Table S2). At Zako, 5 orders, 16 families, and 32 taxa (including 15 species) were identified from 13 cobbles (Table S3). At Ohyama, diversity was significantly lower in H than in L for all diversity orders examined (Fig. 2a), indicating a shift in community composition accompanied by reduced diversity. At Zako, none of the Rényi diversity measures was significantly associated with *C. janischii* coverage, although all estimated correlation coefficients were negative (Fig. 2b).

The nMDS stress values were 0.105 for Ohyama and 0.210 for Zako (Fig. 3). PERMANOVA showed significant differences in community composition between L and H in both rivers (Table 1). At Ohyama, the difference was pronounced (PERMANOVA: $F = 20.347$, $R^2 = 0.693$, $p = 0.004$; Table 1). Multivariate dispersion was significantly lower in H (mean distance = 0.038) than in L (0.428; PERMDISP: $F = 19.696$, $p = 0.001$; Table 1). As shown in Fig. 3a, species significantly associated with the Ohyama ordination were Diptera sp. ($p = 0.001$), *Teleganopsis punctisetae* (Ephemeroptera; $p = 0.006$), *Stenopsyche marmorata* (Trichoptera; $p = 0.008$), *Torleya japonica* (Ephemeroptera; $p = 0.023$), *Ephemerella ishiwatai* (Ephemeroptera; $p = 0.026$), *Cheumatopsyche infascia* (Trichoptera; $p = 0.032$), and *Rhyacophila yamanakensis* (Trichoptera; $p = 0.036$). Diptera sp. was more abundant toward H, whereas all other significant taxa were associated with L. Among environmental variables, *C. janischii* coverage was associated with H ($p = 0.002$) and water depth with L ($p = 0.002$); water temperature ($p = 0.281$) and current velocity ($p = 0.767$) were not significant.

Table 1
PERMANOVA and PERMDISP results for benthic macroinvertebrate communities in the H and L groups at Ohyama and Zako

Analysis	Ohyama	Zako
PERMANOVA		
F	20.347	2.648
Pr (> *F*)	0.004	0.006
R^2	0.693	0.194
PERMDISP		
F	19.696	0.068
Pr (> *F*)	0.001	0.800
Group L mean distance to median	0.428	0.417
Group H mean distance to median	0.038	0.400

At Zako, community composition also differed significantly between groups (PERMANOVA: $F = 2.648$, $R^2 = 0.194$, $p = 0.006$; Fig. 3b). Multivariate dispersion did not differ between L (mean distance = 0.417) and H (0.400; PERMDISP: $F = 0.068$, $p = 0.800$). Taxa significantly associated with the ordination were *Rhyacophila kisoensis* (Trichoptera; $p = 0.010$), Orthocladiinae sp. (Diptera; $p = 0.024$), *Tadamus* sp. (Plecoptera; $p = 0.026$), and *Stenopsyche marmorata* (Trichoptera; $p = 0.048$). As at Ohyama, only the dipteran Orthocladiinae sp. was associated with H. None of the measured environmental variables was significantly related to the Zako ordination.

Taxonomic and functional responses

The results of the taxonomic analyses are shown in the top-row graphs in Fig. 4a and 4b. At Ohyama, Ephemeroptera was significantly less abundant in H ($t = -4.527$, $p = 0.002$), whereas Diptera increased ($t = 86.719$, $p < 0.001$). Trichoptera tended to decrease ($t = -2.328$, $p = 0.070$), and Plecoptera showed little change ($t = -1.079$, $p = 0.333$). At Zako, Ephemeroptera ($r = -0.633$, $p = 0.020$) and Trichoptera ($r = -0.626$, $p = 0.022$) were negatively correlated with *C. janischii* coverage. Diptera showed a nonsignificant positive tendency ($r = 0.405$, $p = 0.170$), whereas Plecoptera showed little relationship with cover ($r = -0.199$, $p = 0.514$).

