

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 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) 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 $\delta^{13}\text{C}$ but not in $\delta^{15}\text{N}$, 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 $\delta^{13}\text{C}$ 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

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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,

physical factors (Downes, Lake & Schreiber, 1993), resource availability (Sinsabaugh, Weiland & Linkens, 1991; Maar *et al.*, 2002), interspecific competition (Rader & McArthur, 1995; Harrison & Hildrew, 2001), parasitism (Mouritsen & Poulin, 2002) and predation (Zerba & Collins, 1992). Even in seemingly uniform habitats such as the pelagic sea, food webs show high spatial variability (e.g. Maar *et al.*, 2002).

Compartmentalisation and coupling of habitats are key to constructing food webs (Pimm & Lawton, 1980; Post, Conners & Goldberg, 2000; Krause *et al.*, 2003; Rooney *et al.*, 2006). Habitat heterogeneity and inhabitant immobility lead to the compartmentalisation of local communities embedded within a food web (Pimm & Lawton, 1980; Krause *et al.*, 2003). However, mobile predators can trophically link multiple food chains derived from heterogeneous habitats, as in the well-known coupling of terrestrial and riverine ecosystems (Vannote *et al.*, 1980; Junk, Bayley & Sparks, 1989; Thorp & DeLong, 1994), marine and riverine ecosystems (MacAvoy *et al.*, 2000) and marine and terrestrial ecosystems (Anderson & Polis, 1998; Bouchard & Bjorndal, 2000).

In aquatic ecosystems, spatial variability of primary producers is an essential component characterising food-web structure. For example, lake and marine food webs are supported by periphyton and macrophytes from the littoral area and phytoplankton from the pelagic area (France, 1995a,b; Vander Zanden & Rasmussen, 1999; Syvaranta, Hamalainen & Jones, 2006). These two compartments are usually coupled by mobile predators such as fish, resulting in 'littoral-pelagic coupling' or 'benthic-pelagic coupling' (Raffaelli & Hall, 1992; Schindler & Scheuerell, 2002; Vadeboncoeur, Vander Zanden & Lodge, 2002; Vander Zanden & Vadeboncoeur, 2002). The entirety of such a food web can be viewed on large spatial scales, sometimes reaching tens of kilometres (Ulanowicz & Baird, 1999). In contrast, aquatic ecologists recently have focused on the spatial heterogeneity of trophic structures on smaller scales (Deegan & Garritt, 1997; Guest, Connolly & Loneragan, 2004; Doi *et al.*, 2007). Since the pattern of community organisation depends on spatial scaling (Woodward & Hildrew, 2002; Brose *et al.*, 2004; Thompson & Townsend, 2005), one must recognise the minimum unit of habitat compartmentalisation to understand the hierarchical structure of food webs on varying scales, from microhabitat to landscape levels.

Peatland ecosystems have recently received attention because of their unique fauna and flora, including many rare and endemic species (Rosenberg & Danks, 1987; Finnamore & 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 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) 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 (Vanderklift & 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- μ m 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

