ECOSYSTEMS

Ecosystem Linkages Between Lakes and the Surrounding Terrestrial Landscape in Northeast Iceland

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ABSTRACT

Despite a recent emphasis on understanding cross-habitat interactions, few studies have examined the ecological linkages between lakes and surrounding terrestrial habitats. The current paradigm of land–lake interactions is typically unidirectional: the view is that nutrients and matter are transported downslope from the surrounding watershed to their ultimate lacustrine destination. Emergent aquatic insects, which spend their larval stages in lake sediments and emerge as adults to mate over land, can act as vectors of material, energy and nutrients from aquatic to terrestrial habitats. In this study, we document a gradient of midge (Diptera: Chironomidae) infall rates into terrestrial habitats (measured as g dw midges m^{-2} d^{-1}) surrounding eight lakes in Northern Iceland ($\approx$66°N latitude). Lakes ranged from having virtually no midge infall (for example, Helluvaðstjörn, 0.03 g m^{-2} d^{-1}) to extreme levels (for example, Mývatn, 19 g m^{-2} d^{-1}) with abundances of midges decreasing logarithmically with distance from shore. Annual midge input rates are estimated as high as 1200–2500 kg midges ha^{-1} y^{-1}. As midges are approximately 9.2% total N, this can result in a significant fertilization effect of terrestrial habitats with consequences for plant quality and community structure. In addition, we used naturally-occurring δ^{13}C and δ^{15}N isotopes to examine food web structure and diet sources of terrestrial arthropod consumers surrounding lakes with differing amounts of midge input. Terrestrial arthropods showed increased utilization of aquatic-derived (that is, midge) C relative to terrestrial sources as midge infall increased. This pattern was particularly pronounced for predators, such as spiders and opiliones, and some detritivores (Collembola). These findings suggest that, despite being largely ignored, aquatic-to-terrestrial linkages can be large and midges can fuel terrestrial communities by directly serving as resources for predators and decomposers.

Key words: allochthonous resources; subsidy; food webs; landscape ecology; spatial flows; emergent aquatic insects.

INTRODUCTION

Subsidies of resources, organisms, and energy emanating from one habitat or ecosystem have the potential to significantly affect the dynamics of trophic interactions within a recipient system (Polis and others 1997). Such effects have been documented in a diversity of coupled systems including oceans and inland riparian areas linked through the

migration of anadromous salmon (Moore and others 2007), oceans and islands through deposition of marine-mammal carrion or seabird derived guano (Polis and Hurd 1996; Anderson and Polis 1999), and streams and adjacent riparian areas via the emergence of aquatic insects (Henschel and others 2001; Sabo and Power 2002), infall of arthropods (Nakano and others 1999), or litterfall (Hall and others 2000). A common finding of these studies is that ignoring allochthonous resource inputs into recipient systems significantly limits the ability to understand and predict the abundance, biomass and dynamics of organisms within a recipient habitat. The view of ecosystems as ''open'' (Milner and others 2007) suggests the need for a landscape perspective to the study of food webs that explicitly examines the influence of cross-habitat ecological flows on food web and species interactions (Polis and others 2004).

Despite the emerging appreciation of cross-habitat linkages and their importance for food web dynamics in recipient ecosystems (Polis and Winemiller 1996; Polis and others 1997; Polis and others 2004) studies examining how freshwater productivity affects terrestrial trophic dynamics have focused on lotic systems (Sabo and Power 2002; Ballinger and Lake 2006), whereas lentic systems have been the subject of little attention (but see Knight and others 2005). Reasons for this difference are several-fold. First, the study of insect secondary production is a common subject of stream ecology, whereas studies of lakes have focused on pelagic productivity and processes, often at the expense of benthic (insect) production (Vadeboncoeur and others 2002). Furthermore, theory predicts strong cross-habitat trophic linkages in riverine systems due to the high prevalence of edges in riverine landscapes (that is, high perimeter:area of habitat, Polis and others 1997). In contrast, lakes have relatively little edge per unit habitat area and have been thought of as having weak interactions with the surrounding terrestrial landscape. Our present understanding of land–lake interactions is wholly unidirectional: the view is that nutrients and matter are transported downslope from the surrounding watershed to their ultimate lacustrine destination. Yet, the large lake area (per unit perimeter) also has the potential to create strong linkages from the lake to the land, particularly because lakes can have high rates of insect secondary production (Lindegaard and Jonasson 1979).

Lakes can influence terrestrial ecosystems through the export of emergent aquatic insects. Many lakes have significant benthic production of larval insects which emerge as adults and enter the terrestrial system (Likens 1985). Among the many well-known examples are phantom midges (Chaoboridae) from Lake Malawi (Irvine 2000), midges (Chironomidae) from Wisconsin lakes (Hilsenhoff 1967), and mayflies from Lake Michigan (MacKenzie and Kaster 2004). Most of the studies of aquatic-terrestrial linkages, however, have examined interactions between streams and land. These have shown that adult aquatic insects often move into riparian areas (Jackson and Fisher 1986) where they are fed upon by terrestrial consumers such as birds (Murakami and Nakano 2002), lizards (Sabo and Power 2002), spiders (Sanzone and others 2003) and beetles (Paetzold and others 2005). There are currently few studies (for example, Knight and others 2005) that have examined how lake ecosystems affect terrestrial food webs in the adjacent landscape. Given the prevalence of lakes in landscapes, ignoring these linkages will limit our ability to understand potentially significant factors that affect interactions among organisms in terrestrial food webs.

