Spatial heterogeneity of trophic pathways in the invertebrate community of a temperate bog

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SUMMARY
1. To examine spatial heterogeneity of trophic pathways on a small scale (<5 m diameter), we conducted dual stable isotope (δ¹³C and δ¹⁵N) analyses of invertebrate communities and their potential food sources in three patchy habitats [sphagnum lawn (SL), vascular-plant carpet (VC) and sphagnum carpet] within a temperate bog (Mizorogaike Pond, Kyoto, Japan).

2. In total, 19 invertebrate taxa were collected from the three habitats, most of which were stenotopic, i.e. collected from a single habitat. Amongst the habitats, significant variation was observed in the isotopic signatures of dominant plant tissues and their detrital matter [benthic particulate organic matter (BPOM)], both of which were potential organic food sources for invertebrates. Site-specific isotopic variation amongst detritivores was found in δ¹³C but not in δ¹⁵N, reflecting site-specificity in the isotopic signatures of basal foods. The eurytopic hydrophilid beetle Helochares striatus was found in all habitats, but showed clear site variation in its isotopic signatures, suggesting that it strongly relies on foods within its own habitat.

3. The most promising potential foods for detritivores were the dead leaf stalks of a dominant plant in the VC and BPOM in the SL and carpet. An isotopic mixing model (IsoSource version 1.3.1) estimated that aquatic predators rely on unknown trophic sources with higher δ¹³C than detritus, whereas terrestrial predators forage on allochthonous as well as autochthonous prey, suggesting that the latter predators might play key roles in coupling between habitats.

4. Our stable isotope approach revealed that immobile detritivores are confined to their small patchy habitats but that heterogeneous trophic pathways can be coupled by mobile predators, stressing the importance of habitat heterogeneity and predator coupling in characterising food webs in bog ecosystems.

Keywords: compartmentalisation, coupling, food web, peatland, stable isotopes

Introduction

Ecologists are interested in how spatial heterogeneity in the environment affects community organisation and food-web structure (Persson et al., 1992; Polis, Anderson & Holt, 1997; Thompson & Townsend, 2005). Spatial variability in trophic organisation has been reported in a variety of ecosystems (e.g. marine: Vetter, 1998; Pakhomov et al., 2004; terrestrial: Moore & de Ruiter, 1991; freshwater: Stone & Wallace, 1998; Garvey et al., 2003). The primary factors responsible for this pattern include heterogeneity of biotic and abiotic environments within habitats, for example,
Peatland ecosystems have recently received attention because of their unique fauna and flora, including many rare and endemic species (Rosenberg & Danks, 1987; Finnimore & Marshall, 1994; Rydin & Jeglum, 2006; Spitzer & Danks, 2006; Warner & Asada, 2006). The ecological attributes of peatland plant communities are well studied, particularly in terms of species diversity (Warner & Asada, 2006), ecological interactions between plant species (Vanbreemen, 1995; Ohlson et al., 2001; Malmer et al., 2003) and ecosystem function as a carbon sink (Harden et al., 1997; Weltzin et al., 2001). One of the most striking features of peatland ecosystems is their spatial heterogeneity in vegetation (Nungesser, 2003; Warner & Asada, 2006). Because of strong dependence on their environment, few plant species characterise specific vegetation types, serving as good indicators for local abiotic conditions such as pH, wetness and water level (Sjörs, 1948; Jeglum, 1971; Gignac et al., 1991; Nicholson & Gignac, 1995; Tiner, 1999). These indicator species form two unique vegetation types, ‘hummock’ and ‘hollow’, characteristic of bog (ombrotrophic and nutrient-poor peatland) ecosystems (Wheeler & Proctor, 2000; Gunnarsson, Malmer & Rydin, 2002; Belyea & Baird, 2006). The hummock–hollow transition is defined by the elevation of the ground surface above the water table (Sjörs, 1948). Hummocks are 5–50 cm above the water table and are characterised by dwarf shrubs and peat mosses, whilst hollows occur below the water table and are dominated by vascular plants and bryophytes tolerant of water-logged conditions. Such patchiness of vegetation types provides spatially heterogeneous habitats for invertebrate communities in bog ecosystems, often resulting in patchy distributions of immobile small animals (e.g. Batzer & Wissinger, 1996; Lamentowicz & Mitchell, 2005). Considering that spatial variability of plant-derived matter can influence the site-specificity of trophic pathways, patchy and heterogeneous vegetation might create a mosaic of local communities within bog ecosystems, leading to food-web compartmentalisation.