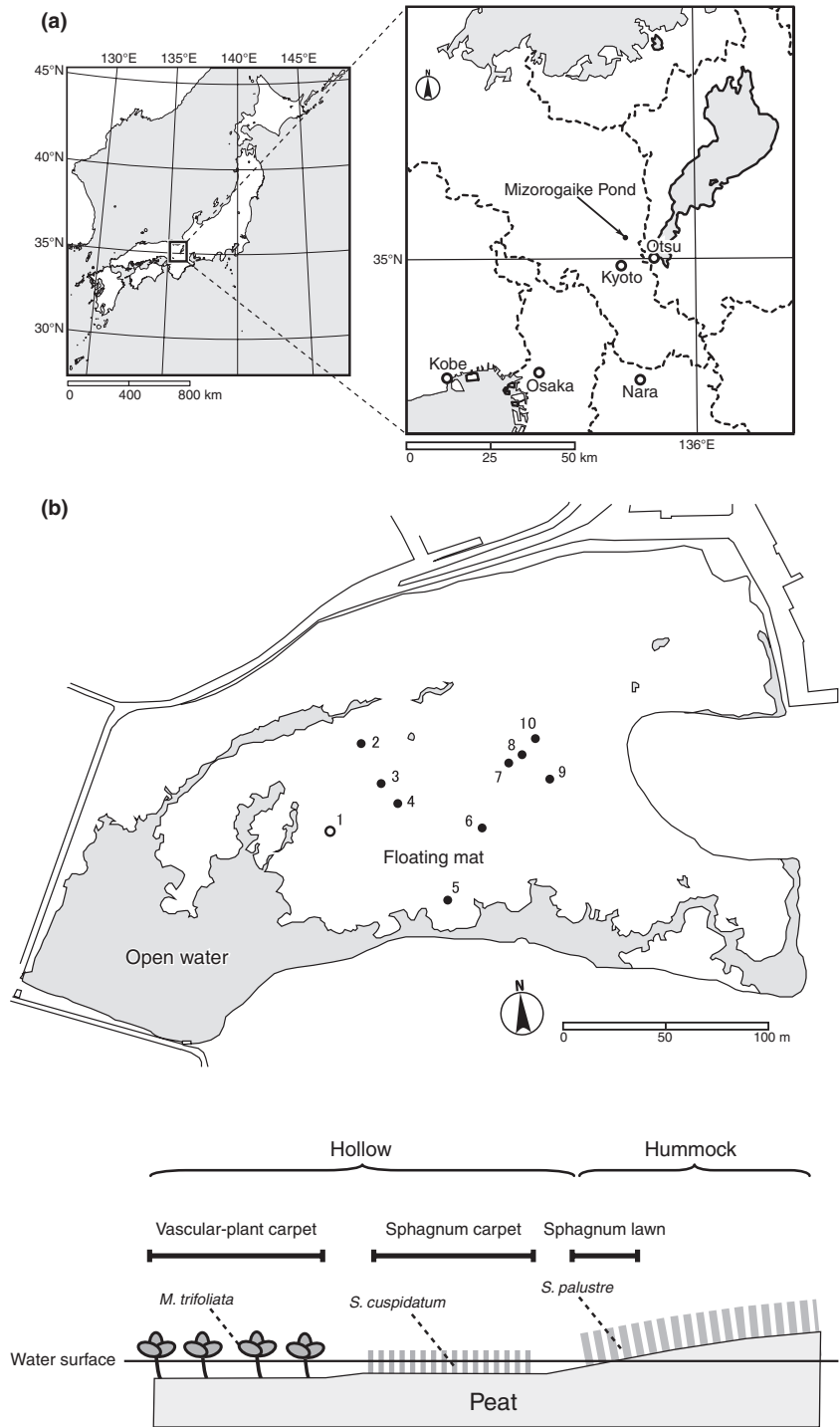


Fig. 1 (a) Maps showing the location of Kyoto City and Mizorogaikae Pond. (b) Study sites on the floating mat in Mizorogaikae Pond. Circles show the location of patches ($n = 10$) which consists of three vegetation types. All isotopic samples were collected only in site no. 1 (open circle).

Fig. 2 Cross-sectional diagram of three habitat types (sphagnum lawn, vascular-plant carpet and sphagnum carpet) on the floating mat in Mizorogaikae Pond.

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 desiccated 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 δ notation as deviations from a standard: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ (‰). Here R is $^{13}\text{C}/^{12}\text{C}$ for $\delta^{13}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{15}\text{N}$. The standards were PeeDee belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. We used DL-alanine as working standard. The analytical precision was ± 0.2 ‰ for $\delta^{13}\text{C}$ and ± 0.2 ‰ for the $\delta^{15}\text{N}$.

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 isoto-

pic 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 $\delta^{13}\text{C}$ ($\Delta\delta^{13}\text{C}$) and $\delta^{15}\text{N}$ ($\Delta\delta^{15}\text{N}$) for each detritivore. Since detritivores do not assimilate living plant tissues, we used the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of dead plant tissues and BPOM as potential food sources in the SL and the SC. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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‰) $\delta^{13}\text{C}$ values of potential trophic sources for all predators following the $\Delta\delta^{13}\text{C}$ 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 \pm 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.).