We explored the magnitude of lake-to-land linkages via aquatic insects that originate from lakes in northern Iceland and enter the surrounding terrestrial landscape, and measured to what extent terrestrial arthropod consumers utilize these allochthonous resources. The principal lake studied in this research is Lake Mývatn, a lake well known for its spectacular annual chironomid midge (Diptera) emergences. We hypothesized that a significant quantity of the benthic secondary production (midges) from this lake enters the terrestrial system. Midge inputs are then utilized both by terrestrial consumers, such as spiders, directly as prey, and by decomposers which utilize midges as they decompose on the ground. Thus terrestrial food webs on the shores surrounding lakes can be trophically linked to lake production through the flux of mobile aquatic insects that acts as an allochthonous resource.

Study Areas and Chironomid Midges

Lake Mývatn in northern Iceland (Digital Supplement 1, 65.55° N 17.00° W), is a well-studied limnetic system (Jonasson 1979a; Einarsson and Gulati 2004). Mývatn is a young ($\approx$2300 years BP), shallow, eutrophic lake with a mean depth of around 2.5 m and an area of 38 km^2 (Jonasson 1979b) and is highly productive due to high levels of solar input, high pH and inputs of N, P and Si from warm and cold artesian springs entering the lake, as well as high rates of wind-driven nutrient resuspension (Olafsson 1979).
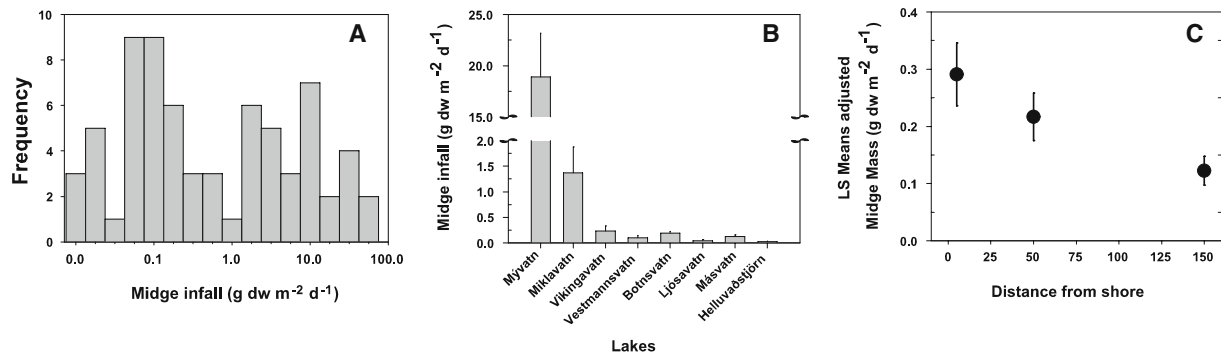
Figure 1. (**A**) Frequency distribution of midge infall (g dw m^{-2} d^{-1}) captured in midge collectors placed at different distances around eight lakes in Northern Iceland. Note log-scale of x-axis. (**B**) Average midge infall (+SEM) captured in infall collectors (g dw m^{-2} d^{-1}) around lakes in northern Iceland over a 5–7 days period in early August 2006 and (**C**) midge infall as a function of distance (m) from shore along transects. Values are back-transformed least-squares means (±SEM) from the ANOVA analysis, adjusting for differences between lakes.

The English translation of Mývatn is ''midge lake,'' owing to the abundance of chironomid midges (Diptera) that periodically emerge from the lake. A total of 41 species of chironomids occur at Mývatn (Gardarsson and others 2000), but one species, *Tanytarsus gracilentus* (Holmgren), represents on average 80% of the adult assemblage with *Chironomus islandicus* (Kieffer) representing an additional 2% of total captures (Gardarsson and others 2004). During a period of high midge abundance (1972–1974) these two species together represented 91% of the zoobenthic biomass (Lindegaard and Jonasson 1979). Midge larvae live within the soft sediments of the lake bottom and feed on periphyton and detritus (Ingvason and others 2004).

After completing their larval development, midges pupate and emerge from the lake as adults. During peak midge emergence, large and dense mating swarms form on the shoreline and midges and carcasses accumulate on vegetation and on the ground. Adult midges do not feed except for potentially nectaring at flowers (Armitage 1995). Mated females return to the lake where they deposit their eggs. The lake annually supports two adult generations of *T. gracilentus* with emergence periods in early to mid-June and early-August, whereas *C. islandicus* has a two-year life cycle with adults emerging in late-May to early-June (Jonsson and others 1986). *T. gracilentus* populations fluctuate cyclically at approximately 5–7 year periods with densities in high and low phases of a cycle differing by as much as 4 orders of magnitude. The periodicity appears to be internally driven, as it is unrelated to climactic variation (Einarsson and others 2004; Ives and others 2008), and is likely the result of consumer-resource interactions between the midges and benthic resources, rather than predator (fish or predatory chironomids)-prey interactions within the lake (Einarsson and others 2002).

Like other terrestrial habitats at the water-land ecotone (Polis and Hurd 1995; Henschel 2004), terrestrial arthropod assemblages are dominated by predatory taxa, primarily spiders. The assemblage includes seven species of spiders (three Lycosidae, four Linyphiidae) that comprise over 80% of the total abundance, with one lycosid species, *Pardosa sphagnicola* (Dahl), accounting for 30% of all spiders. Web builders are primarily linyphiids with *Allomengea scopigera* (Grube), representing over 30% of the guild in wetland areas (Hoffman 1997). Herbivore assemblages are less diverse with one species of planthopper (Delphacidae, *Javasella pellucida* [F.]) and one leafhopper (Cicadellidae) dominant. The terrestrial plant community is dominated by C3 plants typical of heathland vegetation (for example, Chapin and others 1995) such as grasses, ericaceous shrubs (*Vaccinium* spp., *Calluna vulgaris*, and *Empetrum nigrum*), and dwarf trees (*Salix lanata, S. phylicifolia, and Betula nana*).

