

Regional-Level Inputs of Emergent Aquatic Insects from Water to Land

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ABSTRACT

Emergent aquatic insects can provide inputs to terrestrial ecosystems near lentic and lotic waterbodies, producing ecosystem linkages at the aquatic–terrestrial interface. Although aquatic insect emergence has been examined for individual sites, the magnitude and spatial distribution of this phenomenon has not been examined at regional spatial scales. Here, we characterize this cross-habitat linkage for the state of Wisconsin, USA (169,639 km²). We combined GIS hydrological data with empirical data and predictive models of aquatic insect production to estimate annual aquatic emergence for the state of Wisconsin. Total emergence (lentic + lotic) was estimated to be about 6,800 metric tons of C y⁻¹. Lentic systems comprised 79% of total estimated insect emergence, primarily due to the large amount of lake surface area relative to streams. This is due to both basic ecosystem geometry and the overall abundance of lakes in Wisconsin. Spatial variation was high: insect emergence in southwestern Wisconsin was dominated by streams, whereas

for most of the rest of the state insect emergence was dominated by lakes. Lentic inputs to land were highly concentrated (relative to lotic inputs) because lakes have a high ratio of surface area to buffer area. Although less concentrated, the spatial extent of lotic influence was greater: statewide, four times more land area fell within the 100 m buffer zones of streams compared to lakes. Large waterbodies (almost all of which were lakes) were hotspots of insect emergence and input to land. Aquatic insect inputs exceed estimated terrestrial secondary production in 13% of buffer area, and by a factor of 100 or more adjacent to large lakes (> 50,000 ha). The model sensitivity analysis showed that the simplifying assumptions and sources of potential error in the input variables had a minor impact on the overall results.

Key words: aquatic insects; emergence; lentic; lotic; lakes; streams; landscape; terrestrial–aquatic linkages; food webs; Wisconsin.

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INTRODUCTION

Habitats and ecosystems are often linked via the movement of organisms, nutrients, matter, and energy across traditionally-defined ecosystem boundaries (Polis and others 1997, 2004). The classic view of linkages between aquatic and terrestrial systems has been largely unidirectional, emphasizing the downhill movement of terrestrial-derived nutrients and matter into lakes and streams (Carpenter and others 1998; Pace 2004). In recent

decades, stream ecologists have shifted toward viewing streams as a tightly integrated part of the broader watershed system (Hynes 1975; Ormerod and Tyler 1991; Nakano and Murakami 2001; Baxter and others 2005). In contrast, lake-to-land linkages have rarely been examined; though recently some studies have examined the role of emergent aquatic insects in linking lakes and the surrounding terrestrial landscape (Finlay and Vredenburg 2007; Gratton et al. 2008).

It is now widely accepted that cross-ecosystem food web linkages can have important implications for the structure, function, and trophic dynamics of recipient ecosystems (Polis and others 1997, 2004). Yet although cross-habitat linkages are widely-cited and viewed as important, it is notable that research on cross-habitat linkages is generally conducted at the local scale, and focusing on individual sites (Ballinger and Lake 2006; Milner and others 2007; Jonsson and Wardle 2009; Macdade and others 2011; Dreyer and others 2012; Greig and others 2012). This leaves open questions such as: What is the magnitude of these cross-habitat linkages at regional scales? How are these inputs distributed in space and how variable are they? What is the relative importance of inputs from different habitats types, for example, stream-to-land and lake-to-land on real landscapes? Addressing these questions pertaining to cross-habitat linkages at the regional level will require “scaling up” the results of individual site-specific studies.

As a start in this direction, Gratton and Vander Zanden (2009) developed a model of the flux of emergent aquatic insects to land for both lotic and lentic systems. A key concept was the central role of ecosystem geometry, specifically that the strength of water-to-land linkages increases as a function of the

ratio of aquatic habitat area to perimeter. Although this simulation was based on empirical insect production and emergence data, the analysis was largely abstract, and the objective was to highlight general patterns and processes, and was not specific to any particular location. The goal of this study is to apply the general modeling framework of Gratton and Vander Zanden (2009) to assess the aquatic-to-terrestrial inputs of emergent aquatic insects for an actual landscape, focusing on the contrasts between lotic and lentic systems. This study represents both an application to a real landscape and an effort to “scale-up” earlier more conceptual modeling efforts (Gratton and Vander Zanden 2009; Vander Zanden and Gratton 2011). We performed the analysis for the state of Wisconsin because lake, stream, and hydrological GIS layers were readily available, and the landscape is sufficiently large and geographically diverse to allow for potentially strong regional contrasts.