To determine the configuration of food webs in bog ecosystems, one of the best techniques is dual stable isotope (δ13C and δ15N) analysis of consumers and their basal food resources. In bog ecosystems, invertebrate communities are generally dominated by detritivorous groups (Rosenberg & Danks, 1987). For this group of animals feeding on detritus in bogs,
determining food sources on the basis of gut contents is difficult. However, stable isotope analysis is a powerful tool for disentangling complicated trophic relationships in invertebrate communities, especially between detritivores and their food sources (France, 1996; Hershey et al., 2006; Solomon et al., 2008; Zeug & Winemiller, 2008). This method is based on the fundamental assumptions that basal foods derived from primary products show unique isotopic signatures that depend on plant physiology and the geochemical environment (Maberly, Raven & Johnston, 1992), that consumers fractionate the carbon and nitrogen isotope ratios of their foods in predictable ways (DeNiro & Epstein, 1978, 1981) specific to taxonomic and functional feeding groups (Vandeklif & Ponsard, 2003) and that consumers’ isotopic signatures reflect the mass balance of assimilated foods, enabling estimation of the relative contributions of multiple food sources with a mixing model (Phillips, 2001). Stable isotope analysis can also integrate consumers’ dietary information over time periods from weeks to years, depending on body size and turnover rate, an advantage over gut content analysis, which can only detect the current diet.

In this study, we characterised the food-web structure in the temperate bog ecosystem of Mizorogaike Pond, Kyoto, Japan, using carbon and nitrogen stable isotope analysis. We demonstrate compartmentalisation of food webs into patchy habitats associated with vegetation types on the bog and habitat coupling mediated by mobile predators, focusing on the spatial heterogeneity of trophic pathways on the scale of a few metres.

**Methods**

The field study was conducted in Mizorogaike Pond (Fig. 1; 9 ha, 1 km in circumference) located in northern Kyoto City (35°03’N, 135°50’E; 75 m a.s.l.), Japan. This pond contains a large (5 ha) floating mat that is held afloat by gases such as methane and carbon dioxide, emitted by the decomposition of terrestrial organic matter. The vegetation on the floating mat contains two peat moss species, *Sphagnum cuspidatum* Ehrh. and *S. palustre* L., and some emergent plants (Fujita & Endo, 1994). *Sphagnum cuspidatum* and the emergent bogbean *Menyanthes trifoliata* L. predominate in hollows and are patchily distributed (Investigation Group for Mizorogaike Pond in the Research Institute of Plant Biology in Kyoto University, 1981), whilst *S. palustre* predominates in hummocks.

In this study, we define three types of vegetation [sphagnum lawn (SL), vascular-plant carpet (VC) and sphagnum carpet (SC)] as habitats for bog-dwelling invertebrates (Fig. 2). A SL is the edge of a hummock dominated by *S. palustre*. The centre of the hummock was not considered a specific habitat since it was so elevated and dry that bog-dwelling aquatic invertebrates were not found there. A VC is a muddy flat hollow dominated by *M. trifoliata*. A SC is a flat hollow covered with *S. cuspidatum*. To characterise the abiotic environmental features of each habitat, we established 10 monitoring sites covering these three habitats within a 5-m-diameter area (Fig. 1b). We measured water temperature, pH, electrical conductivity (EC), dissolved oxygen (DO) and the elevation of the peat surface above the water table on 6 November 2006. We used the following instruments for the environmental measurements: Horiba D-50 (Horiba Ltd., Kyoto, Japan) for pH, YSI model 30 (YSI/Nanotech Inc., Kawasaki, Japan) for EC and YSI model 550A (YSI/Nanotech Inc.) for DO and water temperature. We tested for differences in environmental variables amongst habitat types using one-way ANOVA. Principal components analysis (PCA) was also used to determine how the environmental characteristics differed amongst the three habitat types.

