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Quantifying aquatic insect deposition from lake to land

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Abstract. Adjacent ecosystems are influenced by organisms that move across boundaries, such as insects with aquatic larval stages and terrestrial adult stages, which transport energy and nutrients from water to land. However, the ecosystem-level effect of aquatic insects on land has generally been ignored, perhaps because the organisms themselves are individually small. At the naturally productive Lake Mývatn, Iceland, we used two readily measured quantities: total insect emergence from water and relative insect density on land, to demonstrate an approach for estimating aquatic insect deposition (e.g., kg $N{\cdot}m^{-2}{\cdot}yr^{-1}$) to shore. Estimates from emergence traps between 2008 and 2011 indicated a range of 0.15–3.7 $g{\cdot}m^{-2}{\cdot}yr^{-1}$, or a whole-lake emergence of 3.1–76 Mg/yr; all masses are given as dry mass. Using aerial infall trap measurements of midge relative abundance over land, we developed a local-maximum decay function model to predict proportional midge deposition with distance from the lake. The dispersal model predicted midge abundance with $R^2 = 0.89$, a pattern consistent among years, with peak midge deposition occurring 20–25 m inland and 70% of midges deposited within 100 m of shore. During a high-midge year (2008), we estimate midge deposition within the first 50 m of shoreline to be 100 $kg{\cdot}ha^{-1}{\cdot}yr^{-1}$, corresponding to inputs of 10 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ and 1 kg $P{\cdot}ha^{-1}{\cdot}yr^{-1}$, or about three to five times above background terrestrial N deposition rates. Consistent with elevated N input where midges are most dense, we observed that soil available nitrate in resin bags decreases with increasing distance from the lake. Our approach, generalizable to other systems, shows that aquatic insects can be a major source of nutrients to terrestrial ecosystems and have the capacity to significantly affect ecosystem processes.

Key words: aquatic insects; aquatic–terrestrial linkages; Chironomidae; cross-ecosystem subsidy; Iceland; nutrient deposition.

Introduction

Many ecosystems are influenced by the movement of energy or nutrients across boundaries in the landscape (Polis et al. 2004, Townsend et al. 2004, Lovett et al. 2010). These transfers are often facilitated by organisms moving between distinct ecosystems. Aquatic insects that emerge from the water as adults and move into nearby terrestrial habitats to feed or mate are one example of this process (Ballinger and Lake 2006). It is estimated that 75–99% of aquatic insects that disperse to land never return to the water (Jackson and Fisher 1986, Gray 1989, Petersen et al. 1999). On land, aquatic insects are prey for terrestrial consumers and/or their carcasses fuel detrital food webs (Hoekman et al. 2011). Aquatic insect deposition (mass falling per unit area per unit time) could thus provide an input of nitrogen and phosphorus to land that significantly affects primary production in nutrient-limited ecosystems adjacent to water. Understanding the potential ecosystem-level effects of insects requires quantification of fluxes of insects in terms relevant to other ecosystem processes, such as g $N{\cdot}m^{-2}{\cdot}yr^{-1}$. Yet, studies of aquatic insects on land have focused on describing their dispersal among habitats or their role as prey for terrestrial consumers (Griffith et al. 1998, Sabo and Power 2002), rather than considering these fluxes as potentially important sources of nutrients to terrestrial ecosystems (e.g., Milner et al. 2007).

Flying insects are usually quantified using various aerial intercept traps (malaise, window, sticky, or pan traps) that passively capture moving insects, providing information useful for estimating relative abundances (Irwin 1980, Southwood and Henderson 2009). Such insect trap catches can be easily converted into estimates of deposition by dividing the total number of insects collected by the surface area of the trap. For example, using aerial cup traps (infall traps) at Lake Mývatn in

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northeast Iceland, Gratton et al. (2008) suggested that as much as 2000 $kg \cdot ha^{-1} \cdot yr^{-1}$ of aquatic midge carcasses might be deposited on land near the lake. This approach assumes that each insect collected would have remained, but these traps offer no opportunity for insects to leave once they have been captured, and probably inflate deposition rates. Thus, the deposition estimates of Gratton et al. (2008) from "lethal" infall traps far exceed the total estimated export of midges from the lake (Lindegaard and Jónasson 1979). Typical methods of insect collection therefore can provide relative estimates of insect activity on land, but are unlikely to accurately estimate actual deposition of insects to land.

Several recent studies suggest approaches to estimate the flux of aquatic insects to terrestrial ecosystems (Gratton and Vander Zanden 2009, Vander Zanden and Gratton 2011, Sabo and Hagen 2012, Muehlbauer et al. 2014). These authors propose using measures of aquatic insect emergence from a given waterbody to set the upper limit on how much aquatic insect material could potentially move over land. Aquatic insect emergence is then distributed spatially over land using relative estimates of insect activity derived from passive traps. Because the density of adult aquatic insects is typically greatest close to the water's edge (Kuusela and Huusko 1996, Petersen et al. 1999), the dispersal of emergent insects from water onto land has been modeled with an exponential decay or inverse power functions (Gratton and Vander Zanden 2009, Sabo and Hagen 2012). Deposition can be constrained by total emergence to provide a mass-balance approach to estimate insect-driven C, N, or P deposition on land using empirical observations of emergence rates and dispersal patterns. Although this approach is straightforward and well established theoretically, examples that quantify the strength of linkages between aquatic and terrestrial systems using empirical measurements are lacking.

Lake Mývatn ("lake of midges") in northeast Iceland provides a model system to estimate the magnitude and extent of aquatic insect deposition to land. Midges emerge from Lake Mývatn and form immense mating swarms around the lakeshore during the summer months. Mated females attempt to return to the lake to lay eggs, but most midges die on the ground after mating, their carcasses providing a substantial but unknown input to the terrestrial detrital pool. Experiments in Iceland show that the addition of midge carcasses to subarctic heathlands increases detritivorous arthropod abundance (Hoekman et al. 2011), and observations show that midges around Icelandic lakes increase the abundance of both predators and detritivores and herbivores, likely due to consumption of midges or through bottom-up nutrient effects, respectively (Gratton et al. 2008, Dreyer et al. 2012). In addition, plants in high-midge areas tend to be of higher quality (lower C:N ratio) than those of the same species in low-midge areas (Bultman et al. 2014), suggesting that midge-derived N increases leaf N concentrations. Together, these patterns suggest that aquatic insect deposition on land has a pervasive and significant effect on the entire terrestrial community within the dispersal range of these small aquatic insects.

The discrete nature of the insect source (Lake Mývatn), with no other major sources of aquatic insects in the landscape, provides the opportunity to couple emergence and infall data to estimate the terrestrial input from an aquatic source. Between 2008 and 2011, we measured midge emergence rates from the south basin of Lake Mývatn and simultaneously estimated relative midge abundance on land at various distances from shore using infall cups to develop a model to predict the mass of deposition of insects into the terrestrial ecosystem. Our approach is general and adaptable to other systems for which emergence (or some rate of production that is exported) and the shape of the dispersal function can be estimated. This enables a spatially and temporally explicit quantification of the strength of the linkage between adjacent ecosystems.