The results of the functional category analyses are shown in the graphs starting from the second row in Fig. 4a and 4b. In the life types, Crawlers decreased in both rivers (Ohyama: $t = -4.314$, $p = 0.008$; Zako: $r = -0.658$, $p = 0.014$). Net-spinners were negatively correlated with cover at Zako ($r = -0.562$, $p = 0.046$) and tended to decrease at Ohyama ($t = -2.271$, $p = 0.076$). Swimmers (Ohyama: $t = -0.486$, $p = 0.647$; Zako: $\rho = 0.224$, $p = 0.463$) and burrowers, which were analyzed only at Ohyama ($t = -1.843$, $p = 0.109$), showed no significant response. For the dietary groups and FFGs, Detritus feeder (Ohyama: $t = -4.499$, $p = 0.002$; Zako: $r = -0.585$, $p = 0.036$), Predator/Parasite (Ohyama: $t = -2.739$, $p = 0.033$; Zako: $r = -0.557$, $p = 0.048$), and Predator (Ohyama: $t = -2.739$, $p = 0.033$; Zako: $r = -0.561$, $p = 0.046$) decreased significantly in H or were negatively correlated with cover in both rivers. In addition, Collector-gatherer decreased significantly at Ohyama ($t = -4.189$, $p = 0.005$), whereas Algal feeder ($r = -0.612$, $p = 0.026$), Filter feeder ($r = -0.562$, $p = 0.046$), and Grazer ($r = -0.612$, $p = 0.026$) decreased significantly at Zako. Omnivore ($r = -0.551$, $p = 0.051$) and Collector-gatherer ($r = -0.548$, $p = 0.053$) also tended to decrease at Zako. In contrast, Algal feeder ($t = -0.142$, $p = 0.891$) and Grazer ($t = -0.142$, $p = 0.891$) showed no clear difference between H and L at Ohyama.

Order-level analyses within functional categories that showed significant responses are shown in Fig. 5. At Ohyama, the decline in Crawlers was attributable to a significant decrease in Ephemeroptera ($t = -3.049$, $p = 0.031$) and a tendency toward a decrease in Trichoptera ($t = -2.338$, $p = 0.051$). Ephemeroptera also decreased significantly among Detritus feeder ($t = -4.527$, $p = 0.002$) and Collector-gatherer ($t = -3.838$, $p = 0.008$), whereas Trichoptera tended to decrease among Predator/Parasite ($t = -2.338$, $p = 0.051$). At Zako, Ephemeroptera declined significantly among Crawlers ($r = -0.643$, $p = 0.018$), Algal feeder ($r = -0.612$, $p = 0.026$), Predator/Parasite ($\rho = -0.702$, $p = 0.007$), Grazer ($r = -0.612$, $p = 0.026$), and Predator ($\rho = -0.747$, $p = 0.003$). Trichoptera declined significantly among Net-spinners ($r = -0.562$, $p =$

0.046) and Filter-feeder (r = -0.562, p = 0.046). Nonsignificant negative tendencies were also observed for Ephemeroptera among Detritus feeder (r = -0.537, p = 0.058) and for Trichoptera among Predator/Parasite (ρ = -0.508, p = 0.077). Plecoptera did not decrease significantly in any category in either river.

Discussion

Common responses of diversity and community composition

At Ohyama, a significant loss of diversity was observed in H (Fig. 2a), whereas at Zako, diversity showed a negative but nonsignificant correlation with coverage (Fig. 2b). Community composition differed significantly between H and L in both rivers (Fig. 3). Furthermore, at Ohyama, dispersion within H was substantially lower than within L (Fig. 3a and Table 1), indicating community homogenization under high cover. Among the taxonomic groups, Ephemeroptera and Trichoptera decreased or tended to decrease in both rivers, whereas Diptera increased or tended to increase (Fig. 4). Taxa belonging to these orders also characterized the multivariate differences: several ephemeropteran and trichopteran taxa were associated with L, whereas dipteran taxa were associated with H in both rivers (Fig. 3). These responses broadly resemble those reported for the invasive stalk-forming diatom Didymo. Didymo blooms have been associated with shifts in community composition and taxonomic homogenization (e.g., Kilroy et al. 2009; Ladrera et al. 2018; Brand and Grech 2020), together with decreases in the proportion of EPT and increases in small-bodied groups such as Chironomidae, Oligochaeta, and Nematoda (e.g., Larned et al. 2007; Brand and Grech 2020; Bray et al. 2020). Our findings suggest that blooms of *C. janischii* can produce broadly comparable effects.