We collected animal specimens for stable isotope analysis at one of the 10 monitoring sites, site no. 1 (Fig. 1b), from 23 November to 1 December 2006. At this sampling site, we collected macro- and meioinvertebrates from each of the three habitats by handpicking. We collected animals for 2 h at each habitat type with the same sampling effort. Handpicking is not a quantitative sampling method but is effective in obtaining presence/absence data for each species. Aquatic invertebrates were all kept in pond water, filtered through a 125-µm mesh sieve, for approximately 24 h to allow for gut content excretion. Terrestrial invertebrates were kept in Petri dishes for approximately 24 h to allow for excretion. We identified these animal specimens to the species or genus level, according to Wiederholm (1983), Ueno, Kurosawa & Sato (1985), Merritt & Cummins (1996), Mori & Kitayama (2002) and Kawai & Tanida (2005). These animals were categorised into two groups, eurytopic and stenotopic taxa, based on their distribution on the
floating mat. Eurytopic taxa were defined as those found in two or more habitat types and stenotopic taxa as those found in a single habitat. Details of bog-dwelling invertebrate communities in this pond is reported in Kato, Takemon & Hori (2009), which demonstrates a high habitat specificity of its local community structure, thus confirming that our animal community data from one sampling site can be representative of each habitat.

We also collected living and dead plant tissues of the dominant species in five replicates as potential food sources for invertebrates in each habitat: leaves...
of *S. palustre* in the SL, leaves and leaf stalks of *M. trifoliata* in the VC and leaves of *S. cuspidatum* in the SC. As detrital food sources for the invertebrates, benthic particulate organic matter (BPOM) was also collected in five replicates from each habitat. The BPOM was sieved into a size fraction of 0.5–1.0 mm. All these samples were dessicated at 60 °C for 48 h and stored in the desiccator (13 °C, 20% humidity) for the stable isotope analysis.

We ground the samples for isotope analysis into a powder using agate mortar and pestle. For small animal samples whose dry weight was <1 mg, we analysed them in bulk. We measured carbon and nitrogen stable isotope ratios for the living and dead plant samples, BPOM and the animal samples using a mass spectrometer: EA1108 (Fisons, Milan, Italy), conflo II and Delta-S (Finnigan MAT, Bremen, Germany). The stable isotope ratios are expressed in notation as deviations from a standard: δ13C or δ15N = (Rsample/Rstandard — 1) × 1000 (%). Here R is 13C/12C for δ13C or 15N/14N for δ15N. The standards were PeeDee belemnite for δ13C and atmospheric nitrogen for δ15N. We used DL-alanine as working standard. The analytical precision was ± 0.2‰ for δ13C and ± 0.2‰ for the δ15N.

To examine variation amongst habitats in the basal foods of the invertebrate communities, we compared the isotopic values of dead plant tissues and BPOM amongst the three habitat types using one-way ANOVA. We also compared the isotopic signatures of the invertebrate communities amongst habitats to test if they strongly relied on organic matter associated with their habitat. The invertebrate taxa were categorised into two functional feeding groups, detritivores and predators, and analysed separately. We tested for isotopic differences in the detritivore group amongst habitat types by one-way ANOVA, incorporating the mean isotopic value of each taxon as an independent variable. Since the species composition of the invertebrate communities varied greatly amongst habitats (see the Results), their isotopic variation may have been as a result of interspecific differences in food niche determined by phylogenetic constraints rather than because of habitat differences in basal food sources. To test such a possibility, we examined the variation amongst habitats in individual isotopic signatures of the eurytopic hydrophilid beetle *Helochares striatus* Sharp. If its inter-habitat variation was significant and corresponded to isotopic variation in its basal foods amongst habitat types, the spatial pattern could be attributed to its strong reliance on detritus derived from its natal habitat, suggesting that detritivores tend to be confined to patchy habitats.

To determine which potential food sources were assimilated by detritivores, we selected *H. striatus* as the standard detritivore since it appeared in all types of habitat. We estimated the contributions for each possible food source of *H. striatus* and determined the most feasible food source of *H. striatus* as the possible trophic source of other detritivores in the same habitat. Then we calculated the enrichment in δ13C (Δδ13C) and δ15N (Δδ15N) for each detritivore. Since detritivores do not assimilate living plant tissues, we used the δ13C and δ15N of dead plant tissues and BPOM as potential food sources in the SL and the SC. The δ13C and δ15N of dead leaves, dead leaf stalks (DS) and BPOM were used for the VC.