Materials and Methods

Study system

Lake Mývatn, Iceland (65°36′ N, 17°0′ W) is a large (38 km^2), shallow (4 m maximum depth) lake divided into two large basins that function mostly as independent hydrologic bodies (Ólafsson 1979; Appendix A: Fig. A1). The number of non-biting midge (Diptera: Chironomidae) larvae on the lake bottom is high, but variable; midge production between 1972 and 1974 ranged from 14 to 100 (ash-free) $g \cdot m^{-2} \cdot yr^{-1}$, averaging 28 $g \cdot m^{-2} \cdot yr^{-1}$ (Lindegaard and Jónasson 1979); all masses presented as dry mass. The midge assemblage is mostly comprised of two species (>90% of total individuals), *Chironomus islandicus* (Kieffer) and *Tanytarsus gracilentus* (Holmgren), which feed as larvae in the sediment in silken tubes by scraping diatoms, algae, and detritus off the lake bottom (Lindegaard and Jónasson 1979). At maturity (May–August), midge pupae float to the lake surface, emerge as adults, and fly to land, forming large mating swarms around the lake (Einarsson et al. 2004, Gratton et al. 2008; Appendix B: Fig. B1). On land, midges are consumed by terrestrial predators (Gratton et al. 2008, Dreyer et al. 2012), or enter the detrital pool upon death (Gratton et al. 2008, Hoekman et al. 2012). Midge populations naturally cycle with 5–8-year periodicity, with abundances fluctuating by three to four orders of magnitude (Einarsson et al. 2002, Ives et al. 2008).

General approach

Our objective was to estimate midge deposition on land around the south basin of Lake Mývatn (Appendix B: Fig. B1). For four summers (2008–2011), we measured the dry mass of midges emerging from the basin, expressed on a per unit area basis ($g \cdot m^{-2} \cdot yr^{-1}$) and referred to as emergence (Appendix B: Fig. B1A). Simultaneously, we collected midges (g/yr) in aerial

infall traps at sampling stations on land to estimate the relative infall rates (Appendix B: Fig. B1B) used to develop a dispersal function of expected midge input to land as a function of distance from the lake. Deposition (Appendix B: Fig. B1C), or the dry mass of midges falling to land per unit area ($g \cdot m^{-2} \cdot yr^{-1}$), is modeled by combining information on the measured midge emergence and the spatial and temporal patterns of midge infall.

Midge emergence

We used submerged conical traps to estimate midge emergence from Lake Mývatn (Appendix B: Fig. B1A). Traps were constructed of 2-mm clear polycarbonate plastic (Laird Plastics, Madison, Wisconsin, USA) formed into a cone with a large-diameter opening of 46 cm (0.17 m^2). The tops of the cones were open to a diameter of 10 cm, with a clear jar affixed at the apex. The trap was weighted to approximately neutral buoyancy, with the jar at the top containing air to allow mature midges to emerge. Traps were suspended with a nylon line ~1 m below the surface of the lake from an anchored buoy. For sampling, traps were raised to the surface and rapidly inverted, preventing midges from escaping. Jars and traps were thoroughly rinsed with lake water to collect all trapped midges, including unmetamorphosed larvae and pupae, and scrubbed before being returned to the lake to prevent growth of epiphytic algae and colonization by midges. We assumed that the emergence traps collected all potentially emerging midges from the sampling area, though it is likely an underestimate, since some midges initially captured could fall out of the trap. Thus, our results should be considered a conservative estimate of potential midge emergence from the surface of the lake.

We sampled midge emergence throughout the south basin of Lake Mývatn. Emergence was sampled at six sites in 2008 and 2011 and 10 sites in 2009 and 2010, with locations relocated using GPS and natural sightlines (Appendix A: Fig A1). Each site had two traps within 5 m of each other that were monitored during midge activity, from the last week of May to the first week of August (third week of July in 2009 and 2011; Appendix C: Table C1). Midge emergence outside of this time frame is extremely low (Lindegaard and Jónasson 1979) and we assumed it to be zero, again erring toward conservative estimates of annual midge emergence from the lake. Traps were checked weekly during periods of high emergence (initial and final 2–3 weeks of the study), and biweekly during low-emergence periods in the middle of the study (July). Midges were identified as *Chironomus islandicus* (>5 mm) or *Tanytarsus gracilentus* (<5 mm); these two species account for 90% of midge production in Lake Mývatn (Lindegaard and Jónasson 1979). From a sample of 100 midges of each size collected in 2008 and 2011, we determined the average dry mass of *Chironomus* midges to be 1.0 ± 0.1 mg (mean ± SE) and *Tanytarsus* midges to be 0.1 ± 0.05 mg. Total annual midge emergence rate per unit area ($g \cdot m^{-2} \cdot yr^{-1}$) at each site was computed as the annual sum of the count of *Chironomus* and *Tanytarsus* midges collected by the trap multiplied by the average midge dry mass and divided by the area of the trap.

Total annual emergence from Lake Mývatn (g/yr) was estimated as the product of midge emergence ($g \cdot m^{-2} \cdot yr^{-1}$) and lake-bottom area ($m^2$) suitable as midge habitat (Appendix A: Fig. A1). We considered the midge-producing area of the lake to be away from rocky shorelines and dominated by epibenthic algae (Einarsson et al. 2004). A Voronoi tessellation (a set of polygons whose interiors are closer to their centroid than any other point) centered at trap locations was used to extrapolate emergence over areas we did not directly sample. Because we did not measure emergence from the north basin of Lake Mývatn, all data reported here are for the south basin and its surroundings only. Finally, we estimated the mean and 95% confidence intervals of total annual emergence from 999 permutations of a randomized selection of one trap per site per sampling period.

Midge infall on land

We deployed 11 transects of passive, lethal aerial infall traps arrayed at variable distances from Lake Mývatn to estimate relative midge abundance on shore during the summers 2008–2011 (Appendix B: Fig. B1B). Each transect was perpendicular to the lake edge, with traps located at approximately 5, 50, 150, and 500 m (where possible) from shore for a total of 31 traps around the lake. Sampling locations were recorded using GPS and precise distances from the lake were calculated within a geographic information system. Traps consisted of a single 1000-mL clear plastic cup (0.0095-m^2 opening) affixed 1 m above the ground on a stake and filled with 300–500 mL of a 1:1 mixture of water and ethylene glycol (ESSO antifreeze/coolant, Imperial Oil, Toronto, Ontario, Canada) and a trace amount of unscented detergent to capture, kill, and preserve insects landing on the surface of the liquid (Gratton et al. 2008, Dreyer et al. 2012). Midges and other insects were emptied from the traps weekly and the traps were reset immediately, thus collections span the entirety of each summer. To determine rates of midge infall, the count of both midge types from each infall cup was multiplied by its average dry mass, summed, and standardized by the number of days the traps were active to get midge infall (g) per day for each sample period.