Possible mechanisms inferred from functional structure

The functional structure analysis excluding Diptera suggested that physical alteration of the riverbed by *C. janischii* mats affected the life and feeding characteristics of benthic macroinvertebrates. Crawlers decreased in both rivers, and Net-spinners decreased or tended to decrease (Fig. 4); an analysis of taxonomic groups of these types revealed that these responses were linked to Ephemeroptera and Trichoptera losses (Fig. 5). This was likely because the *C. janischii* cover of stone surfaces reduced suitable habitats for crawling and net construction, thereby affecting taxa with these life types. In contrast, large numbers of Diptera, chironomids, occurred within the mats at Ohyama. As reported for Didymo, the interstitial spaces created by *C. janischii* stalks may provide both habitat and food for small-bodied invertebrates (Kilroy et al. 2009; Ladrera et al. 2018; Brand and Grech 2020). In fact, in field and microscopic observations, no impairment of movement was observed in small, flexible-bodied organisms with no or short legs, such as chironomids; they were also observed feeding within the mat. Swimmers, which in both rivers consisted of Ephemeroptera (Supplementary Tables S2 and S3), did not respond significantly to the cover. A similar contrast has been reported for Didymo: crawling mayflies decreased as Didymo increased, whereas swimming mayflies showed no clear response (Brogan et al.

2024). This study also suggested that Swimmers may be less susceptible to the effects of *C. janischii* cover.

In the dietary groups and FFGs, Detritus feeder, Predator/Parasite, and Collector-gatherer decreased or tended to decrease in both rivers, and Algal feeder, Filter-feeder, and Grazer also declined at Zako (Fig. 4). Order-level analyses showed that these responses primarily reflected decreases in Ephemeroptera and/or Trichoptera assigned to the corresponding functional categories, whereas Plecoptera showed no significant change (Fig. 5). Thus, the reorganization of functional structure was closely linked to the loss of Ephemeroptera and/or Trichoptera assigned to those functional categories.

Environmental factors

We examined relationships between community composition and water temperature, water depth, and current velocity to investigate environmental differences other than *C. janischii* cover. Water temperature and current velocity have been related to macroinvertebrate community patterns in some Didymo studies (e.g., Kilroy et al. 2009; Sanmiguel et al. 2016; Green et al. 2019; Bray et al. 2020), but neither variable was related to community composition in either river here. This indicates that variation in these environmental conditions among the sampled cobbles remained within a range that did not affect the community composition, suggesting that the sampling design was suitable for isolating associations with *C. janischii* cover. At Ohyama, in addition to *C. janischii* cover, water depth was associated with community composition, with L being slightly deeper than H (L: mean 23.4 cm, SD 1.5; H: mean 18.7 cm, SD 1.9). This difference probably arose because sampling sites L and H were in distinct, spatially restricted areas. Although the difference was less than 5 cm and was unlikely to represent an environmental factor driving community shift, the independent effect of depth requires future investigation.

Differences between rivers

In the more recently invaded Zako, diversity did not decline significantly with increasing coverage, although community composition changed significantly and the abundances of several taxonomic orders and scores for several functional categories decreased. Community composition can respond more sensitively than taxon richness or diversity indices and may therefore reveal ecological change before clear diversity loss becomes detectable (Schindler 1987; Dornelas et al. 2014; Hillebrand et al. 2018). Zako results may represent such an early response. Furthermore, because changes in benthic community structure have been reported to persist even after Didymo blooms have subsided (Sanmiguel et al. 2016), future changes in community structure at Zako should be closely monitored. In addition, Zako supports a wild population of white-spotted charr managed without stocking (Nakamura and Iida 2009). Further research is needed to assess the potential effects of *C. janischii* blooms on this population.

Algal feeder and Grazer declined significantly at Zako but were already uncommon at the low-cover Ohyama sites and did not differ between H and L. The Ohyama site lies immediately downstream of a dam and has experienced extensive *C. janischii* blooms over a long period. Consequently, these

categories may already have been depleted throughout the surrounding reach. Additionally, downstream macroinvertebrate communities can also be affected by dam-related changes in benthic algal communities and their accumulation (Ward and Stanford 1983; Tanida and Takemon 1999), and additional changes in macroinvertebrate communities have been reported where Didymo blooms occur downstream of dams (Ladrera et al. 2015). However, since the Ohyama study compared only H and L sites and did not independently evaluate the effects of the dam, the reason for the low abundances of these categories at the L sites remains unclear.