METHODS

We developed a spatial model of aquatic to terrestrial linkages by expanding on the conceptual framework of Gratton and Vander Zanden (2009) (Figure 1; Table 1), and applying it to the landscape of Wisconsin, USA. Wisconsin has an area of 169,639 km², and includes a diverse mix of lentic (lakes, ponds, and impoundments) and lotic (streams and rivers) systems, including several of the most lake-rich regions in the world (Magnuson and others 2006). We conducted all spatial analyses on the Wisconsin Department of Natural Resources 1:24,000-scale hydrography, which is the highest resolution hydrography dataset available for this region. The general approach was to estimate mean

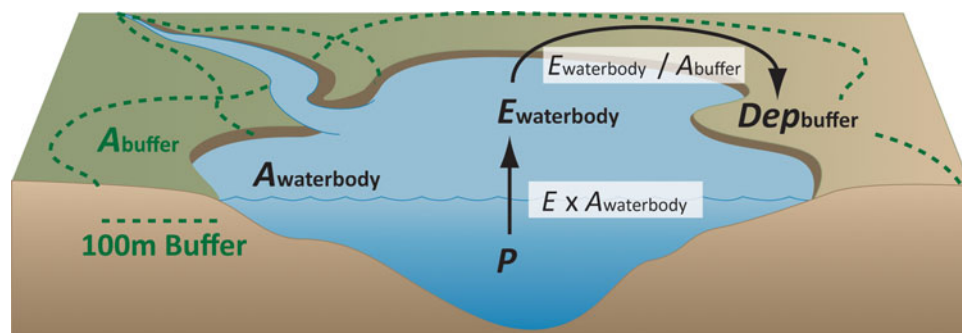


Figure 1. The conceptual model for linking aquatic production to land via the emergence of aquatic insects. Aquatic insect production (P , $\text{gC m}^{-2} \text{y}^{-1}$) is estimated for individual lentic and lotic systems for a real landscape from empirical relationships with environmental predictors. Emergent aquatic insects represent a flux across the water–land boundary and are distributed to the adjacent land area (insect inputs to land, $\text{Dep}_{\text{buffer}}$, $\text{gC m}^{-2} \text{y}^{-1}$). $\text{Dep}_{\text{buffer}}$ is a function of the total insect emergence ($E_{\text{waterbody}}$, gC y^{-1}), and the total land area adjacent to each waterbody. We assumed the aquatic insect influence was constrained to a 100 m buffer (A_{buffer} , m^2).

Table 1. Variables Used in This Study

Variable	Abbreviation	Units	Equation or source
Waterbody area	$A_{\text{waterbody}}$	m^2	
Buffer area (100 m width)	A_{buffer}	m^2	
Buffer area in watershed	$A_{\text{buffer-watershed}}$	m^2	ΣA_{buffer}
Total watershed area (excluding waterbodies)	$A_{\text{total-watershed}}$	m^2	
Benthic insect production	P	$\text{gC m}^{-2} \text{y}^{-1}$	Eq. 1, $f(\text{Secchi})_{\text{lentic}}$ Eq. 2, $f(\text{Temperature})_{\text{lotic}}$
Insect emergence	E	$\text{gC}^{-2} \text{y}^{-1}$	$P \times (E/P)_{\text{literature}}$
Total insect emergence per waterbody	$E_{\text{waterbody}}$	gC y^{-1}	$E \times A_{\text{waterbody}}$
Total insect emergence per watershed	$E_{\text{watershed}}$	gC y^{-1}	$\Sigma E_{\text{waterbodies}}$
Total insect emergence in Wisconsin	E_{state}	gC y^{-1}	$\Sigma E_{\text{watersheds}}$
Insect inputs to land per square meter of buffer for a waterbody	Dep_{buffer}	$\text{gC m}^{-2} \text{y}^{-1}$	$E_{\text{waterbody}}/A_{\text{buffer}}$
Insect inputs to land per square meter of buffer in a watershed	$Dep_{\text{buffer-watershed}}$	$\text{gC m}^{-2} \text{y}^{-1}$	$E_{\text{watershed}}/A_{\text{buffer-watershed}}$
Insect inputs to land per square meter of watershed	$Dep_{\text{total-watershed}}$	$\text{gC m}^{-2} \text{y}^{-1}$	$E_{\text{watershed}}/A_{\text{total-watershed}}$