In addition to Mývatn we identified seven other lakes (Digital Supplement 1) in the northeastern Icelandic landscape that where known, based on historical sampling or anecdotal observations (A. Einarsson, *unpublished data*), to span a gradient from high- (for example, Miklavatn and Vikingavatn) to low-midge production (for example, Helluvaðstjörn and Ljósavatn). Lakes are interspersed in the landscape along an approximate 100 km N to S transect with ''high'' and ''low'' midge lakes occurring near each other across the area.

METHODS

Midge Infall Sampling

To quantify the amount of aquatic insect production entering the terrestrial community, we placed midge infall collectors at each of our study lakes. Midge collectors consisted of 1000 ml clear plastic cups (95 cm^2 opening) filled with about 250 ml of 50% ethylene glycol and a small amount of unscented detergent to capture and kill insects that landed in the container. Although concerns about attractiveness of traps and surfactants have been raised (Southwood 1966), similar methods have been used to capture insect infall (Jonsson and others 1986; Kawaguchi and Nakano 2001) with no apparent bias in captures. Collection cups were attached with rubber bands to a bamboo stake pushed into the ground with the top of the cup positioned at a height of about 50 cm above the ground.

Midge collectors were placed at stations along two parallel transects spaced 50 m apart with stations at distances 5, 50, and 150 m perpendicular to shore at all lakes. Due to the relatively large size of Mývatn and heterogeneity in terrestrial habitats around the lake, we placed ten different transects around the perimeter of the lake with no two transects closer than 100 m to each other. Cup collectors remained in the field for 4–7 days between 1st August 2006 and 8th August 2006. This time period coincides with the typical peak activity of adult flight for the second generation of *T. gracilentus* at Mývatn (Gardarsson and others 2000).

Upon collection, contents of the cups were cleaned of insects that were clearly not of lake origin (occasional bumblebees, moths, and large muscoid flies), leaving primarily chironomids. The contents of the midge collectors were poured over a 200-µm sieve, and transferred to a vial with 70% ethanol. Insect samples were returned to the lab, identified to family and the number of chironomids were counted and dried at 70°C for 48 h to constant mass. If midge abundance in the collector was too great to fit in a 50-ml sampling tube then a subsample of the cup was taken by bringing the volume of the cup collector to a total volume of 1000 ml, briskly stirring the contents of the cup and removing a 50-ml subsample with a large bulb pipette and the sample was treated as described above. The retained subsample was used to estimate species composition. The remainder of the sample was filtered, squeezed of excess liquid, placed in a paper bag and dried to constant mass before being removed from the bag and weighed to estimate insect mass. In addition, for a subset of samples ($n = 28$), we counted midges before drying them to estimate an average dry mass per midge. For each sample midge infall is expressed as g dry weight (dw) m^{-2} d^{-1} adjusting for the total number of days a collector was exposed in the field.

Stable Isotope Sampling

To estimate the degree of reliance on terrestrial compared to aquatic (midge) resources, we collected terrestrial arthropods for analyses of naturally occurring stable isotope ratios of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N). Samples for isotope analyses were taken only at a subset of the lakes and distances from shore: Helluvaðstjörn, Botnsvatn, Miklavatn, and Mývatn (2 transects each), at the 5 m (near) and 150 m (far) distances from shore along the same transects established for midge collections (above). At each of the 16 locations, an area approximately 0.61 m^2 around each sampling station was sampled by vacuuming vegetation and the soil for arthropods. Samples were taken with a small gasoline-powered handheld vacuum (Stihl Inc., Virginia Beach, VA, model SH85), fitted with a 200-µm mesh collecting bag over the vacuum opening. Collection bags were kept separate for each sampling location, brought back to the lab and frozen at −20°C within 4 h to kill all arthropods. Contents of the bags were then sorted for analyses. At each site, we also collected live leaf tissue from the dominant grasses (bulked) and leaf litter. Arthropod samples were sorted to taxonomic groupings (Table 1) and bulked when necessary for analysis (minimum 0.5 mg dry mass).

Samples were analyzed for stable isotopes of C and N using by CF-IRMS (continuous flow-isotope ratio mass spectrometry) on a Carlo Erba NA 1500 series 2 analyzer coupled with a Europa Scientific Tracermass at the University of Wisconsin, Department of Horticulture (Arlington, Wisconsin). Ratios of ^{13}C/^{12}C and ^{15}N/^{14}N are expressed relative to a known standard (Vienna PeeDee Belemnite [VPDB] and atmospheric N, respectively) in per mil (‰) notation (for example, $\delta^{13}C_{sample} = [(^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{standard})-1] \times 1000$). Percent total nitrogen for midges was calculated from CF-IRMS analysis and total phosphorus was determined on an Astoria Pacific nutrient autoanalyzer following NaOH-$K_2S_2O_8$ digestion in an autoclave following the method of Valderrama (1981).