Conclusions

This study demonstrated that *C. janischii* cover can lead to reduced benthic macroinvertebrate diversity, changes and simplification of community structure, and alterations in functional structure. It also showed that *C. janischii*, a mat-forming stalked diatom distinct from Didymo, can have effects similar to those of Didymo. These findings suggest that such responses may represent common ecological consequences of blooms of mat-forming stalked diatom. However, this study was limited to two rivers that differed in geographic setting and sampling season, and the sample sizes were relatively small. Therefore, further validation using data collected from a wider range of environmental conditions is needed to determine the extent to which these findings can be generalized and whether such effects are common to Didymo and other mat-forming stalked diatoms.

Declarations

Competing interests

The authors declare no competing interests.

Ethics approval and consent to participate

This study did not involve human participants or animal experiments.

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Author Contribution

YK: Conceptualization, Methodology, Investigation, Formal analysis, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing. YH: Methodology, Resources, Writing –

review & editing. NK and TT: Investigation, Writing – review & editing. JT: Funding acquisition, Writing – review & editing. SS: Resources, Writing – review & editing

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Data Availability

All data supporting the findings of this study are available within the paper and its supplementary materials.

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Figures

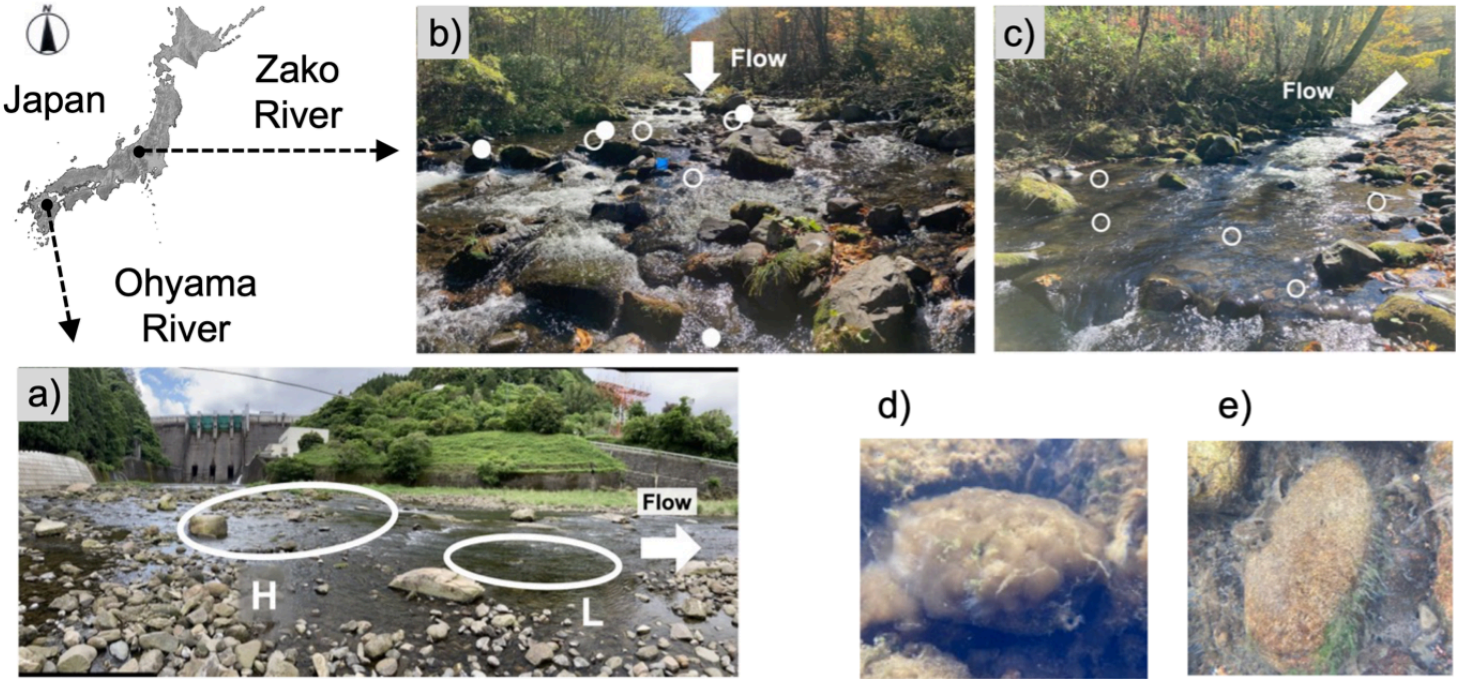


Figure 1

Overview of the sampling sites. (a) Sampling site at Ohyama shown in a panoramic photograph. H indicates the area where cobbles with high *C. janischii*cover (≥ 95%) were collected, and L indicates the area where cobbles with low cover (≤ 20%) were collected. (b, c) Two sampling locations at Zako; location (c) was approximately 50 m downstream of location (b). Filled white circles indicate cobbles with high *C. janischii*cover (≥ 90%), and open white circles indicate cobbles assigned to the low-to-moderate group (0–60%). Arrows indicate flow direction. Examples of cobbles with high (d) and low (e) *C. janischii* cover