Since the trophic position of predators was unknown, determining which of the potential food sources were assimilated by predators was difficult. Therefore, we estimated the feasible contributions for each food source via isotope mixing models for δ13C using IsoSource version 1.3.1 (Phillips & Gregg, 2003). Essentially, the model iteratively creates all possible combinations of source proportions (with each combination equaling 100%) at preset increments (1% in this study) to create a set of predicted mixtures of sources (see Phillips & Gregg, 2003 for details). For the model, the most feasible trophic sources for detritivores in each habitat (BPOM in the SL and SC; DS in the VC; see the Results) were selected as the potential food sources. Tolerance was initially set at 0.1‰, if mixture isotope values were out of bounds, we incrementally increased the tolerance value by 0.1‰ up to a maximum of 1.0‰. We used enriched (+0.80‰) δ13C values of potential trophic sources for all predators following the Δδ13C of detritivorous invertebrates (+0.4‰, McCutchan et al., 2003). Prior to statistical comparisons, we examined the homogeneity of variance for each data set with a Bartlett test. If criteria for ANOVA were not satisfied, we performed a rank transformation. We used Tukey or Tukey-Kramer tests for post hoc comparisons. For descriptive purposes, means ± SE are given. P values are two-tailed. For all tests, a significance level of 0.05 was used. All statistical analyses were performed in SPSS version 13.0 (SPSS Inc., Chicago, IL, U.S.A.).

Results

Physical and chemical parameters of each habitat type are shown in Table 1. Water temperatures were significantly lower in SC than in VC, whilst DO was significantly higher in SC than in VC and SL. Peat surface height, which is an indicator of dryness, was the only abiotic factor with which to discriminate amongst these three habitats. PCA revealed differences in physical and chemical variables amongst the three habitat types (Fig. 3). PCA axis 1 was related to water temperature, pH, DO and peat surface height, and PCA axis 2 was related to EC. In total, 19 different invertebrate taxa were collected from the three habitats (Table 2): five taxa in the SL, 11 in the VC and 10 in the SC. Species composition was variable amongst habitats, indicating that many species were stenotopic (Table 2). One eurytopic taxon (7%) was shared between the SL and the VC, two (15%) between the SL and carpet and four (31%) between the VC and the SC. The only species that appeared in all habitats was *H. striatus*. Fourteen and five taxa had aquatic and terrestrial life-forms respectively. All habitats included aquatic and terrestrial invertebrates, regardless of environmental features, especially wetness (Tables 1 and 3).

The $\delta^{13}$C and $\delta^{15}$N of invertebrates and their potential trophic sources are shown in Fig. 4. A significant variation was observed amongst sites in the isotopic signatures of dead plant tissue and BPOM (Table 3). The $\delta^{13}$C of BPOM was higher in the SC than in the other two habitats, whereas the $\delta^{15}$N of BPOM was lowest in the SL, intermediate in the VC and highest in the SC. For dead plant tissues, isotopic differences amongst habitats were also significant for both $\delta^{13}$C and $\delta^{15}$N (Table 3). In the VC, the $\delta^{13}$C of

<table>
<thead>
<tr>
<th>Variables</th>
<th>Sphagnum lawn</th>
<th>Vascular-plant carpet</th>
<th>Sphagnum carpet</th>
<th>d.f.</th>
<th>F-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water temperature</td>
<td>11.1 ± 0.4$^{ab}$</td>
<td>11.9 ± 0.5$^{b}$</td>
<td>10.3 ± 0.2$^a$</td>
<td>2, 27</td>
<td>4.74*</td>
</tr>
<tr>
<td>pH</td>
<td>4.3 ± 0.1$^a$</td>
<td>4.5 ± 0.1$^a$</td>
<td>4.4 ± 0.1$^a$</td>
<td>2, 27</td>
<td>1.13</td>
</tr>
<tr>
<td>Conductivity</td>
<td>45.7 ± 5.5$^a$</td>
<td>41.7 ± 2.9$^b$</td>
<td>32.1 ± 3.1$^a$</td>
<td>2, 27</td>
<td>3.02</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>2.9 ± 0.6$^b$</td>
<td>1.6 ± 0.5$^a$</td>
<td>5.0 ± 0.6$^b$</td>
<td>2, 27</td>
<td>9.10**</td>
</tr>
<tr>
<td>Peat surface height</td>
<td>2.3 ± 0.3$^c$</td>
<td>–4.5 ± 0.5$^a$</td>
<td>0.7 ± 0.2$^b$</td>
<td>2, 27</td>
<td>95.35**</td>
</tr>
</tbody>
</table>