Midge density decay function

For each transect and sampling period, we standardized midge infall measurements to a proportion as a function of the area under the curve defined by infall per cup (y-axis) and distance (x-axis). This facilitated comparison of decay functions between transects and across sampling periods in which there were sometimes orders-of-magnitude differences in total midge abun-

dance. Some trapping periods at a single transect were removed from our analysis because of missing observations, or when the most distant sample on a transect (~150 m or ~500 m) had higher infall than closer samples, as this prevented integrating infall with distance. This circumstance only occurred when midge infall approximated low background levels across the length of a transect, and therefore had little effect on estimates of total midge infall on the landscape. Data from two short transects (103 m and 123 m) were also excluded because they did not capture enough distance from shore to characterize a decay function with distance from Lake Mývatn. Proportion data were arcsine square-root-transformed for further analysis.

We developed a local-maximum decay function model to predict the proportion of midge infall as a function of distance from the lake edge. An examination of our data indicated a local-maximum model form best described the infall pattern where midge abundance increases from zero at the lake edge to a maximum some short distance from the lake and then declines to zero with increasing distance. The model form was

$$\arcsin\sqrt{I_{\hat{p},d}} = ad^b e^{cd} \quad (1)$$

where $I_{\hat{p},d}$ is the proportion ($\hat{p}$) of infall at distance d from the lake, and a, b, and c represent empirically fit parameters which describe the shape of the curve and its decay with distance, and are generated when fitting a three parameter local-maxima model. Note that the value of d at the first derivative of Eq. 1 is the distance at which maximum infall occurs. We solved for a, b, and c using PROC NLMIXED in SAS v. 9.3 (SAS Institute, Cary, North Carolina), weighting observations by total infall at a sample site, so that periods with greater total infall along a transect influenced the model more than periods with lower midge infall. We initially tested a mixed-effects version of the model in which year of sampling was treated as a random effect, but found no statistically significant differences in parameters a, b, and c by year. Therefore, we combined all years for analysis, and the derived parameters are applicable to any year, regardless of midge activity.

We also examined alternative distance functions for insect deposition, including negative exponential and inverse power decay functions, which are suggested as being common for aquatic insects dispersing from lakes (Gratton and Vander Zanden 2009). For these comparisons, we used a subset of the infall data restricted to sample sites with non-zero predicted values for the negative exponential model. Nevertheless, the local-maxima model (even with an additional parameter) was a superior fit to the data (adjusted pseudo $R^2 = 0.674$, Akaike's information criterion [AIC] = 144.1) compared to either the negative exponential (adjusted pseudo $R^2 = 0.274$, AIC = 188.5) or the inverse power model (adjusted pseudo $R^2 = 0.515$, AIC = 164.7). Thus, for the remainder of this study, we used the local-maxima decay function to describe midge dispersal from shore.

We developed local-maximum decay functions on six variants of our data: the infall generated from weekly sampling (weekly model, based on total infall per station per week for all four years, $N = 603$ samples), and the cumulative data summed for each station during a year (annual model, $N = 108$ samples). In addition, weekly and annual models were generated separately for *Chironomus* only, *Tanytarsus* only, and all midges (sum of *Chironomus* and *Tanytarsus*), for a total of six models (three midge types × two temporal aggregation schemes). We evaluated the robustness of each model through jackknifed cross-validation. Specifically, we dropped each year of sampling sequentially, redeveloped our predictive model, and tested that model on the dropped year. Model evaluation included analyses of both arcsine square-root-transformed data as well as the data back-transformed from proportions to total infall.

Midge deposition model

We developed a spatial model to map deposition of midges (Appendix B: Fig. B1C) as a function of the total mass of emergent midges from the lake and the local-maximum decay function (Eq. 1) describing the distribution of midges on land with distance from the lake. The spatial version of the model was area-weighted in 5-m bands from the lakeshore to the maximum distance beyond which midge infall approximates background levels of aerial insect activity (which we defined as <0.01% of total midge infall along a transect). This accounts for differing areas of land at different distances from the lake due to its irregular shape (Mývatn shoreline development factor, $D_L = 4.34$). Proportion of deposition is therefore estimated by 5-m distance bands, as weighted by the area within each concentric band. Mapping was conducted using custom Python (v. 2.7; Python, Wilmington, Delaware, USA) scripts. Since the model is independent of time, the only inputs required to generate maps of midge deposition are the total midge emergence over a desired time period and the proportion of emerged midges estimated to move onto and remain on land (and not to return to the lake).

We compared model-predicted midge deposition to land ($g \cdot m^{-2} \cdot yr^{-1}$) at Lake Mývatn to another estimate of deposition that can be directly estimated from the lethal midge infall traps. Since infall traps have a known area over which midges are captured (0.0095-m^2 openings), we can use the mass of midges collected in a cup over the entire sampling period (g/yr) to calculate deposition by dividing by the cup area ($g \cdot m^{-2} \cdot yr^{-1}$; e.g., Gratton et al. 2008). This alternative estimate measured from the lethal traps on land was compared to the predicted deposition based on the emergence-constrained midge-deposition model described. For these tests, all data were natural-log-transformed to meet assumptions of normality of residuals. We included year and transect as random effects to determine the importance of time and location around the lake on the models.

Relative soil N availability

Midge deposition to land is expected to contribute nutrients into the terrestrial system. To measure whether the predicted midge deposition has a relationship with soil N availability, in May 2008 we buried 10-g ion exchange resin (Rexyn I-300, Thermo Fisher Scientific, Waltham, Massachusetts, USA) bags 8 cm deep at 19 of the infall cup stations and an additional eight sites 20 m from shore. Bags were retrieved in August 2008 and frozen until laboratory N extractions were performed following standard methods (Binkley et al. 1986, Kalra et al. 2007), and samples were run using a flow injection analyzer (Flow Solution 3100, OI Analytical, College Station, Texas, USA). To examine the relationship between midge deposition and available nitrogen in the soil, we fit a least squares regression of extracted nitrate ($\mu g\ NO_3^-\cdot[g\ resin]^{-1}\cdot d^{-1}$) from the resin bags as a function of our local-maximum modeled deposition (log-transformed). All analyses were performed using R 2.13.2 (R Development Core Team 2011).

Results

Midge emergence

Midge emergence measured from in-lake emergence traps (Appendix B: Fig. B1) was greatest at the beginning (late May/early June) and near the end of summer (late July), with lowest emergence during early July (Appendix C: Table C1). Cumulative whole-lake annual midge emergence was highest in 2008, with 76 Mg midges/yr emerging from the lake, and declined to less than 4 Mg/yr in 2011 (Appendix C: Fig. C1), representing the natural declining phase of the midge population cycle over this time period (Ives et al. 2008). These annual emergence values represent an average midge emergence rate from the surface of the lake of 0.15–3.7 $g\cdot m^{-2}\cdot yr^{-1}$.