Statistical Analyses

Variation in midge infall (log-transformed) was analyzed by 2-way ANOVA with lake (8 lakes),

Table 1. Summary (Means and SEM) of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of Main Arthropod Taxa Collected at Four Lakes in Northern Iceland, Mývatn, Miklavatn, Botnsvatn, and Helluvaðstjörn, in August 2006, Which Range in Degree of Midge Inputs From High to Low, Respectively

| Taxon | $\delta^{13}C$ | | | | | | | | | | | | $\delta^{15}N$ | | | | | | | |
| | Mývatn | | | Miklavatn | | | Botnsvatn | | | Helluvaðstjörn | | | Mývatn | | Miklavatn | | Botnsvatn | | Helluvaðstjörn | |
	n	$\delta^{13}C$	(SEM)	n	$\delta^{13}C$	(SEM)	n	$\delta^{13}C$	(SEM)	n	$\delta^{13}C$	(SEM)	$\delta^{15}N$	(SEM)	$\delta^{15}N$	(SEM)	$\delta^{15}N$	(SEM)	$\delta^{15}N$	(SEM)
Grass	4	-28.10	(0.19)[a,b]	4	-29.44	(0.58)[b]	4	-27.77	(0.33)[a]	4	-27.50	(0.57)[a]	-0.66	(1.14)	1.13	(1.19)	-3.13	(1.00)	-2.11	(1.63)
Litter	4	-26.79	(0.80)	4	-27.56	(0.23)	4	-27.91	(0.22)	4	-26.98	(0.30)	-0.79	(1.46)	0.19	(0.92)	-2.86	(0.57)	-1.42	(0.93)
Plant–Litter average*	8	-27.44	(0.45)	8	-28.50	(0.46)	8	-27.84	(0.19)	8	-27.24	(0.31)	-0.71	(0.82)	0.66	(0.72)	-2.99	(0.54)	-1.76	(0.88)
Midges*	7	-11.29	(1.08)	2	-16.39	(1.77)	2	-16.34	(2.89)	1	-17.27	–	-0.82	(0.21)	0.51	(0.52)	0.26	(0.71)	0.52	–
Coccidae	4	-30.39	(1.33)	4	-29.56	(1.44)	4	-31.60	(0.92)	4	-30.38	(0.67)	-2.92	(1.27)	-2.46	(0.47)	-2.73	(0.93)	-1.27	(1.34)
Delphacidae	4	-23.28	(1.06)	3	-26.04	(1.04)	2	-26.91	(4.90)	4	-23.74	(1.42)	-2.59	(1.26)	-0.43	(0.89)	-3.20	(0.66)	-1.85	(0.72)
Cicadellidae†	4	-25.29	(1.98)	–			–			–			-0.73	(0.87)	–		–		–	
Miridae*†	4	-12.59	(1.74)	1	-21.05	–	–			–			1.39	(0.22)	4.15	–	–		–	
Herbivore average*	8	-26.83	(1.56)	7	-28.05	(1.12)	6	-30.04	(1.71)	8	-27.06	(1.45)	-2.75	(0.83)	-1.59	(0.59)	-2.88	(0.62)	-1.56	(0.71)
Collembola	5	-15.75	(1.04)[a]	4	-23.57	(1.12)[a]	6	-26.32	(1.25)[b]	5	-23.25	(1.04)[b]	0.73	(0.52)	0.56	(0.63)	-3.03	(0.92)	-1.59	(1.15)
Acari	10	-19.51	(1.45)	5	-20.59	(0.93)	7	-25.30	(1.47)	4	-22.54	(1.33)	0.92	(0.76)	0.15	(1.34)	-1.60	(1.00)	-2.75	(1.51)
Detritivore average*	15	-18.26	(1.11)	9	-21.91	(0.85)	13	-25.77	(0.95)	9	-22.94	(0.78)	0.86	(0.52)	0.33	(0.75)	-2.26	(0.69)	-2.10	(0.89)
Carabidae	5	-21.17	(0.96)[a]	5	-23.18	(0.98)[a]	3	-23.01	(1.17)[a]	2	-28.16	(0.25)[b]	4.53	(0.66)	4.88	(0.76)	1.31	(0.81)	2.02	(0.28)
Beetle average*	10	-22.08	(0.98)	11	-22.92	(0.53)	4	-23.13	(0.84)	6	-25.30	(1.22)	4.56	(0.37)	3.21	(0.68)	1.47	(0.59)	2.23	(0.18)
Linyphiidae	5	-14.05	(1.50)[a]	6	-21.23	(0.57)[b]	4	-21.85	(0.96)[b]	7	-22.56	(0.77)	3.15	(1.26)	3.95	(0.73)	2.12	(0.86)	1.99	(1.04)
Lycosidae	7	-13.19	(1.12)[a]	7	-20.84	(0.75)[b]	7	-19.56	(0.66)[b]	8	-24.06	(0.64)	2.81	(0.24)	3.23	(0.22)	2.14	(0.40)	1.59	(0.74)
Other spiders	6	-13.13	(2.12)[a]	2	-23.07	(0.98)[b]	4	-22.77	(1.29)[b]	4	-24.49	(0.71)[b]	2.70	(0.39)	3.40	(0.77)	0.76	(0.57)	2.16	(0.86)
Spider average*	18	-13.41	(0.88)	15	-21.29	(0.45)	15	-21.03	(0.61)	19	-23.60	(0.44)	2.87	(0.36)	3.54	(0.32)	1.76	(0.34)	1.85	(0.50)
Opiliones*	6	-8.17	(0.85)[a]	6	-19.84	(0.72)[b]	3	-19.04	(1.07)[b]	4	-21.52	(0.81)[b]	2.12	(0.14)	1.94	(0.23)	0.04	(0.42)	-0.16	(0.43)

Notes: Different letters across a row indicate significant differences in isotopic values between lakes as indicated by Tukey HSD, post-hoc test.
*values plotted in Figure 2.
†not used in analyses due to rarity at several lakes. Presented for illustrative purposes.

distance from shore (5, 50, 150 m) and their interaction as fixed factors. Potential spatial correlations of midge catches between sampling stations within transects, transects within sites or lakes were not modeled in the ANOVA.