Different superscripts across rows denote a significant difference (Tukey’s test, $P < 0.05$) among the habitat types. *$P < 0.05$; **$P < 0.01$ in ANOVA.

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Table 1 Environmental conditions (mean ± SE) for each vegetation types ($n = 10$) on the floating mat in Mizorogi Pond

Table 2 \(\delta^{13}C\) and \(\delta^{15}N\) (\(^\circ\)) of macroinvertebrates in each vegetation type on the floating mat, Mizorogaike Pond

<table>
<thead>
<tr>
<th>Order</th>
<th>Taxon</th>
<th>Feeding habit</th>
<th>Aquatic/ terrestrial Distribution type</th>
<th>Sample code Mean SE</th>
<th>Collect individual no. (sample no.)</th>
<th>Sample code Mean SE</th>
<th>Collect individual no. (sample no.)</th>
<th>Sample code Mean SE</th>
<th>Collect individual no. (sample no.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isopoda</td>
<td>Asellus hilgendorfii Bovallius</td>
<td>Detritivore</td>
<td>Aquatic E</td>
<td>−26.6 −0.4 3 (2) 1</td>
<td>−23.0 0.2 0.7 1.0 25 (9) 17</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>Arctosa sp.</td>
<td>Predator</td>
<td>Terrestrial S</td>
<td>−23.2 0.5 5.1 0.2 3 (3) 6</td>
<td>−23.2 4.4 1 (1) 18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colembola</td>
<td>Isotominae gen. spp.</td>
<td>Detritivore</td>
<td>Terrestrial S</td>
<td>−24.1 0.5 4.2 0.5 3 (3) 7</td>
<td>−23.2 4.4 1 (1) 18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Odonata</td>
<td>Nanophyia pygmaea Rambur</td>
<td>Predator</td>
<td>Aquatic S</td>
<td>−23.8 0.0 −1.1 0.0 &gt;500 (10) 8</td>
<td>−21.9 2.0 1.0 5 (5) 19</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neuroptera</td>
<td>Sialis yamatoensis Hayashi et Suda</td>
<td>Predator</td>
<td>Aquatic S</td>
<td>−23.2 4.4 1 (1) 18</td>
<td>−21.5 0.3 0.2 0.2 4 (4) 20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Helochares striatus Sharp</td>
<td>Detritivore</td>
<td>Aquatic E</td>
<td>−27.2 −0.5 2 (2) 2</td>
<td>−25.9 0.1 0.1 1.0 3 (3) 21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Helochares palens MacLeay</td>
<td>Detritivore</td>
<td>Aquatic E</td>
<td>−25.5 0.1 −0.1 0.0 23 (3) 10</td>
<td>−23.9 0.2 −0.1 0.1 15 (4) 22</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coelostoma stadtnam (Walker) Breede</td>
<td>Detritivore</td>
<td>Aquatic S</td>
<td>−24.6 1.5 1(1) 11</td>
<td>−21.3 2.7 58 (2) 25</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Enochrus japonicus (Sharp) Orchiyont</td>
<td>Detritivore</td>
<td>Aquatic S</td>
<td>−29.9 1.3 2 (2) 3</td>
<td>−24.7 3.8 1 (1) 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tachinus impunctatus Sharp</td>
<td>Predator</td>
<td>Terrestrial S</td>
<td>−26.2 0.1 2.4 0.9 23 (3) 4</td>
<td>−25.4 0.1 0.7 1.0 4 (4) 12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tabanidae gen. spp.</td>
<td>Predator</td>
<td>Terrestrial S</td>
<td>−25.2 0.1 0.7 0.1 4 (4) 12</td>
<td>−23.2 0.9 2.2 23</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ceratopogonidae gen. spp.</td>
<td>Predator</td>
<td>Aquatic S</td>
<td>−24.4 1.3 2.1 7 (2) 14</td>
<td>−22.5 3.1 2 (2) 24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Branchiura gen. sp.</td>
<td>Predator</td>
<td>Aquatic S</td>
<td>−23.2 2.8 2 (2) 15</td>
<td>−21.3 2.7 58 (2) 25</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clitellata</td>
<td>Branchiura gen. sp.</td>
<td>Detritivore</td>
<td>Aquatic S</td>
<td>−25.4 −0.3 13 (2) 16</td>
<td>−22.7 1.0 1.0 15 (3) 26</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Archiellochaeta gen. sp.</td>
<td>Branchiura gen. sp.</td>
<td>Detritivore</td>
<td>Aquatic S</td>
<td>−25.4 −0.3 13 (2) 16</td>
<td>−22.7 1.0 1.0 15 (3) 26</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Sample code is corresponding to that in Fig. 4. Sample number is defined as the number of measured sample. Distribution type is referred to the text for definition: E, eurytopic; S, stenotopic.
the dominant plant *M. trifoliata* was markedly different in dead leaves and DS. The BPOM in the VC had a δ^{13}C close to that of the dead leaves of *M. trifoliata* (Fig. 4). A similar pattern was found in the SL and carpet, where no clear difference was seen between the dead tissues of moss species and BPOM in δ^{13}C.