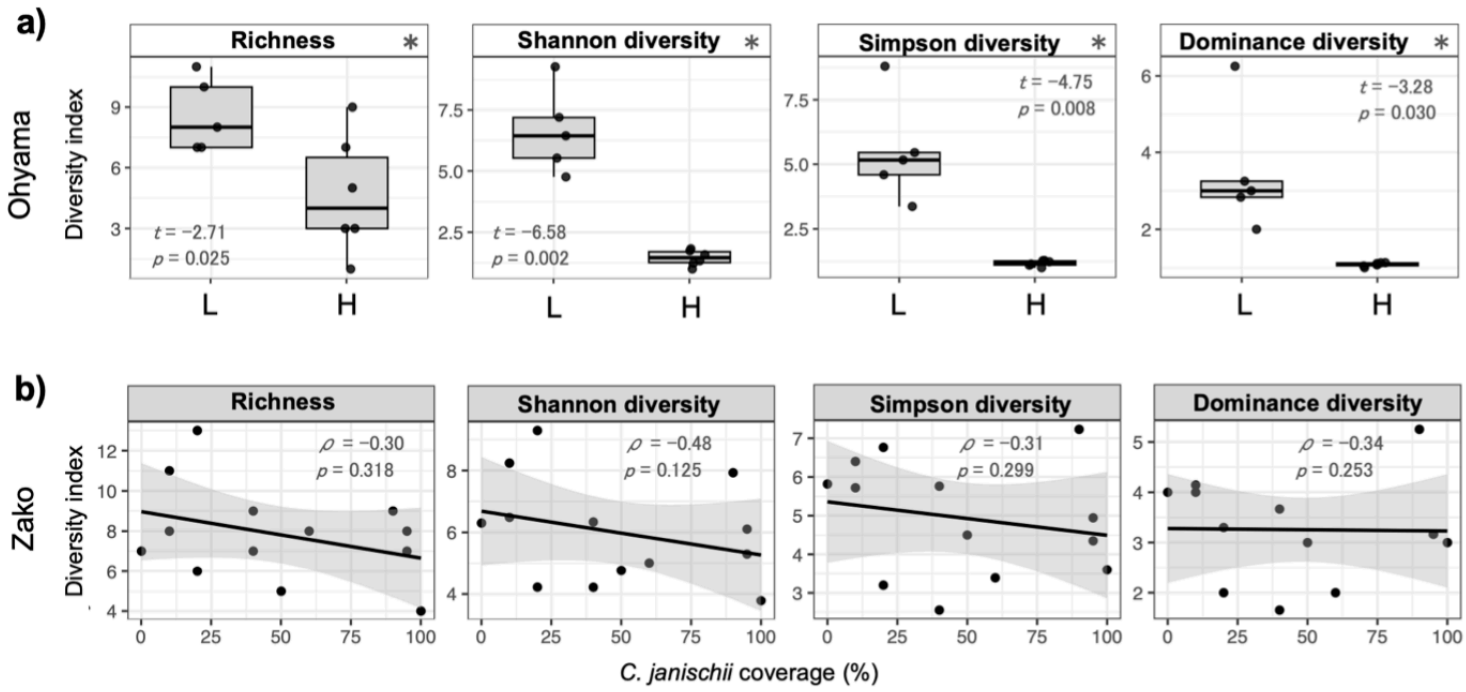


Figure 2

Diversity of macroinvertebrates. (a) Diversity indices in the low-cover (L) and high-cover (H) groups at Ohyama (*n*= 11). Values of *t* and *p* are from Welch's t-tests calculated as H minus L. (b) Relationships between *C. janischii* cover and diversity indices at Zako (*n* = 13). Values of "*ρ*" and "*p*" are Spearman's rank correlation coefficient and its *p*value. Asterisks indicate statistical significance ($p < 0.05$)