Midge infall

Midge infall also varied considerably over the 4-yr period. The 5- and 50-m stations averaged >200 g/yr during 2008, but those same locations averaged only 25 g/yr in 2011. Moreover, within a year, midge abundance decreased with increasing distance from shore (Fig. 1A; Appendix D: Table D1). For example, in 2008, infall collection stations 5 m from the lake edge averaged >300 g/yr while those at 500 m collected <20 g/yr. From 50 m on, midge infall decreased as distance from the lake increased, a pattern that was consistent across years (Fig. 1A; Appendix D: Fig. D1).

Decay function

The decay functions showed a congruent pattern of midge density slightly increasing and then rapidly decreasing with distance from lake edge (Fig. 1B). The model form did not differ significantly among formulations that used either all midges combined, or split out small (i.e., mostly *Tanytarsus*) or large (*Chironomus*) midges (Fig. 1B), or where midge emergence and infall was aggregated at either annual or weekly time intervals. Differences between model parameters and fit to the data (Appendix E: Table E1) were minor compared to the overall decay pattern represented in all models. Thus, all data reported here are derived from the all midges, annual aggregation model unless otherwise noted. The ability of the decay model to predict observed midge infall using the yearly summary of all midges was high ($R^2 = 0.89$) and did not vary by year ($F_{3,95} = 0.34$, $P = 0.79$) or transect ($F_{8,95} = 1.04$, $P = 0.41$; Fig. 2A inset). The high R^2 values, coupled with a lack of significance of year or transect, demonstrate that the pattern of decreasing midge infall with increasing distance from shore is consistent over time, as well as space. Cross-validation efforts dropping each year and rebuilding the model with the remaining years indicated consistent model performance (Appendix E: Table E2). Poorest performance in the cross-validation effort was when infall abundance was low (<0.2 g/yr, at some locations in 2008 and 2011), when the model underpredicted midge infall (Fig. 2A inset). At these levels, however, midge activity is near background levels and does not significantly affect subsequent deposition calculations on an absolute basis.

Midge deposition

Our model of midge deposition on the landscape adjacent to Lake Mývatn indicates that midge inputs to the landscape are large in both magnitude and extent. Using the weekly sample data summed within a year, our model predicted peak deposition at 20 m from the lake for all midges, 19 m for *Tanytarsus*, and 52 m for *Chironomus* midges (Appendix E: Table E1). In the peak midge year of 2008, the first 50 m of shoreline adjacent to the lake received an average estimated midge deposition of 100 $kg\cdot m^{-2}\cdot yr^{-1}$ midges (Table 1, Fig. 2A). In 2009–2011, this number declined to approximately 50, 30, and 4 $kg\cdot ha^{-2}\cdot yr^{-1}$, respectively. At Lake Mývatn, we estimate that 35% of midge deposition occurs within the first 50 m of shoreline (330 ha in extent) and 60% within the first 100 m (590 ha, Fig. 2B). Our model predicts that almost 100% of emergent midges are deposited within 2300 ha adjacent to the lake. Since midges are 10% N and 1% P by mass (Fagan et al. 2002, Gratton et al. 2008), this amount of deposition adds 0.4–10 kg $N\cdot ha^{-1}\cdot yr^{-1}$ and 0.04–1 kg $P\cdot ha^{-1}\cdot yr^{-1}$ to the terrestrial ecosystem, depending on the proximity to shore. Similarly, using our polynomial local-maximum deposition model with the "all annual" parameters, we found that nitrate mineralization in resin bags placed in the soil at various distances from shore during a high-midge year (2008) was higher close to the lake (Fig. 3), with $\log(NO_3^-)$ significantly related to distance from shore ($F_{1,25} = 8.66$, $P = 0.007$, adjusted $R^2 = 0.23$).

There was a strong positive relationship ($F_{1,99} = 240.1$, $P \ll 0.0001$, adjusted psuedo $R^2 = 0.701$) between

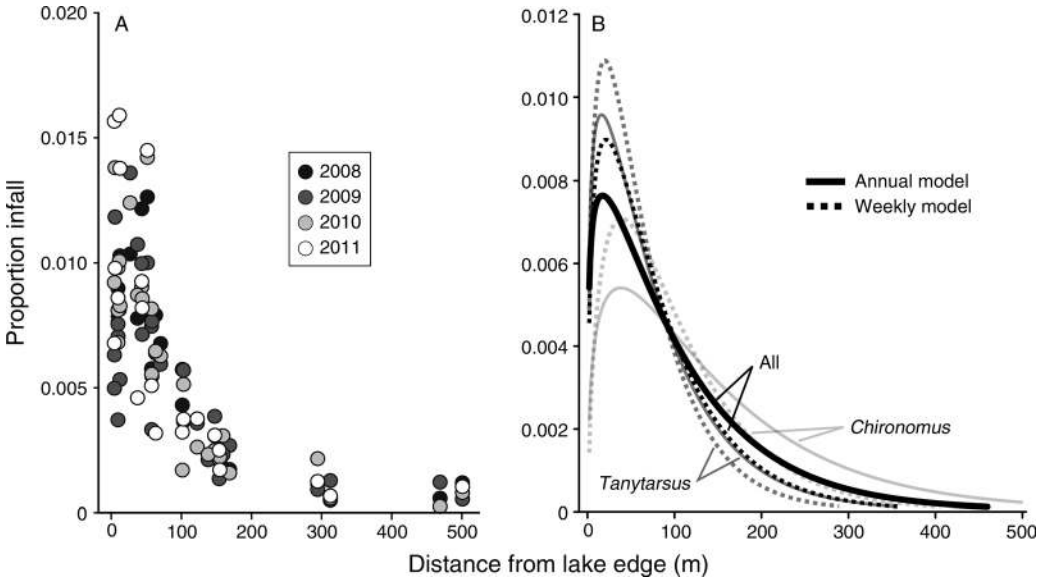

FIG. 1. (A) Proportion of total midge mass collected in infall traps as a function of distance from lake edge at Lake Mývatn, Iceland, during May–August 2008–2011. (B) Model predictions of the proportion of midge biomass deposited as a function of distance from the lake edge from models of different taxonomic identity (*Chironomus* midges shown as light gray lines, *Tanytarsus* midges shown as dark gray lines, and all [sum of all midges] shown as black lines) and collection period (annual or weekly, solid and dashed lines, respectively).

estimated midge deposition from the emergence-constrained model and deposition measured from midge infall cup traps, with year ($F_{3,88} = 2.92$, $P = 0.038$) and transect ($F_{8,88} = 6.51$, $P \ll 0.0001$) having significant effects as well. However, midge deposition estimated with midge infall traps (i.e., by simply dividing cumulative midge catches by the area of the infall cup) was about 25 times higher when compared to the emergence-constrained model across all midge deposition predictions (Appendix E: Fig. E1).