The δ^{13}C of detritivorous taxa was significantly different amongst habitats, although no habitat variation was observed in δ^{15}N (Table 3). This amongst-habitat pattern was also seen in the δ^{13}C of the eurytopic species *H. striatus* (*F* = 29.69; *P* < 0.05) in the VC (−25.9 ± 0.1‰) and 24.0 ± 0.5‰ in the SC). The most promising candidate for the food source of *H. striatus* was BPOM in the SL (Δδ^{13}C = 0.1‰; Δδ^{15}N = 1.4‰) and in the SC (Δδ^{13}C = 0.3‰; Δδ^{15}N = 0.3‰) and DS of *M. trifoliata* in the VC (Δδ^{13}C = −0.2‰; Δδ^{15}N = 0.0‰). The δ^{15}N in the VC and the SC showed a moderate reliance on both autochthonous and allochthonous products (Table 4). However, terrestrial predators in the VC and the SC appeared to rely on BPOM in the SC. The aquatic predators seemed to rely more on BPOM in the SC or other unknown food resources with a higher δ^{13}C.

**Table 3** δ^{13}C and δ^{15}N (‰; mean ± SE) of possible trophic origins [dead plant tissues and benthic particulate organic matter (BPOM)] and detritivore, and estimated enrichment factors (Δ) of C and N in each habitat type on the floating mat, Mizorogaike Pond

<table>
<thead>
<tr>
<th>Trophic groups</th>
<th>Sphagnum lawn</th>
<th>Vascular-plant carpet</th>
<th>Sphagnum carpet</th>
<th>F-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead plant tissue</td>
<td>−27.4 ± 0.2b</td>
<td>−28.1 ± 0.1* (leaf)</td>
<td>−25.6 ± 0.2* (leaf stalk)</td>
<td>−24.5 ± 0.4*</td>
</tr>
<tr>
<td>BPOM</td>
<td>−27.4 ± 0.0*</td>
<td>−27.3 ± 0.0*</td>
<td>−24.3 ± 0.0b</td>
<td>1042.46**</td>
</tr>
<tr>
<td>Detritivore</td>
<td>−27.9 ± 1.0*</td>
<td>−29.0 ± 0.3*</td>
<td>−23.4 ± 0.3b</td>
<td>22.33**</td>
</tr>
<tr>
<td>Predator</td>
<td>−26.4 ± 1.0*</td>
<td>−23.6 ± 0.4b</td>
<td>−22.1 ± 0.3b</td>
<td>14.72**</td>
</tr>
<tr>
<td>δ^{13}C</td>
<td>−4.1 ± 0.2*</td>
<td>−0.3 ± 0.2b (leaf)</td>
<td>−0.2 ± 0.3b (leaf stalk)</td>
<td>−1.1 ± 0.2b</td>
</tr>
<tr>
<td>BPOM</td>
<td>−1.9 ± 0.1*</td>
<td>−0.5 ± 0.0b</td>
<td>−0.1 ± 0.1c</td>
<td>169.77**</td>
</tr>
<tr>
<td>Detritivore</td>
<td>0.1 ± 0.6*</td>
<td>0.6 ± 0.3*</td>
<td>0.5 ± 0.2a</td>
<td>0.50</td>
</tr>
<tr>
<td>Predator</td>
<td>2.3 ± 0.9a</td>
<td>3.5 ± 0.7b</td>
<td>2.7 ± 0.9b</td>
<td>1.25</td>
</tr>
<tr>
<td>δ^{15}N</td>
<td>−0.9 ± 0.2*</td>
<td>−0.6 ± 0.3*</td>
<td>−0.8 ± 0.3*</td>
<td>2.90</td>
</tr>
<tr>
<td>BPOM</td>
<td>−0.9 ± 0.2*</td>
<td>−0.6 ± 0.3*</td>
<td>−0.8 ± 0.3*</td>
<td>1.25</td>
</tr>
</tbody>
</table>