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

Variables	Sphagnum lawn	Vascular-plant carpet	Sphagnum carpet	d.f.	F-value
Water temperature(°C)	11.1 \pm 0.4 ^{ab}	11.9 \pm 0.5 ^b	10.3 \pm 0.2 ^a	2, 27	4.74*
pH	4.3 \pm 0.1 ^a	4.5 \pm 0.1 ^a	4.4 \pm 0.1 ^a	2, 27	1.13
Electric conductivity ($\mu\text{S cm}^{-1}$)	45.7 \pm 5.5 ^a	41.7 \pm 2.9 ^a	32.1 \pm 3.1 ^a	2, 27	3.02
Dissolved oxygen (mg L ⁻¹)	2.9 \pm 0.6 ^b	1.6 \pm 0.5 ^a	5.0 \pm 0.6 ^b	2, 27	9.10**
Peat surface height from water table (cm)	2.3 \pm 0.3 ^c	-4.5 \pm 0.5 ^a	0.7 \pm 0.2 ^b	2, 27	95.35**

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.

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ of BPOM was higher in the SC than in the other two habitats, whereas the $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 3). In the VC, the $\delta^{13}\text{C}$ of

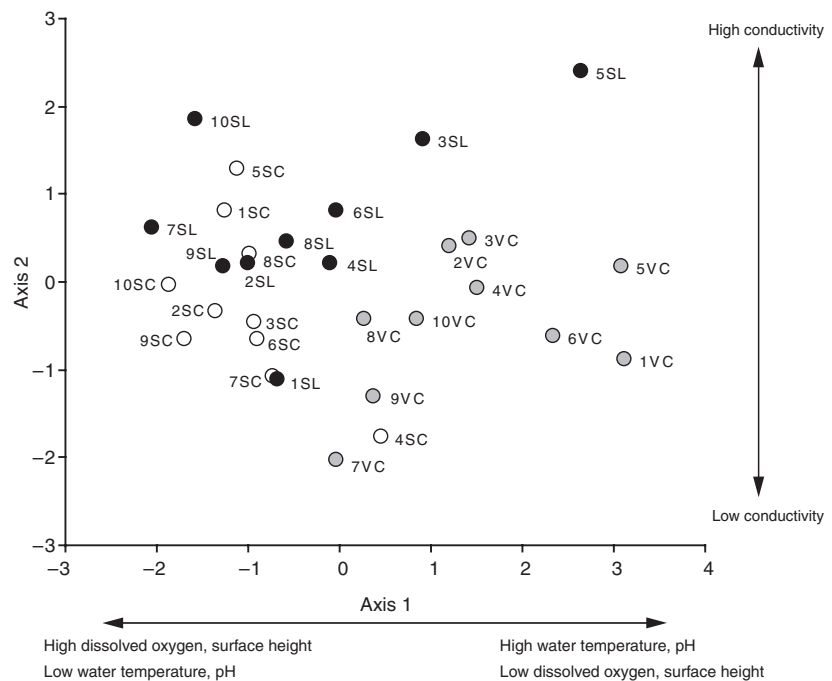


Fig. 3 Results of principal component analysis of physical and chemical variables collected from the three habitat types on the floating mat, Mizorogaike Pond. Numbers beside plots indicate the patch numbers shown in Figure 1. SL, sphagnum lawn; VC, vascular-plant carpet; SC, sphagnum carpet.

Table 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) (mean \pm SE) of macroinvertebrates in each vegetation type on the floating mat, Mizorogaike Pond