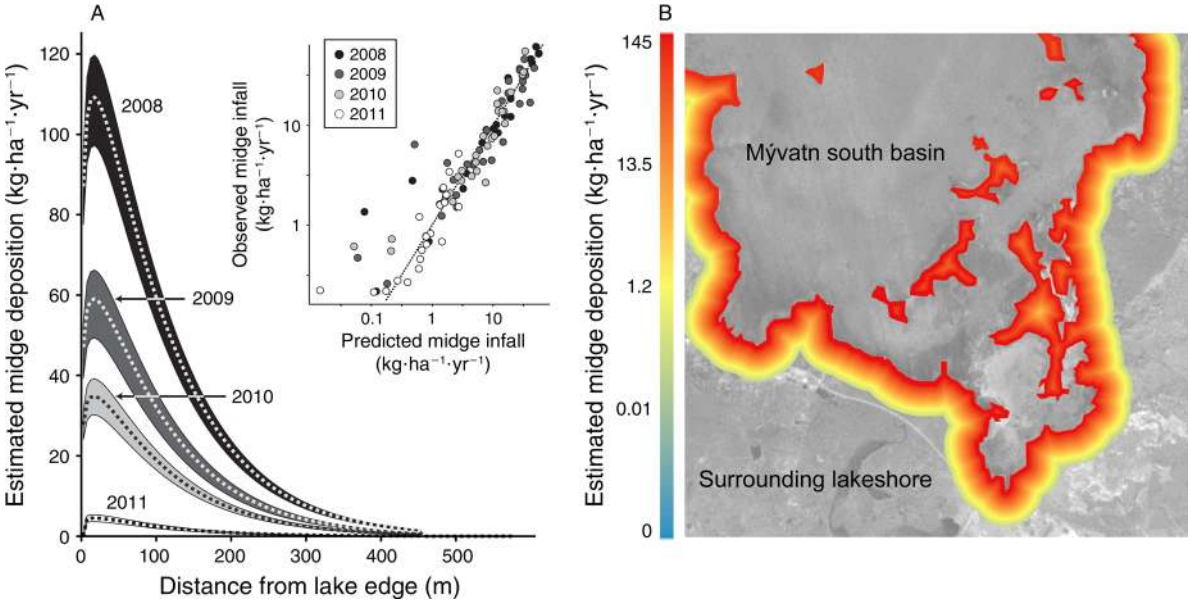

FIG. 2. (A) Predicted midge deposition around Lake Mývatn, Iceland May–August 2008–2011, with ±95% confidence interval (CI) uncertainty, as a function of distance from the lake edge; deposition is shown as a dashed line, CI as the shading around each line. Color scheme is as in Fig. 1. Inset shows the model-predicted estimated deposition (dashed line) vs. the observed calculations for all midges (circles), under the annual aggregation model. (B) Spatial representation of the intensity of midge deposition around the southeastern shore of Lake Mývatn in 2008. Deposition beyond 500 m is assumed to be zero. All masses are measured as dry mass.

TABLE 1. Predicted total annual midge deposition derived from weekly sample data, proportion deposited in 50-m distance bands, and cumulative deposition within 50-m bands moving outward from the Lake Mývatn, Iceland shoreline 2008–2011.

Deposition measure	Maximum deposition	Distance class (m)								
		0–50	51–100	101–150	151–200	201–250	251–300	301–350	351–400	401–450
Predicted mean deposition ($kg \cdot ha^{-1} \cdot yr^{-1}$)										
2008	110	100	75	47	28	17	10.0	5.8	3.4	2.0
2009	59	55	41	25	15	9.1	5.4	3.2	1.8	1.1
2010	35	32	24	15	9.1	5.4	3.2	1.9	1.1	0.63
2011	4.5	3.9	3.1	1.9	1.2	0.69	0.41	0.24	0.14	0.081
Proportion in class		0.35	0.25	0.16	0.10	0.06	0.03	0.02	0.01	0.01
Cumulative proportion		0.35	0.61	0.77	0.87	0.93	0.96	0.98	0.99	1.00

Note: Distance classes (i.e., 0–50) are presented in in 50-m increments. Maximum deposition occurred at 20–25 m from lakeshore for all years sampled. Cells left blank indicate no data.

DISCUSSION

Determining the importance of aquatic insects to terrestrial ecosystems requires estimates of deposition to land. We created a model that takes the estimated emergence of aquatic insects, here coming from a lake, and distributes the organisms to the adjacent terrestrial landscape using an empirically derived abundance decay curve. From in-lake emergence traps, we estimate that the emergence rate of midges from Lake Mývatn was as high as 32 $kg \cdot ha^{-1} \cdot yr^{-1}$ in a high-abundance year. This scales to 75 Mg/yr from the productive south basin of Lake Mývatn, a testament to the sizeable insect secondary production that can be exported by a large lake, though this is likely an underestimate due to the conservative nature of the lake sampling approaches used in this study (Gratton and Vander Zanden 2009, Vander Zanden and Gratton 2011, Bartrons et al. 2013). Midge abundance decreased exponentially as a function of distance from shore, but with a peak in relative abundance about 20 m inland. The pattern of decreasing midge density with distance from shore was consistent even among years that varied significantly in total midge emergence. Though model performance varied slightly from year to year, overall there was very good agreement between model predictions and field observations of infall. Our method shows that during a year of high midge emergence, 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ of midges, equivalent to ~10 kg $N \cdot ha^{-1} \cdot yr^{-1}$, are deposited within the first 50 m of land adjacent to the lake edge. We demonstrate a generalizable method by which aquatic–terrestrial insect fluxes can be empirically quantified, and suggest that aquatic insects can be a major source of nutrients to terrestrial ecosystems.

Modeling insect deposition to land

Our results build on recent modeling studies that explore insect fluxes between water and land (Sabo and Hagen 2012, Bartrons et al. 2013, Muehlbauer et al. 2014), specifically expanding on Gratton and Vander Zanden (2009) by using empirical estimates of the total amount of organisms produced in a waterbody. Because constraining terrestrial deposition by the total amount of aquatic insect emergence is a key feature of these approaches, accurate measurement of insect emergence provides the greatest payoff to improving estimates of terrestrial deposition of aquatic insects. Using a conceptually similar approach, Whiles et al. (2001) derived estimates of insect deposition from one terrestrial habitat (belowground) to another (aboveground litter) when studying the emergence of periodical cicadas in Kansas, USA. From emergence traps placed on the ground and cicada emergence hole counts, they estimated how many cicadas emerged from the soil and, under the assumption of no dispersal (i.e., all insect emergence ended up in the same place), estimated likely insect deposition back to the soil as carcasses. The approach we espouse in this study is generalizable to other systems in which emergence rates (or secondary production) of mobile organisms can be estimated from source habitats to areas of deposition and can include terrestrial-to-terrestrial linkages as well (e.g., Dreyer and Gratton 2014).