Stable isotope patterns in terrestrial communities surrounding lakes were examined using three complementary approaches. First, we examined the degree of stable isotope change of the entire assemblage of terrestrial arthropod consumers among lakes using a multivariate analysis based on calculating a euclidean distance matrix between $\delta^{13}C$ and $\delta^{15}N$ values of all detritivores, beetles, spiders, and harvestmen taxa collected at each lake. These analyses excluded plants and their herbivores because they were not expected to vary among lakes (see *Results*). We then tested whether the degree of similarity (distance) among the taxonomic groups was greater between lakes compared to the similarity within lakes using ANOSIM (Clarke and Warwick 2001). Pair-wise tests among lakes were performed post-hoc (using Bonferroni-corrected α values) to determine which lakes differ from each other. ANOSIM was performed in PRIMER v.6 (Clarke and Gorley 2006). This analysis allowed us to examine if there were differences in the stable isotope patterns among the dominant consumers when examining the entire assemblage simultaneously. For the remainder of isotope analyses, we focused exclusively on $\delta^{13}C$ because of the large differences in these isotope ratios between terrestrial and aquatic resources.

Second, we examined by ANOVA how $\delta^{13}C$ of different taxonomic groups varied as a function of from which lake they were collected (Mývatn, Miklavatn, Botnsvatn, and Helluvaðstjörn) and distance from shore (near and far from shore, 5 and 150 m, respectively). Multiple comparisons among treatment levels were performed using Tukey's HSD post-hoc test. This allowed us to examine more specifically which taxonomic groups changed in isotopic composition between lakes.

Finally, we examined how the carbon isotope values of terrestrial arthropod consumers changed as a function of midge infall. Shifts (Δ) in $\delta^{13}C$ for a particular taxon (at each sampling location) were calculated as the difference from the average $\delta^{13}C$ of that same taxon estimated at Helluvaðstjörn, a no-midge baseline lake. This makes the assumption that $\delta^{13}C$ of taxa collected at Helluvaðstjörn adequately reflect values of taxa primarily consuming terrestrial resources. Δ $\delta^{13}C$ was calculated separately for each taxon and each sampling location. We then correlated (using Pearson and Spearman statistics) estimates of Δ $\delta^{13}C$ for each sampling location to the amount of midge infall (g m^{-2} d^{-1}, log transformed) at the same collection station (see *Midge infall sampling* above). Analyses were performed using JMP v.7 (SAS Institute 2007) and means are reported ± SEM.

RESULTS

Midge Infall into Terrestrial Communities

Across all sampling stations and lakes there was a gradient of midge abundance that ranged from 0 to 89.5 g dw m^{-2} d^{-1} (Figure 1A). Midge infall into the terrestrial community varied significantly among lakes (Figure 1B). Average midge abundance was highest at Mývatn, with daily infall rates of 18.91 ± 4.28 g dw m^{-2} d^{-1}, whereas Helluvaðstjörn, only 5 km away, had the lowest midge infall over the same period, (0.026 ± 0.0095 g dw m^{-2} d^{-1}, Lake effect, $F_{7,59} = 61.45$, $P < 0.0001$). After accounting for significant differences among lakes, midge abundance was on average over 2.5-times greater nearest to the lake shore compared to far from shore (Figure 1C, Distance effect, $F_{2,59} = 4.44$, $P = 0.016$). Lake × Distance effect was not significant ($F_{14, 45} = 1.03$, $P = 0.45$). The pattern of higher midge infall near shore was most pronounced at Mývatn with infall (combining 5 and 50 m distances) averaging 23.85 compared to 6.58 g dw m^{-2} d^{-1} at distances far (150 m) from shore (Distance effect, $F_{2,19} = 8.3$, $P = 0.003$). Average nitrogen (N) and phosphorous (P) content of midges caught in collectors (>99% *T. gracilentus*) was 9.19 ± 0.55% ($n = 13$) and 1.30 ± 0.06% ($n = 6$), respectively.