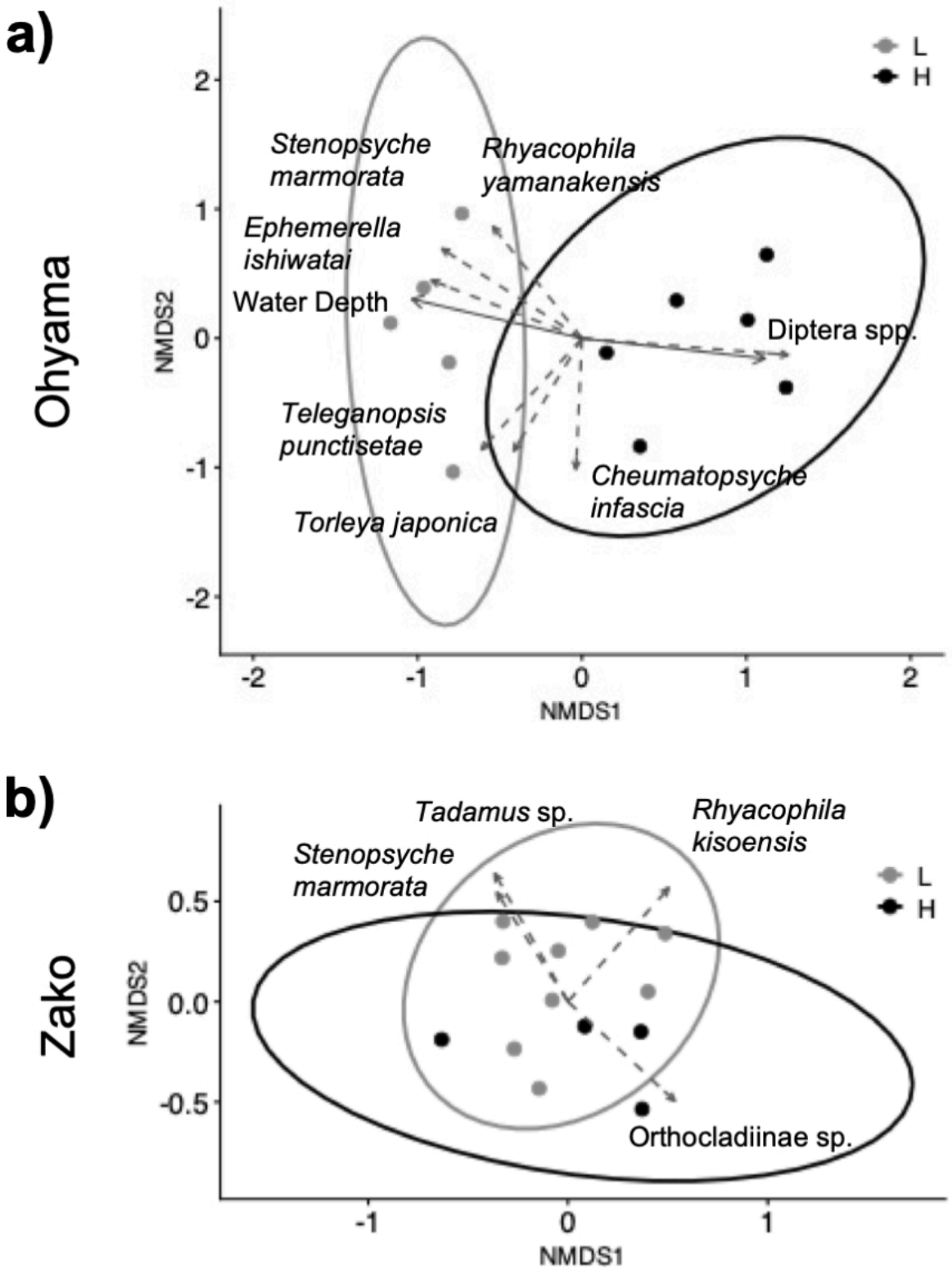


Figure 3

Non-metric multidimensional scaling (nMDS) ordinations of macroinvertebrate communities at Ohyama and Zako. (a) Ohyama. (b) Zako. Low- (L) and high-cover (H) samples are indicated by gray and black circles, respectively; ellipses show 95% confidence regions. Vectors indicate taxa (dashed) and environmental variables (solid) significantly associated with community composition ($p < 0.05$)