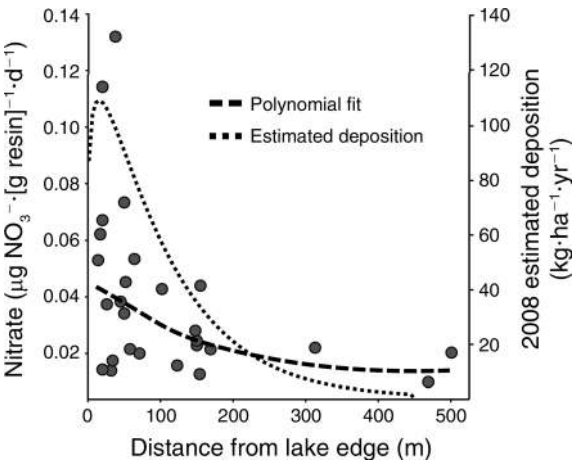

FIG. 3. Nitrate (solid circles) captured by resin bags buried in the soil at different distances from the shore of Lake Mývatn between May and August 2008, with fit using our polynomial local-maximum deposition model showing log(NO_3^-) significantly related to distance from shore ($F_{1,25} = 8.66$, $P = 0.007$, adjusted $R^2 = 0.23$; long dashed line), and the predicted midge deposition in 2008 overlaid for illustrative purposes (short dashed line).

In addition to emergence rates, insect dispersal from the source must be known to estimate deposition. Gratton and Vander Zanden (2009) used literature values to derive two decay functions (negative exponential and inverse power decay) for aquatic insect abundance around bodies of water. For Lake Mývatn, we derived a system-specific dispersal function, including an extra parameter allowing a non-zero maximum deposition distance. The variable distance of peak deposition seen between "large" *Tanytarsus* and "small" *Chironomus* midges (Fig. 1B) is likely the result of differences in mobility or other life-history traits (e.g., *Chironomus* spp. observed affinity for elevation). Other factors (wind direction, bank geomorphology, vegetation, etc.) not directly addressed in this model may further vary the dispersal pattern, but could be incorporated in more refined versions of dispersal models. Still, our estimates of insect dispersal patterns are consistent across years of widely variable midge abundance, suggesting that midge dispersal is accurately characterized by our infall traps.

Notably, we assumed that all insects emerging from the lake moved to land and remained there. Although the actual proportion of midges remaining on land is less than 1, the basic life history of midges suggests that male midges remain on land to wait for females, thus at least 50% of all emerging individuals are expected to stay in the terrestrial system (Lindegaard and Jónasson 1979). It is unknown what fraction of females never returns to the lake to oviposit in the water or what fraction returns to land to mate again after oviposition. Given that most aquatic insects remain in the terrestrial system (70–99%; Jackson and Fisher 1986, Gray 1989, Petersen et al. 1999), assuming that most midges stay on land is probably a close approximation of what actually occurs. Nevertheless, improved estimates of the proportion of insects remaining on land will help refine deposition estimates, which at this point should be considered maximal rates.

From a practical perspective, it would be convenient to calculate deposition directly from measurements taken on land, but measuring insect emergence directly from the lake was a key feature of our model. Using infall traps as estimators of deposition proved problematic; we found a considerable mismatch between deposition estimates from infall traps and the emergence-constrained deposition model. When simply dividing the mass of midges in the infall cups by the area of the cup opening, the estimated deposition at Lake Mývatn is 20–30 times more than emergence-constrained estimates. This overestimation is likely due to the lethality of infall traps; that is, given enough time, a single lethal trap could theoretically capture all insects within its vicinity. Unless constrained by the amount of insect biomass in a system, equating lethal methods of insect abundance measurement with deposition overestimates deposition rates. Thus, infall traps provide measures of relative, but not absolute, abundance on land as needed to estimate spatial patterns of movement of aquatic insects to land (Petersen et al. 1999).

Aquatic insects and N deposition

From our model of midge deposition, we can estimate ecosystem-relevant measures of material and nutrient transfers from lake to land, estimates that were previously unavailable or unreliable. With midge deposition peaking at 12 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ nearshore during a high midge-emergence year, N contributions from midges are three to five times the level of background atmospheric deposition in the subarctic (Bobbink et al. 2010), which includes Iceland, and approach ~20% of the rates of synthetic fertilization application in pastures by local farmers near Lake Mývatn (50–75 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$). The nitrogen-absorbing resin bags placed near infall traps during 2008 showed increased nitrate concentrations coincident with our modeled increase in midge deposition (Fig. 3), supporting the notion that midges can influence soil-available N concentrations, similar to the findings of Yang (2004), who investigated the impact of cicada carcass deposition. With the concomitant transfer of P to land (around 1 kg $P{\cdot}ha^{-1}{\cdot}yr^{-1}$), the addition of these two elements to nutrient-limited arctic heathlands could significantly shift vegetative cover and primary productivity (Bobbink et al. 1993, Shaver et al. 2001, Britton and Fisher 2007, Marczak et al. 2007).

The movement of N by midges to land is comparable to other measured fluxes of nutrients between ecosystems (Table 2). For example, heavy gypsy moth defoliation can result in nutrient deposition from the forest canopy to the litter layer of 30 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ (Townsend et al. 2004; P. A. Townsend and K. N. Eshleman, *unpublished data*), and deposition of cicada carcasses after a mass emergence event also deposited 30 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ (Whiles et al. 2001). Cross-ecosystem nitrogen deposition from well-studied examples, including seabird guano on islands and salmon carcasses on stream banks, may reach up to 20 and 70 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$, respectively (Erskine et al. 1998, Gende et al. 2007). Likewise, anthropogenic industrial atmospheric sources in China add up to 21 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ (Liu et al. 2013), and many areas in North America and Europe experience similar levels of N deposition from atmospheric sources (Holland et al. 2005). In general, however, there are few estimates of insects as major conduits of nutrients across ecosystem boundaries from water to land (but see Muehlbauer et al. 2014, Scharnweber et al. 2014), though from land to water there are more (e.g., Mehner et al. 2005, Nowlin et al. 2007, Pray et al. 2009). This could either be due to the relative rarity of such linkages, or that measuring these fluxes is difficult or commonly ignored (Yang and Gratton 2014).

Yet, in some landscapes, such as riparian areas, the transport of aquatic nutrients to terrestrial ecosystems by insects may be common (Bartrons et al. 2013) and

TABLE 2. Examples of cross-ecosystem nitrogen deposition caused by various sources, biological as well as aeolian.