Stable Isotope Evidence for Food Web Linkages

Grasses and plant litter in the areas adjacent to subarctic lakes in northeast Iceland had on average $\delta^{13}C = -28.20 \pm 0.29\text{‰}$ and $-27.31 \pm 0.23\text{‰}$, respectively (Figure 2, Table 1). There was no difference in $\delta^{15}N$ of plants among lakes (overall mean = $-1.19 \pm 0.70\text{‰}$, Table 1, $P = 0.85$). Midges collected in terrestrial habitats had significantly enriched isotopic values, $\delta^{13}C = -13.47 \pm 1.01\text{‰}$, compared to plants ($F_{1,20} = 207.4$, $P < 0.0001$) and did not vary significantly among lakes (Figure 2, Table 1, Appendix 1 in Electronic Supplementary Material, $P = 0.07$). Stable isotopes of N of midges were not significantly different from that of plants ($F_{1,20} = 2.17$, $P = 0.16$) making this isotope uninformative for discriminating between aquatic and terrestrial resources.
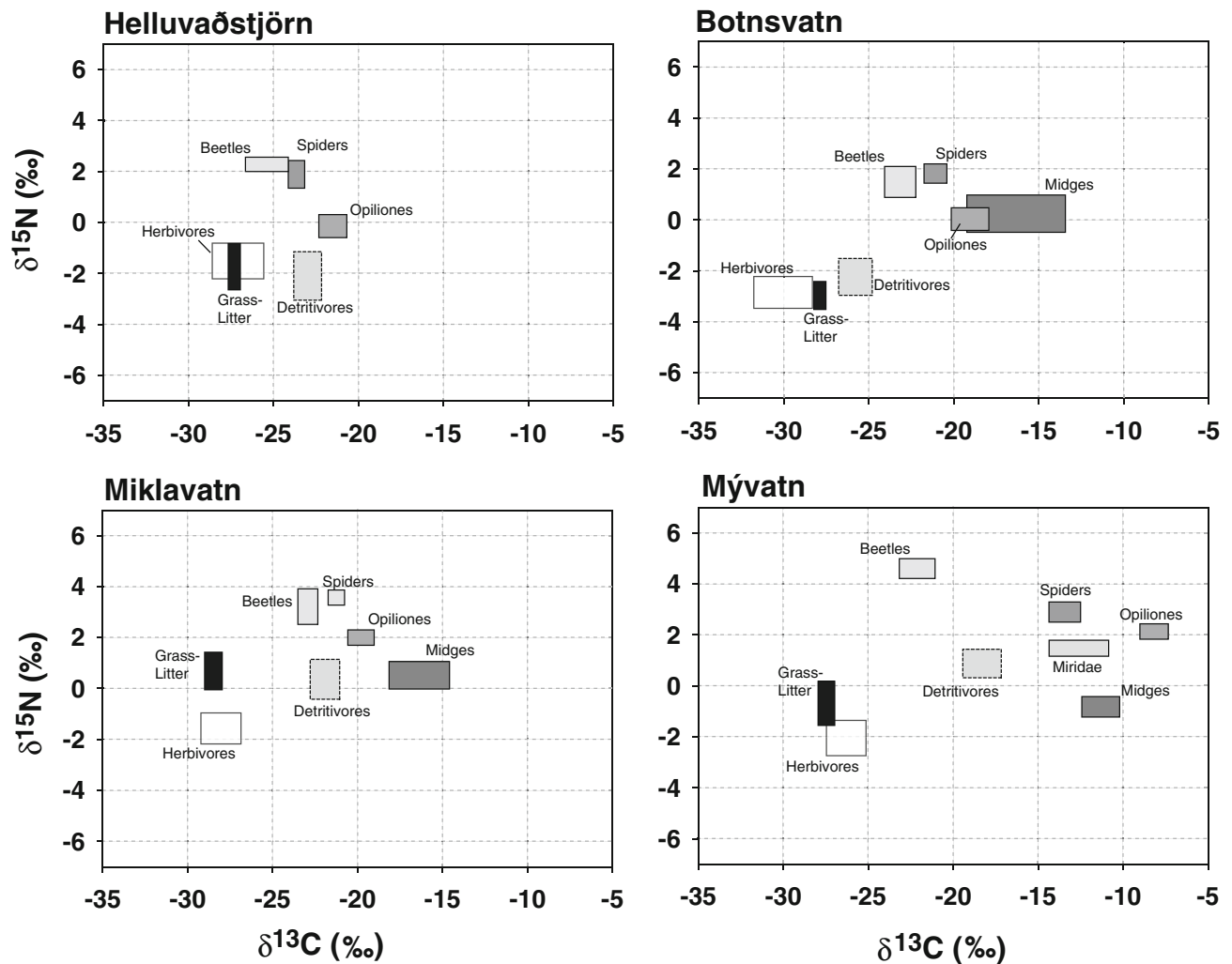
Figure 2. $\delta^{13}C$ and $\delta^{15}N$ (‰) isotope bi-plot of arthropod taxa and terrestrial resources (plants and litter) collected at four lakes in northern Iceland spanning across a gradient of low (Helluvaðstjörn) to high midge inputs (Mývatn) in August 2006. Boxes are centered on mean isotope values and bound ± 1 SEM. See Table 1 for details of specific taxa.

Taken as a group terrestrial arthropod consumers (excluding herbivores) had significantly different $\delta^{13}C$ and $\delta^{15}N$ across lakes (Appendix 2 in Electronic Supplementary Material, $P = 0.004$). Arthropods at Mývatn were significantly different than those of other lakes (Figure 2, Table 1, Appendix 1 in Electronic Supplementary Material) although this difference was most striking when Mývatn taxa are compared to those at Helluvaðstjörn ($P = 0.004$), and only marginally significant ($P = 0.01$–0.02) for comparisons with Miklavatn and Botnsvatn (Appendix 2 in Electronic Supplementary Material).

Examining the patterns of isotopic composition of individual consumers supports the general pattern observed with the multivariate community isotope analyses. Isotopic values of C and N of consumers varied significantly among lakes (Figure 2, Table 1, Appendix 1 in Electronic Supple-

mentary Material). Individual taxa were typically most enriched in $\delta^{13}C$ at Mývatn and most depleted at Helluvaðstjörn (Table 1). This pattern was not observed in sap-feeding herbivores (delphacids and scales) and staphylinid beetles, which had statistically similar $\delta^{13}C$ values across lakes (Appendix 1 in Electronic Supplementary Material).