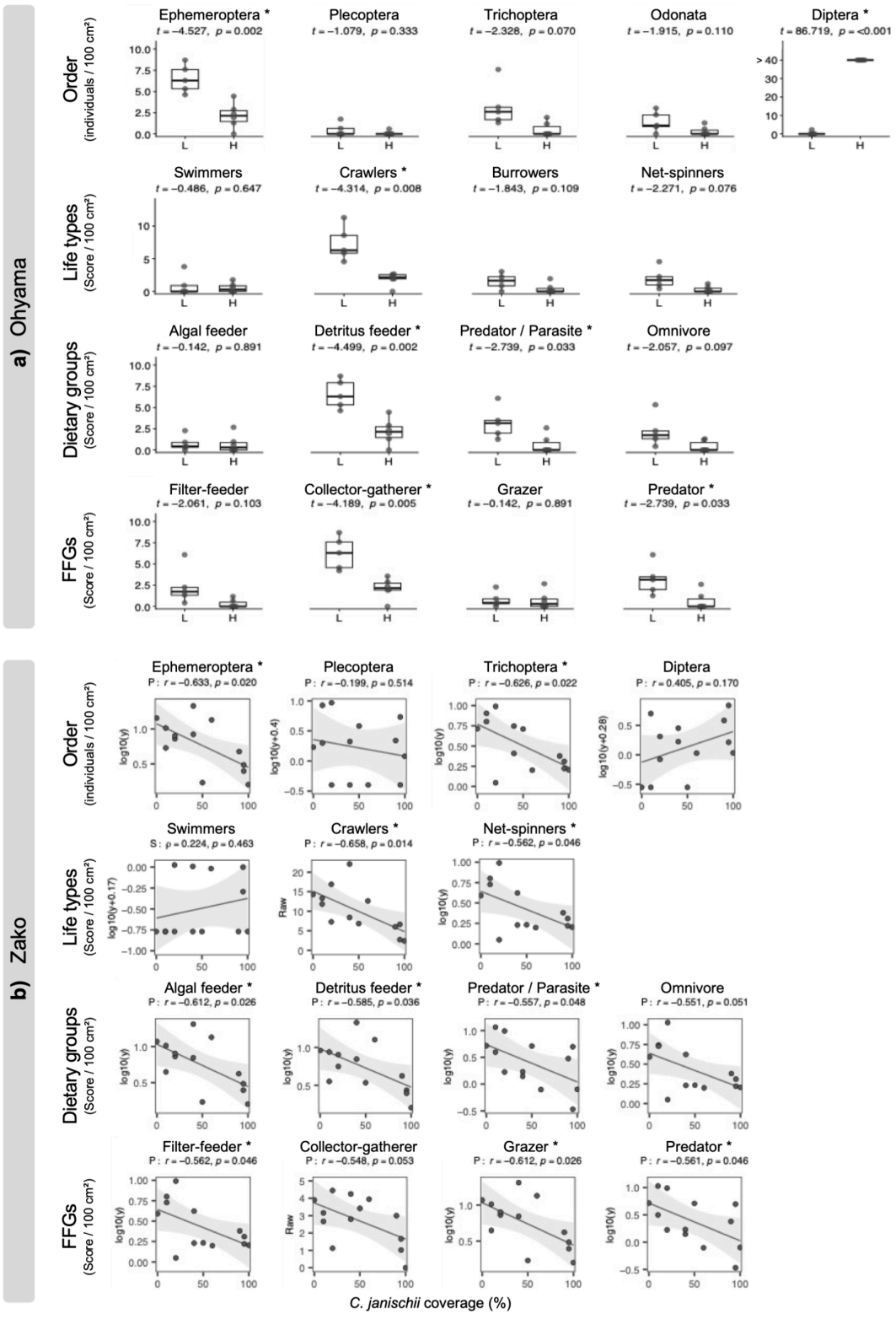


Figure 4

Taxonomic and functional responses of benthic macroinvertebrates to *C. janischii* cover at Ohyama and Zako. (a) Boxplots comparing low-cover (L) and high-cover (H) samples at Ohyama (*n* = 11). Values of *t* and *p* are from Welch's t-tests calculated as H minus L. (b) Correlations between the abundance of each taxonomic order or the score for each functional category and *C. janischii* cover at Zako (*n* = 13). Gray shading indicates the 95% confidence interval. “P” and “S” denote Pearson and Spearman correlations,

respectively; "*r*" or "*ρ*" is the corresponding correlation coefficient. Units are individuals per 100 cm^2 for taxonomic orders and scores per 100 cm^2 for functional categories. Y-axis labels indicate whether raw or log10-transformed values are shown. Asterisks indicate $p < 0.05$