Different superscripts across rows denote a significant difference (Tukey test or Tukey–Kramer test, *P* < 0.05) among habitat types. **P < 0.01 in ANOVA.
δ¹³C of terrestrial predators had some similarities amongst habitats, suggesting that they forage on a variety of prey from the three habitats (Table 4; Fig. 4).

### Discussion

In the bog ecosystem of Mizorogaike Pond, the invertebrate communities varied greatly across patchy habitats associated with vegetation types on the floating mat. The numerical predominance of stenotopic species in each habitat implies that the biodiversity and uniqueness of the invertebrate communities on the floating mat are ultimately maintained by spatial heterogeneity in the abiotic environment, which can determine the dominant plant species of microhabitats. The invertebrate communities also showed discrete variations in their isotopic signatures, especially in δ¹³C, amongst habitats. Marked differences were also observed amongst habitats in the δ¹³C of plant tissues and their detritus, which might be the basal foods of the invertebrate communities. The isotopic variation of the invertebrate communities approximately corresponded to that of the potential food sources.

Invertebrate detritivores generally have lower enrichment of δ¹⁵N, as well as δ¹³C, through their trophic interactions. Across a variety of taxa, a meta-analysis showed that their trophic enrichment factor was 0.4 ± 0.28% for δ¹³C (McCutchan et al., 2003) and 0.59 ± 0.41% for δ¹⁵N (Vanderklift & Ponsard, 2003), including detritivorous/herbivorous invertebrates. Compared with values found in the literature, the deduced trophic sources for *H. striatus* and other detritivores in the bog habitats are appropriate. In the VC, the isotopic signatures of detritivores were closest to those of DS of the dominant plant *M. trifoliata*, suggesting that they selectively consumed the DS. The conclusion is also supported by the fact that the isotopic signature of BPOM was more similar to that of dead leaves than to that of leaf stalks, which might be a consequence of more dead leaves being deposited on the floating mat and DS being consumed more by detritivores. One may point out that our conclusion greatly depends on the assumption of trophic enrichment factor. However, our unpublished work shows that stable isotopic differences between *H. striatus* and its potential food in summer are invariant across a variety of sampling sites with an average of 0.8% for δ¹³C and 1.2% for δ¹⁵N (Y. Kato, unpubl. data), confirming that our assumption is reasonable.

Although our isotopic approach revealed that detritivorous groups of local invertebrate communities rely mainly on autochthonous foods derived from their own habitats, such an isotopic difference can also be because of differences in species composition and thus to interspecific differences in food niches determined by phylogenetic constraints. If this is true, a

![Table 4](image-url)
given species should have a conservative isotopic signature, irrespective of its habitat. However, this possibility can be rejected because the eurytopic species *H. striatus* had different isotopic signatures amongst habitats, implying that its home range was confined to a small area. For small animals, their strong reliance on autochthonous foods may be partly associated with their immobility (Hobson, 1999). In the bog ecosystem of Mizorogaike Pond, most detritivores were aquatic species. For these small aquatic invertebrates, the small ups and downs of the hummock–hollow series may constitute a physical barrier preventing them from moving between patchy habitats, resulting in confinement to one habitat.