In addition to varying across lakes, the isotopic values of terrestrial consumers varied as function of midge input. As the abundance of midges within the terrestrial community increased, the average $\delta^{13}C$ of detritivores and predators became significantly more enriched by about ($\approx + 10$ ‰) relative to the conditions when midges are absent (Figure 3). There was a significant relationship between midge infall and amount of $\delta^{13}C$ change (Δ) for spiders and harvestmen (Table 2, $r > 0.83$, $\rho > 0.70$) and to a lesser degree detritivores such as
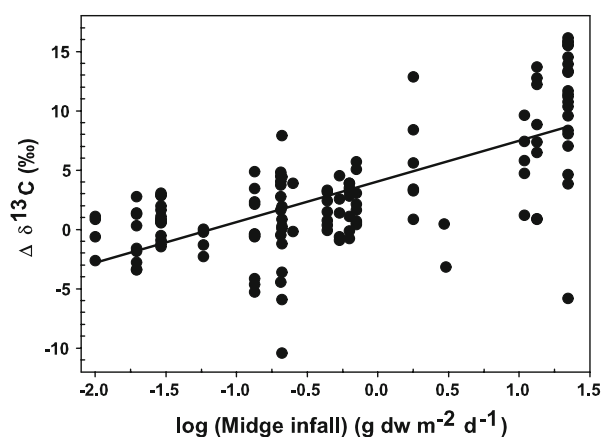
Figure 3. Relationship between the change (Δ) in $\delta^{13}C$ isotope values (‰) of consumers relative to the average $\delta^{13}C$ of that same taxon at a midge-free lake (Helluvaðstjörn) versus the amount of midge infall (g dw m^{-2} d^{-1}, log-transformed) at the sampling station where taxa were collected. Only taxa that showed a significant correlation (Table 2, Collembola, linyphiid, lycosid, and other spiders, and opilionids) are shown. This pattern illustrates that as midge infall into the terrestrial system increases, the average $\delta^{13}C$ value of these arthropods becomes more enriched (positive) suggesting increasing intake of aquatic-derived (that is, midge) C ($\delta^{13}C \approx -13.5$‰) relative to terrestrial C sources ($\delta^{13}C \approx -28.2$‰).

Collembola ($r = 0.65$). Mites ($\rho = 0.52$) and ground beetles ($\rho = 0.55$) showed trends ($P = 0.02$–0.04) in the same direction.

DISCUSSION

Despite the ubiquity of lakes in terrestrial landscapes, there are few studies that have quantified the amount of material entering terrestrial habitats from lakes and their effects on terrestrial communities and thus the strength of the ecological linkages between lakes and land. This study shows that midge emergences from productive subarctic lakes can be large and that lake benthic production can fuel trophic interactions on land. In this system, chironomid midges, by virtue of having aquatic larval stages that are adapted to exploiting high nutrient environments (Kohler and others 2005) and adult life stages that move over land to mate (Armitage 1995), are vectors of material, nutrients and energy that can energetically and trophically link aquatic to terrestrial ecosystems as "mobile links" (sensu Lundberg and Moberg 2003).

The significantly enriched $\delta^{13}C$ isotopes of consumers in areas where midge inputs are high (Figure 2) indicates that terrestrial arthropods are utilizing midges, either directly as prey or indirectly as carcasses decay on the soil surface. The average

Table 2. Summary of Correlations Between Midge Infall (g dw m^{-2} d^{-1}) and the Change (Δ) in $\delta^{13}C$ of a Given Taxon Relative to Taxon Average at a Midge-Free Lake (Helluvaðstjörn)

Taxa	n	Correlation of midge infall[a] (g dw m^{-2} d^{-1})			
		r[b]	P	ρ[c]	P
Coccidae	16	−0.015	0.956	0.018	0.948
Delphacidae	13	0.126	0.681	0.226	0.458
Collembola	20	0.654	**0.002**	0.550	<u>0.020</u>
Acari	26	0.432	<u>0.028</u>	0.516	<u>0.007</u>
Carabidae	15	0.588	<u>0.022</u>	0.547	<u>0.035</u>
Staphylinidae	16	0.232	0.387	0.189	0.483
Linyphiidae	22	0.833	**<0.0001**	0.704	**0.0003**
Lycosidae	29	0.842	**<0.0001**	0.804	**<0.0001**
Other spiders	16	0.848	**<0.0001**	0.863	**<0.0001**
Opiliones	19	0.891	**<0.0001**	0.766	**0.0001**

Notes: In bold are values significant at $\alpha = 0.05/10$ (0.005), values significant at $\alpha = 0.05$ are underlined.
[a]*log transformed.*
[b]*Pearson correlation coefficient.*
[c]*Spearman correlation coefficient.*

$\delta^{13}C$ of the terrestrial arthropod community shifts significantly in magnitude and directionality (toward enriched midge values) in the presence of midge inputs (Figure 3). This pattern is evident whether one examines large-scale patterns across lakes (Figures 1B, 2) or a fine scale, among sampling locations (Figures 1A, 3). In contrast, in the absence of midge inputs, depleted $\delta^{13}C$ isotope values suggest that arthropod communities primarily exploit resources ultimately deriving from terrestrial plants, such as C3 grasses, shrubs or decomposing plant litter.

Aquatic Inputs into Terrestrial Systems

Using Mývatn as the extreme example, our estimates of midge infall into the terrestrial habitats, taken over a one-week period in early August coinciding with peak adult emergence of the second generation of *T. gracilentus* indicate that on average 189 kg ha^{-1} d^{-1} (101–277 kg ha^{-1} d^{-1}, 95% CI) of midges landed around the lake. Gardarsson and others (2000) found that at one location 5 m inland on the eastern shore of Mývatn (Kálfaströnd) a window trap operating continuously during summer months between 1977 and 1996 collected a median of 290 kg midges dw ha^{-1} d^{-1} (122–1630 kg ha^{-1} d^{-1}, 25–75% quantile range) in August indicating that our midge infall estimates are within the observed ranges at Mývatn. Midge infall estimated from cup collectors

or window traps should be viewed as the maximum input of what actually may enter the terrestrial system because traps are lethal to midges as they alight in the collector–a condition that overestimates mortality in the terrestrial system. Reanalysis of Gardarsson and others (2000) gives a rough estimate of midge infall in one location at Mývatn (Digital Supplement 2). From a window trap operating between 1977 and 1996, a median of approximately 2500 kg midges ha^{-1} y^{-1} (1044–12756 kg ha^{-1} y^{-1}, 25–75% quartile range, assuming average 0.15 mg dw midge and 0.03 m^2 traps) was collected.