Nutrient source	Location	Deposition (kg N·ha^{-1}·yr^{-1})	References
Concentrated livestock	Scotland, UK	80	Pitcairn et al. 1998
Salmon carcasses	Alaska, USA	70	Gende et al. 2007
Mammal urine, feces	Midwest, USA	45	Seagle 2003
Fog, rain	Los Angeles Basin, USA	45	Bytnerowicz and Fenn 1996
Industrial NO_x	Beijing, China	38.5	Liu et al. 2006
Gypsy moth frass	Appalachian Mountains, USA	30	P. A. Townsend and K. N. Eshleman, *unpublished manuscript*
Cicada emergence	Konza Prairie, USA	30	Whiles et al. 2001
Industrial NO_x	Mainland China	21	Liu et al. 2013
Penguin and seal excrement	Macquarie Island (subantarctic)	20.4	Erskine et al. 1998
Mammal urine, feces	Indiana, USA	15	Duchamp et al. 2010
Aquatic insects	Lake Mývatn, Iceland	12	Present study
Aeolian dust	Argentinian Pampas	5	Ramsperger et al. 1998
Seabird guano	Anchorage Island, (subantarctic)	4.1	Bokhorst et al. 2007
Mammal urine, feces	Oklahoma, USA	3.7	Clark et al. 2005
Insect frass and defoliation	Pennsylvania, USA	3.5	Lewis 1998
Seabird guano	St. Paul Island, Bering Sea	2.3	Wainwright et al. 1998
Insect herbivore frass	North Carolina, USA	1.1	Hunter et al. 2003

Note: Deposition values are the maximal estimates, and may be very localized (e.g., N deposition associated with an individual salmon carcass).

could generate patterns similar to nutrient "hot spots" formed by vertebrates (Anderson and Polis 1999, Helfield and Naiman 2006, Holtgrieve et al. 2009). As there have been few attempts to measure aquatic insect nutrient deposition to land, it remains to be seen if the case of Lake Mývatn is truly unique, or if the processes we observed in Iceland are more common than currently appreciated. In places where productive waterbodies are bordered by terrestrial ecosystems of low productivity, such as deserts and tundra (Jackson and Fisher 1986), even less extreme levels of insect deposition to land can represent a significant addition of limiting resources. To date, there has been relatively little consideration of fertilization effects by insects, especially in places where they could be important inputs, along streams, rivers, and lakes (but see Francis et al. 2006, Sabo and Hagen 2012, Muehlbauer et al. 2014). While individually, the insects that cross ecosystem boundaries are small, their effects en masse may be both ecologically important and readily quantifiable.

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LITERATURE CITED

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332.

Ballinger, A., and P. S. Lake. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. Marine and Freshwater Research 57:15–28.

Bartrons, M., M. Papeş, M. W. Diebel, C. Gratton, and M. J. Vander Zanden. 2013. Regional-level inputs of emergent aquatic insects from water to land. Ecosystems 1–11.

Binkley, D., J. Aber, J. Pastor, and K. Nadelhoffer. 1986. Nitrogen availability in some Wisconsin forests: comparisons of resin bags and on-site incubations. Biology and Fertility of Soils 2:77–82.

Bobbink, R., G. W. Heil, R. Aerts, and G. W. Heil. 1993. Atmospheric deposition of sulphur and nitrogen in heathland ecosystems. Pages 25–50 *in* Rien Aerts and Gerrit W. Heil, editors. Heathlands: patterns and processes in a changing environment. Kluwer Academic Publishers, Dordrecht, Netherlands.

Bobbink, R., et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications 20:30–59.

Bokhorst, S., A. Huiskes, P. Convey, and R. Aerts. 2007. External nutrient inputs into terrestrial ecosystems of the Falkland Islands and the Maritime Antarctic region. Polar Biology 30:1315–1321.

Britton, A. J., and J. M. Fisher. 2007. Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. Journal of Applied Ecology 44:125–135.

Bultman, H., D. Hoekman, J. Dreyer, and C. Gratton. 2014. Terrestrial deposition of aquatic insects increases plant quality for insect herbivores and herbivore density. Ecological Entomology 39(4):419–426.

Bytnerowicz, A., and M. E. Fenn. 1996. Nitrogen deposition in California forests: a review. Environmental Pollution 92:127–146.

Clark, J. E., E. C. Hellgren, J. L. Parsons, E. E. Jorgensen, D. M. Engle, and D. M. Leslie, Jr. 2005. Nitrogen outputs from fecal and urine deposition of small mammals: implications for nitrogen cycling. Oecologia 144:447–455.

Dreyer, J., and C. Gratton. 2014. Habitat linkages in conservation biological control: lessons from the land–water interface. Biological Control 75:68–76.

Dreyer, J., D. Hoekman, and C. Gratton. 2012. Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways. Oikos 121:252–258.

Duchamp, J. E., D. W. Sparks, and R. K. Swihart. 2010. Exploring the "nutrient hot spot" hypothesis at trees used by bats. Journal of Mammalogy 91:48–53.

Einarsson, A., A. Gardarsson, G. M. Gislason, and A. R. Ives. 2002. Consumer–resource interactions and cyclic population dynamics of *Tanytarsus gracilentus* (Diptera: Chironomidae). Journal of Animal Ecology 71:832–845.

Einarsson, Á., G. Stefánsdóttir, H. Jóhannesson, J. S. Ólafsson, G. Már Gíslason, I. Wakana, G. Gudbergsson, and A. Gardarsson. 2004. The ecology of Lake Mývatn and the River Laxá: variation in space and time. Aquatic Ecology 38: 317–348.

Erskine, P. D., D. M. Bergstrom, S. Schmidt, G. R. Stewart, C. E. Tweedie, and J. D. Shaw. 1998. Subantarctic Macquarie Island: a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. Oecologia 117:187–193.

Fagan, W. F., E. Siemann, C. Mitter, R. F. Denno, A. F. Huberty, H. A. Woods, and J. J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. American Naturalist 160:784–802.

Francis, T. B., D. E. Schindler, and J. W. Moore. 2006. Aquatic insects play a minor role in dispersing salmon-derived nutrients into riparian forests in southwestern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 63: 2543–2552.

Gende, S. M., A. E. Miller, and E. Hood. 2007. The effects of salmon carcasses on soil nitrogen pools in a riparian forest of southeastern Alaska. Canadian Journal of Forest Research 37:1194–1202.

Gratton, C., J. Donaldson, and M. J. Vander Zanden. 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland. Ecosystems 11: 764–774.

Gratton, C., and M. J. Vander Zanden. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. Ecology 90:2689–2699.

Gray, L. J. 1989. Emergence production and export of aquatic insects from a tallgrass prairie stream. Southwestern Naturalist 34:313–318.

Griffith, M. B., E. M. Barrows, and S. A. Perry. 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. Annals of the Entomological Society of America 91:195–201.

Helfield, J., and R. Naiman. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. Ecosystems 9: 167–180.

Hoekman, D., M. Bartrons, and C. Gratton. 2012. Ecosystem linkages revealed by experimental lake-derived isotope signal in heathland food webs. Oecologia 170:735–743.