Many community ecological studies have examined how habitat heterogeneity and animal mobility can affect community organisation on large spatial scales, such as landscapes consisting of heterogeneous ecosystems (Lake, Bond & Reich, 2007). However, ecologists recently have recognised that habitat patchiness and heterogeneity on smaller scales can be important in the organisation of local communities (Williams & Smith, 1996; Sota, Mogi & Kato, 1998; Swan & Palmer, 2000; Yee & Juliano, 2006; Pedersen & Friberg, 2007). Such small-scale heterogeneity will also lead to compartmentalisation of trophic pathways starting from the patchy habitats. In salt marsh and mangrove habitats, the $^{13}$C signatures of gastropods indicate assimilation of carbon from sources 2 to 15 m away (Guest et al., 2004). In estuarine food webs, whilst substantial spatial heterogeneity in organic matter sources exists within a single estuary, consumers tend to utilise sources of organic matter produced in the region of the estuary in which they reside (Deegan & Garritt, 1997). Furthermore, Doi et al. (2007) revealed that the trophic bases of food webs (terrestrial or algal organic sources) in a channel change at comparatively small spatial scales (<10 m$^2$) relative to the degree of canopy cover. The heterogeneity of carbon movement and assimilation at scales smaller than previously realised may be common in wetlands. Using a stable isotope analysis, we demonstrated that the trophic pathways of invertebrate communities, especially detritivorous functional groups, are spatially heterogeneous on a scale of less than a few metres, reflecting the habitat patchiness of vegetation on the bog ecosystem.

Compared with aquatic detritivores, the $^{13}$C of terrestrial predators was similar, regardless of capture site. The isotope mixing model estimated that most terrestrial predators utilise mostly allochthonous foods. As shown by their higher $^{15}$N, wolf spiders (*Arctosa* sp. and *Pirata* sp.) and staphylinid beetles (*Tachinus impunctatus* and *Staphylinidae* sp.) that may hunt in multiple habitats are top predators in the invertebrate communities on the floating mat. Their feeding habits coupled the trophic pathways of separate habitats. Furthermore, the reliance of aquatic predators on other unknown trophic resources with a higher $^{13}$C suggests that they rely on other aquatic trophic resources such as epilithic algae (e.g. $\pm 17 \pm 2\%_o$; France, 1995b). If this literature value of epilithic algal $^{13}$C is incorporated into our IsoSource mixing model as an allochthonous food source for the aquatic predators, we can estimate that their reliance on allochthonous production was on average 31.5%. This implies that the aquatic predators may couple between terrestrial and aquatic trophic pathways. Top terrestrial predators will also couple the trophic pathways based on trophic sources with higher $^{13}$C than detritus.

The compartmentalisation and coupling of food webs are key features of community organisation (Pimm & Lawton, 1980; Post et al., 2000; Krause et al., 2003; Rooney et al., 2006). Many isotopic studies have found that multiple carbon sources exist in aquatic ecosystems and that their trophic pathways are usually coupled by mobile top predators such as fishes, birds and mammals (Anderson & Polis, 1998; Bouchard & Bjorndal, 2000; MacAvoy et al., 2000; Nakano & Murakami, 2001; Bastow et al., 2002). This study demonstrated that habitat heterogeneity on an extremely small scale can be an important factor affecting the uniqueness and diversity of local invertebrate communities in the bog ecosystem of Mizorogaike Pond. Although bog ecosystems often harbour a great deal of endemic species, most of which are endangered, and are thus considered biodiversity hot spots in need of urgent conservation, many bog ecosystems have suffered from habitat destruction and fragmentation (Rydin & Jeglum, 2006; Spitzer & Danks, 2006; Warner & Asada, 2006). As shown here, local invertebrate communities can be supported by heterogeneous vegetation and trophic pathways can be coupled by top predators, both of which facilitate maintain the high biodiversity of bog ecosystems. Stable isotopic approaches will be useful in designing environmental mitigation and rehabilitation of bog ecosystems for biodiversity conservation.
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References


(Human accepted 8 July 2009)