Order	Taxon	Feeding habit	Aquatic/terrestrial type	Distribution	Sphagnum lawn						Vascular-plant carpet						Sphagnum carpet					
					$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Collected individual no. (sample no.)		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Collected individual no. (sample no.)		$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Collected individual no. (sample no.)	
					Mean	SE	Mean	SE	Sample code	Sample code	Mean	SE	Mean	SE	Sample code	Sample code	Mean	SE	Mean	SE	Sample code	Sample code
Isopoda	<i>Asellus hilgendorffi</i>	Detritivore	Aquatic	E	-26.6	-	-0.4	-	3 (2)	1	-23.0	0.2	0.7	0.1	25 (9)	17						
	<i>Bovallius</i>	Predator	Terrestrial	S	-23.2	0.5	5.1	0.2	3 (3)	6												
Araneae	<i>Arcosa</i> sp.	Predator	Terrestrial	E	-24.1	0.5	4.2	0.5	3 (3)	7	-23.2	-	4.4	-	1 (1)	18						
	<i>Isotominae</i> gen. spp.	Detritivore	Terrestrial	S	-23.8	0.0	-1.1	0.0	>500 (10)	8												
Odonata	<i>Nannophya pygmaea</i>	Predator	Aquatic	S	-21.9	0.2	1.2	0.0	5 (5)	19												
Neuroptera	<i>Sialis Rambur</i>	Predator	Aquatic	S	-21.5	0.3	2.0	0.2	4 (4)	20												
	<i>Yamatensis</i> Hayashi et Suda																					
Coleoptera	<i>Heloclares striatus</i> Sharp	Detritivore	Aquatic	E	-27.2	-	-0.5	-	2 (2)	2	-25.9	0.1	-0.2	0.0	22 (22)	9						
	<i>Heloclares pallens</i> MacLeay	Detritivore	Aquatic	E	-25.5	0.1	-0.1	0.0	23 (6)	10	-24.6	-	1.5	-	1 (1)	11						
Diptera	<i>Coelostoma stultum</i> (Walker) Brulle	Detritivore	Aquatic	S	-29.9	-	1.3	-	2 (2)	3	-25.2	0.1	0.7	0.1	4 (4)	12						
	<i>Eiodritus japonicus</i> (Sharp) Orchymont	Detritivore	Aquatic	S	-26.2	0.1	2.4	0.9	23 (3)	4	-24.4	0.0	0.5	0.1	4 (4)	13						
Diptera	<i>Tachinus impunctatus</i> Sharp	Predator	Terrestrial	S	-24.7	-	3.8	-	1 (1)	5	-24.4	-	1.3	-	7 (2)	14						
	<i>Staphylinidae</i> sp.	Predator	Terrestrial	S	-23.2	-	2.8	-	2 (2)	15	-22.5	-	3.1	-	2 (2)	24						
Diptera	<i>Tipula</i> sp.1	Detritivore	Aquatic	S	-25.4	-	-0.3	-	13 (2)	16	-21.3	-	2.7	-	58 (2)	25						
	<i>Tipula</i> sp.2	Detritivore	Aquatic	S	-24.4	-	1.3	-	7 (2)	14	-22.7	0.1	1.0	0.1	15 (3)	26						
Diptera	<i>Tipula</i> sp.3	Detritivore	Aquatic	S	-23.2	-	2.8	-	2 (2)	15	-21.3	-	2.7	-	58 (2)	25						
	<i>Tabanidae</i> gen. spp.	Predator	Aquatic	E	-23.2	-	2.8	-	2 (2)	15												
Clitellata	<i>Ceratopogonidae</i> gen. spp.	Predator	Aquatic	S	-25.4	-	-0.3	-	13 (2)	16	-21.3	-	2.7	-	58 (2)	25						
	<i>Branchiura</i> gen. sp.	Detritivore	Aquatic	S	-25.4	-	-0.3	-	13 (2)	16												
Archiholigochaeta	<i>Archiholigochaeta</i> gen. sp.	Detritivore	Aquatic	S	-22.7	0.1	1.0	0.1	15 (3)	26	-22.7	0.1	1.0	0.1	15 (3)	26						
		Detritivore	Aquatic	S	-22.7	0.1	1.0	0.1	15 (3)	26												