Although both our more spatially widespread measures of daily midge input rates and estimates of annual midge input from Gardarsson and others (2000) appear large, additional evidence suggests that midge inputs to terrestrial habitats around Mývatn are, in fact, substantial. Lindegaard and Jonasson (1979) estimated whole-lake benthic annual midge production from sediment cores during a peak in midge population cycles between 1972 and 1974 at approximately 981 metric tons y^{-1} (325–1636 metric tons y^{-1}, 95% CI), of which they speculate about 50% of this production enters terrestrial habitats. If the majority of this production lands within a 150-m area around the lake (total area 7.7 km^2), this corresponds to annual inputs of 1273 kg ha^{-1} y^{-1} (422–2125 kg ha^{-1} y^{-1}, 95% CI). Taken together, these independent data suggest that the amount of aquatic benthic production entering the terrestrial system annually is large and widespread. Moreover, these estimates of aquatic fluxes to land are comparable to estimates of terrestrial aboveground NPP in heathlands in Iceland of approximately 1200 kg ha^{-1} y^{-1} (range 400–2000 kg ha^{-1} y^{-1}, Kardjilov and others 2006). This suggests that around Mývatn as much C is coming onto land by way of midges as is produced by plants each year.

In addition to transporting C to land midges also represent a flux of N and P. Adult midges are on average 9.2% and 1.3% total N and P, respectively. We estimate that in August 2006 midges carried to land approximately 17 kg N ha^{-1} d^{-1} and 2.5 kg P ha^{-1} d^{-1}. If annual terrestrial midge inputs estimated from Gardarsson and others' (2000) window traps and Lindegaard and Jonasson's (1979) benthic productivity measurements are representative this translates to average annual inputs of 118–250 kg N ha^{-1} y^{-1}. As atmospheric N deposition to high-latitude regions is generally considered to be low ($\ll 5$ kg ha^{-1} y^{-1}, Gordon and others 2001; Wolfe and others 2006), estimated levels of N input by midges to habitats surrounding lakes in northern Iceland suggests that midges have the potential to significantly affect terrestrial communities. For example, the critical nutrient load for arctic heathlands is estimated to be between 5 and 15 kg ha^{-1} y^{-1}. Fertilization experiments in the high arctic of similar plant communities resulted in rapid changes in biomass and shifts in species composition with the addition of 15–30 kg N ha^{-1} y^{-1} (Shaver and others 2001; Shevtsova and others 2005).

The spatial extent of aquatic inputs into terrestrial habitats is dependent on insect dispersal away from shore and inland. Exponential decay of insects away from shore are commonly observed (Jackson and Resh 1989) resulting in few aquatic insects typically collected beyond 50 m from streams (Petersen and others 1999; Power and others 2004). In Iceland, although midges decline in abundance from shore, they are still present in significant numbers up to 150 m inland (Figure 1C). This may simply reflect differences in insect abundance emerging from the lake, with higher abundances near shore, or it may represent inherent differences between lakes and streams in the dispersal of organisms away from water. In either case, understanding the factors that influence dispersal of organisms across ecosystem boundaries will be essential for predicting the spatial extent of the linkages between water and land and how much material is delivered inland.

Midge inputs into terrestrial systems also have the ability to influence food webs by directly and indirectly affecting predators, decomposers, herbivores, and plants. The $\delta^{13}C$ patterns of predators such as spiders show that they are strongly influenced by availability of midge resources (Tables 1 and 2, Figures 2 and 3) and may be consuming midges directly (for example, Power and others 2004; Paetzold and others 2005). Opiliones (harvestmen), which may act as both predators or scavenge recently dead animals (Halaj and Cady 2000), show the greatest changes in carbon isotope values as midges become more prevalent. Collembola are likely acting as detritivores and, along with microbes, decompose dead midges. Other components of the terrestrial food web (for example, herbivores) may also indirectly benefit from lentic inputs via changes in plant quality (increased N or P) although this would not be reflected in their carbon isotope signatures because they are accessing carbon from plants. Further studies will be required to examine how food web interactions and their dynamics are influenced by midge inputs. Nevertheless, this study provides evidence that multiple terrestrial consumers are either directly or indirectly accessing midge-derived carbon.

Conclusions

The degree to which adjacent systems are linked depends on the total flux between systems and the spatial extent of the flux (Baxter and others 2005). The large midge swarms originating from lakes in northern Iceland demonstrate that aquatic subsidies have the capacity to fuel terrestrial arthropod food webs around lakes and this effect is proportional to the quantity of the allochthonous input. Although Mývatn and associated lakes are not unique in producing zoobenthos that is exported to the terrestrial ecosystems, this category of ecosystem linkages is rarely measured or is assumed to be of minor importance (Milner and others 2007). Given that lake exports to land are common and can fuel terrestrial food webs, the challenge lies in understanding the factors that modulate the strength of these linkages, their spatial extent and how their effects may propagate over time. Even though Mývatn may represent an extreme case of insect-derived linkages between lakes and land, our study of lakes in northern Iceland suggest that such linkages represent a largely unexamined, but potentially important interaction that can help understand the dynamics of terrestrial food webs.

ACKNOWLEDGMENTS

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