Hoekman, D., J. Dreyer, R. Jackson, P. Townsend, and C. Gratton. 2011. Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities. Ecology 92:2063–2072.

Holland, E. A., B. H. Braswell, J. Sulzman, and J. F. Lamarque. 2005. Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. Ecological Applications 15:38–57.

Holtgrieve, G., D. Schindler, and P. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 24:1125–1135.

Hunter, M. D., C. R. Linnen, and B. C. Reynolds. 2003. Effects of endemic densities of canopy herbivores on nutrient dynamics along a gradient in elevation in the southern Appalachians. Pedobiologia 47:231–244.

Irwin, M. E. 1980. Sampling aphids in soybean fields. Pages 239–259 *in* M. Kogan and D. C. Herzog, editors. Sampling methods in soybean entomology. Springer, New York, New York, USA.

Ives, A. R., A. Einarsson, V. A. A. Jansen, and A. Gardarsson. 2008. High-amplitude fluctuations and alternative dynamical states of midges in Lake Mývatn. Nature 452:84–87.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67:629–638.

Kalra, Y., J. Crumbaugh, and D. Maynard. 2007. Nitrate and exchangeable ammonium nitrogen. Pages 71–80 *in* M. Carter and E. Gregorich, editors. Soil sampling and methods of analysis. Second edition. CRC Press, Boca Raton, Florida, USA.

Kuusela, K., and A. Huusko. 1996. Post-emergence migration of stoneflies (Plecoptera) into the nearby forest. Ecological Entomology 21:171–177.

Lewis, G. P. 1998. Response of stream chemistry to forest insect defoliation on the Allegheny High Plateau, Pennsylvania. Dissertation. Cornell University, Ithaca, New York, USA.

Lindegaard, C., and P. M. Jónasson. 1979. Abundance, population dynamics and production of zoobenthos in Lake Mývatn, Iceland. Oikos 32:202–227.

Liu, X., et al. 2013. Enhanced nitrogen deposition over China. Nature 494:459–462.

Liu, X., X. Ju, Y. Zhang, C. He, J. Kopsch, and Z. Fusuo. 2006. Nitrogen deposition in agroecosystems in the Beijing area. Agriculture, Ecosystems and Environment 113:370–377.

Lovett, G. M., M. A. Arthur, K. C. Weathers, and J. M. Griffin. 2010. Long-term changes in forest carbon and nitrogen cycling caused by an introduced pest/pathogen complex. Ecosystems 13:1188–1200.

Marczak, L. B., R. R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88: 140–148.

Mehner, T., J. Ihlau, H. Dörner, and F. Hölker. 2005. Can feeding of fish on terrestrial insects subsidize the nutrient pool of lakes? Limnology and Oceanography 50:2022–2031.

Milner, A. M., C. L. Fastie, F. S. Chapin, III, D. R. Engstrom, and L. C. Sharman. 2007. Interactions and linkages among ecosystems during landscape evolution. BioScience 57:237–247.

Muehlbauer, J. D., S. F. Collins, M. W. Doyle, and K. Tockner. 2014. How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. Ecology 95:44–55.

Nowlin, W. H., M. J. González, M. J. Vanni, M. H. H. Stevens, M. W. Fields, and J. J. Valente. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology 88:2174–2186.

Ólafsson, J. 1979. Physical characteristics of Lake Mývatn and River Laxá. Oikos 32:38–66.

Petersen, I., J. H. Winterbottom, S. Orton, N. Friberg, A. G. Hildrew, D. C. Spiers, and W. S. C. Gurney. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. Freshwater Biology 42:401–416.

Pitcairn, C. E. R., I. D. Leith, L. J. Sheppard, M. A. Sutton, D. Fowler, R. C. Munro, S. Tang, and D. Wilson. 1998. The relationship between nitrogen deposition, species composition and foliar nitrogen concentrations in woodland flora in the vicinity of livestock farms. Environmental Pollution 102: 41–48.

Polis, G. A., M. E. Power, and G. R. Huxel, editors. 2004. Food webs at the landscape scale. University of Chicago Press, Chicago, Illinois, USA.

Pray, C. L., W. H. Nowlin, and M. J. Vanni. 2009. Deposition and decomposition of periodical cicadas (Homoptera: Cicadidae: *Magicicada*) in woodland aquatic ecosystems. Journal of the North American Benthological Society 28: 181–195.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ramsperger, B., N. Peinemann, and K. Stahr. 1998. Deposition rates and characteristics of aeolian dust in the semi-arid and sub-humid regions of the Argentinean Pampa. Journal of Arid Environments 39:467–476.

Sabo, J. L., and E. M. Hagen. 2012. A network theory for resource exchange between rivers and their watersheds. Water Resources Research 48:W04515.

Sabo, J. L., and M. E. Power. 2002. River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860–1869.

Scharnweber, K. M., M. J. Vanni, S. Hilt, J. Syväranta, and T. Mehner. 2014. Boomerang ecosystem fluxes: organic carbon inputs from land to lakes are returned to terrestrial food webs via aquatic insects. Oikos. http://dx.doi.org/10.1111/oik.01524

Seagle, S. W. 2003. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? Oikos 103:230–234.

Shaver, G. R., M. S. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin, III. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology 82:3163–3181.

Southwood, T. R. E., and P. A. Henderson. 2009. Ecological methods. John Wiley and Sons, Hoboken, New Jersey, USA.

Townsend, P. A., K. N. Eshleman, and C. Welcker. 2004. Remote sensing of gypsy moth defoliation to assess stream nitrate concentration. Ecological Applications 74:504–516.

Vander Zanden, M. J., and C. Gratton. 2011. Blowin' in the wind: reciprocal airborne carbon fluxes between lakes and land. Canadian Journal of Fisheries and Aquatic Sciences 68: 170–182.

Wainright, S. C., J. C. Haney, C. Kerr, A. N. Golovkin, and M. V. Flint. 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. Marine Biology 131:63–71.

Whiles, M. R., M. A. Callaham, Jr., C. K. Meyer, B. L. Brock, and R. E. Charlton. 2001. Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. American Midland Naturalist 145:176–187.

Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. Science 306:1565–1567.

Yang, L. H., and C. Gratton. 2014. Insects as drivers of ecosystem processes. Current Opinion in Insect Science. 2: 26–32.

Supplemental Material

Ecological Archives

Appendices A–E are available online: http://dx.doi.org/10.1890/14-0704.1.sm

Data Availability

Data associated with this paper are available from the North Temperate Lakes LTER; midge emergence data 2008–2011 is available at https://lter.limnology.wisc.edu/dataset/ltreb-lake-m%C3%BDvatn-midge-emergence-2008-2011, and midge infall data 2008–2011 is available at https://lter.limnology.wisc.edu/dataset/ltreb-lake-m%C3%BDvatn-midge-infall-2008-2011