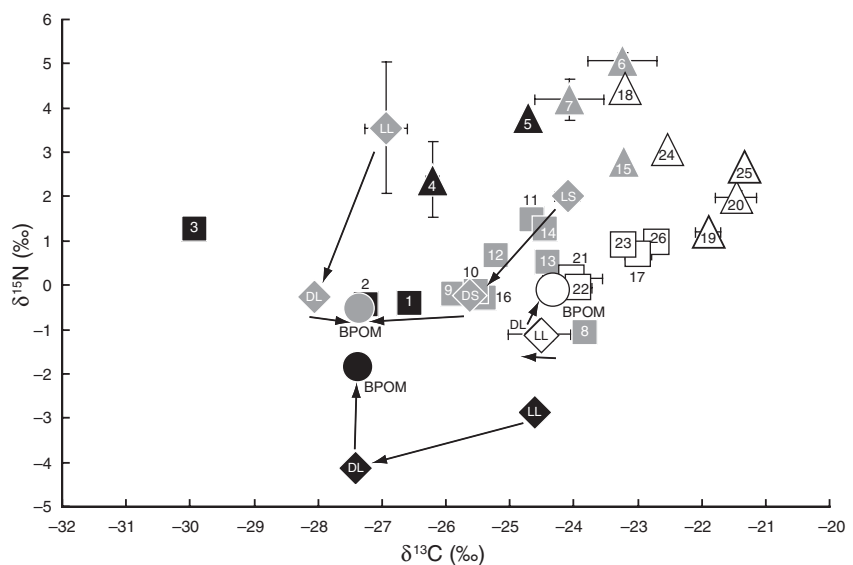
Sample code is corresponding to that in Fig. 4. Sample number is defined as the number of measured sample. Distribution type is referred to the text for definition: E, eurytopic; S, stenotopic.

Table 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰; mean \pm 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

	Trophic groups	Sphagnum lawn	Vascular-plant carpet		Sphagnum carpet	F-value
$\delta^{13}\text{C}$	Dead plant tissue	-27.4 ± 0.2^b	-28.1 ± 0.1^a (leaf)	-25.6 ± 0.2^c (leaf stalk)	-24.5 ± 0.4^c	53.04**
	BPOM	-27.4 ± 0.0^a	-27.3 ± 0.0^a		-24.3 ± 0.0^b	1042.46**
	Detritivore	-27.9 ± 1.0^a	-25.0 ± 0.3^b		-23.4 ± 0.3^c	22.33**
	Predator	-26.4 ± 1.0^a	-23.6 ± 0.4^{ab}		-22.1 ± 0.3^b	14.72**
$\delta^{15}\text{N}$	Dead plant tissue	-4.1 ± 0.2^a	-0.3 ± 0.2^b (leaf)	-0.2 ± 0.3^b (leaf stalk)	-1.1 ± 0.2^b	44.89**
	BPOM	-1.9 ± 0.1^a	-0.5 ± 0.0^b		-0.1 ± 0.1^c	169.77**
	Detritivore	0.1 ± 0.6^a	0.6 ± 0.3^a		0.5 ± 0.2^a	0.50
	Predator	2.3 ± 0.9^a	3.5 ± 0.7^a		2.7 ± 0.5^a	1.25

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.

Fig. 4 Stable isotope features ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of tissues of the dominant plants, BPOM and invertebrates on the floating mat in Mizorogaike Pond (mean \pm SE). Diamonds, circles, triangles and squares show tissues of the dominant plants, BPOM, predators and detritivores respectively. Black, grey and white symbols show the samples collected in the sphagnum lawn, vascular-plant carpet and sphagnum carpet respectively. Arrows show the decomposition process of the dominant plant (living tissue – dead tissue – BPOM) in each vegetation type. Each number with the symbol of invertebrate shows sample code presented in Table 2. LL, living leaf; DL, dead leaf; LS, living leaf stalk; DS, dead leaf stalk.



the dominant plant *M. trifoliata* was markedly different in dead leaves and DS. The BPOM in the VC had a $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$.

The $\delta^{13}\text{C}$ of detritivorous taxa was significantly different amongst habitats, although no habitat variation was observed in $\delta^{15}\text{N}$ (Table 3). This amongst-habitat pattern was also seen in the $\delta^{13}\text{C}$ of the eurytopic species *H. striatus* ($F = 29.69$; -27.2‰ in the SL, $-25.9 \pm 0.1\text{‰}$ in the VC and $-24.0 \pm 0.5\text{‰}$ in the SC). The most promising candidate for the food source of *H. striatus* was BPOM in the SL ($\Delta\delta^{13}\text{C} = 0.1\text{‰}$; $\Delta\delta^{15}\text{N} = 1.4\text{‰}$) and in the SC ($\Delta\delta^{13}\text{C} = 0.3\text{‰}$; $\Delta\delta^{15}\text{N} = 0.3\text{‰}$) and DS of *M. trifoliata* in the VC ($\Delta\delta^{13}\text{C} = -0.2\text{‰}$; $\Delta\delta^{15}\text{N} = 0.0\text{‰}$; Fig. 4). $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ were $-0.9 \pm 1.7\text{‰}$ and $2.3 \pm 0.8\text{‰}$ in the SL,