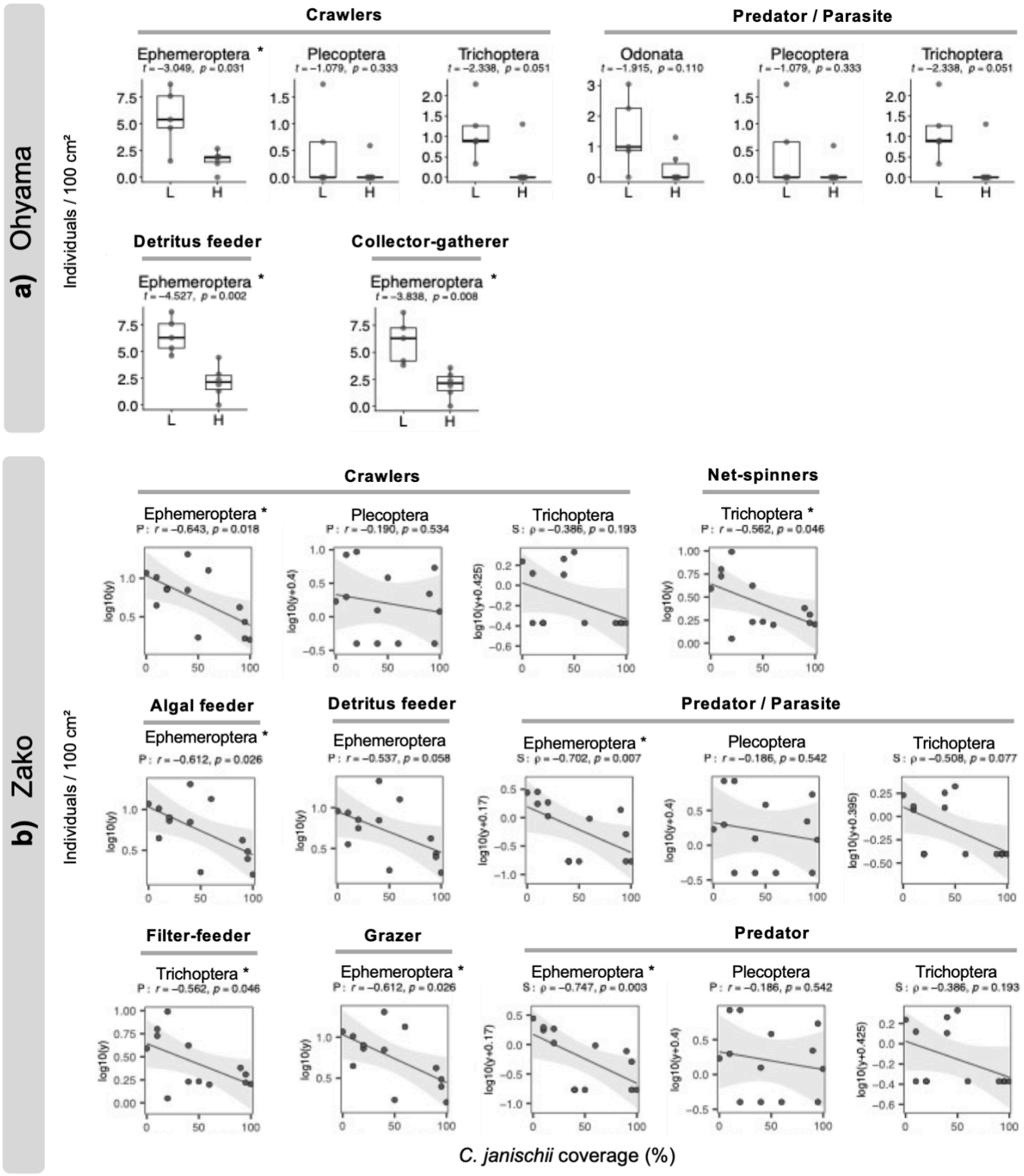


Figure 5

Order-level composition of functional categories that showed significant responses in Fig. 4. (a) Ohyama (*n* = 11). (b) Zako (*n* = 13). Functional category names are shown above groups of panels, and taxonomic order names above individual panels. Other notation follows Fig. 4

Supplementary Files

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