$0.9 \pm 0.2\text{‰}$ and $0.6 \pm 0.3\text{‰}$ in the VC and $1.1 \pm 0.3\text{‰}$ and $0.7 \pm 0.2\text{‰}$ in the SC respectively. Furthermore, $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ of other detritivores were $0.7 \pm 0.3\text{‰}$ and $0.9 \pm 0.3\text{‰}$, respectively, in total.

Predators varied amongst habitats in their $\delta^{13}\text{C}$ but the difference was significant only between the SL and carpet (Table 3). No significant differences were observed in predator $\delta^{15}\text{N}$ amongst habitats (Table 2). Terrestrial predators showed a significantly higher $\delta^{15}\text{N}$ than aquatic predators (terrestrial predators: $4.0 \pm 0.5\text{‰}$; aquatic predators: $2.3 \pm 0.3\text{‰}$; $t = -2.90$). The terrestrial predators in the SL 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 $\delta^{13}\text{C}$. The

Table 4 Means and ranges of feasible contribution of the potential food sources to predators [benthic particulate organic matter (BPOM) in the sphagnum lawn and carpet; dead leaf stalks of *Menyanthes trifoliata* in the vascular-plant carpet] determined using IsoSource mixing model

Life form	Habitat type	Taxon	Sphagnum lawn		Vascular-plant carpet		Sphagnum carpet	
			Mean \pm SD (%)	Range	Mean \pm SD (%)	Range	Mean \pm SD (%)	Range
Terrestrial	Sphagnum lawn	<i>Tachinus impunctatus</i>	82.0 \pm 3.9	73–90	11.5 \pm 7.2	0–27	6.5 \pm 4.2	0–16
		Staphylinidae sp.	19.2 \pm 11.5	0–41	46.7 \pm 27.4	0–100	34.1 \pm 16.1	0–64
	Vascular-plant carpet	<i>Arctosa</i> sp.	0	0	0	0	100	100
		<i>Pirata</i> sp.	9.6 \pm 5.9	0–22	23.6 \pm 14.1	0–53	66.7 \pm 8.7	47–83
Aquatic	Sphagnum carpet	<i>Pirata</i> sp.	0	0	0	0	100	100
	Vascular-plant carpet	Tabanidae gen. spp.	0	0	0	0	100	100
	Sphagnum carpet	<i>Nannophya pygmaea</i>	NC	NC	NC	NC	NC	NC
		<i>Sialis yamatoensis</i>	NC	NC	NC	NC	NC	NC
		Tabanidae gen. spp.	0	0	0	0	100	100
	Ceratopogonidae gen. spp.	NC	NC	NC	NC	NC	NC	

Enrichment factor among predators and food sources was +0.8, following McCutchan *et al.* (2003).

NC, the contribution could not be determined using IsoSource mixing model because of higher isotope values from potential food resources.

$\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$, amongst habitats. Marked differences were also observed amongst habitats in the $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$, as well as $\delta^{13}\text{C}$, through their trophic interactions. Across a variety of taxa, a meta-analysis showed that their trophic enrichment factor

was $0.4 \pm 0.28\text{‰}$ for $\delta^{13}\text{C}$ (McCutchan *et al.*, 2003) and $0.59 \pm 0.41\text{‰}$ for $\delta^{15}\text{N}$ (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 $\delta^{13}\text{C}$ and 1.2‰ for $\delta^{15}\text{N}$ (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

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 $\delta^{13}\text{C}$ 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 m²) 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 $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$, 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 $\delta^{13}\text{C}$ suggests that they rely on other aquatic trophic resources such as epilithic algae (e.g. $-17 \pm 2\text{‰}$; France, 1995b). If this literature value of epilithic algal $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 & Bjørndal, 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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