annual benthic insect production for each individual lentic and lotic system on a per-unit area basis (P , $\text{gC m}^{-2} \text{y}^{-1}$). From benthic insect production P we estimated aquatic insect emergence (E , $\text{gC m}^{-2} \text{y}^{-1}$, Table 1), which when multiplied by the area of the waterbody ($A_{\text{waterbody}}$, m^2) that approximates total annual insect emergence ($E_{\text{waterbody}}$, gC y^{-1}), and hence the potential for movement of insects across the water–land boundary. Emergent aquatic insect inputs to land follow a negative exponential or inverse power function with distance from shore and, on average, decline to near zero at a distance of approximately 100 m (Petersen and others 2004). For the purpose of this study, it was appropriate to simply divide total annual insect emergence from a waterbody ($E_{\text{waterbody}}$, gC y^{-1}) by the total land area within 100 meters of shore for that waterbody (that is, the 100 m buffer, A_{buffer} , m^2). This approximates the average input of aquatic insects to the terrestrial 100 m buffer for that waterbody (Dep_{buffer} , $\text{gC m}^{-2} \text{y}^{-1}$). We apply this approach for lentic and lotic systems across the entirety of the state of Wisconsin, USA.

Estimation of Insect Production for Lentic Systems

To model benthic insect production for lentic systems (lakes and ponds), we assembled a data set of mean annual insect production (P) for 28 lakes, mostly located in temperate regions around the world (see supplementary material: Appendix A). Potential explanatory variables that could be used to model location-specific insect production were latitude, longitude, area (m^2), mean depth (Z_{mean} , m), maximum depth (Z_{max} , m), total phosphorus

(TP, $\mu\text{g L}^{-1}$), chlorophyll a (Chl- a , $\mu\text{g L}^{-1}$) and estimated Secchi depth (m). Other variables that could affect mean annual insect production such as community composition, lake bathymetry, or anthropogenic impacts were not available. Total phosphorus (TP, $\mu\text{g L}^{-1}$) and chlorophyll a (Chl- a , $\mu\text{g L}^{-1}$) were available only for a small proportion of Wisconsin lakes, and were thus excluded from the analysis. All data were log-transformed to attain normality where required (Kolmogorov–Smirnov Goodness-of-fit test, $P < 0.05$). All possible models, including interactions, were fit to the data using the *lme* package in R (R Development Core Team 2013) and evaluated using Bayesian information criterion (BIC). Secchi depth was the best explanatory variable for P for lentic waterbodies ($r^2 = 0.268$, $P = 0.013$, $\text{MSE} = 0.34$):

$$\text{Log}_{10}P = -0.68 \times \text{Log}_{10}\text{Secchi} + 0.48 \quad (1)$$

Secchi depth was estimated from Landsat satellite imagery (<http://www.lakesat.org/>, Chipman and others 2004) for 8,602 of the 87,400 lentic systems (comprising 95% of total lentic surface area) in the Wisconsin Department of Natural Resources (WDNR) 1:24,000-scale hydrography dataset (WDNR 2011). For these lakes, mean annual insect production P was estimated from Eq. 1. Bias in log-transformed allometric equations was corrected as in Newman (1993). For the remaining 78,798 waterbodies lacking Secchi depth estimates (most of which were small: $< 5\%$ total lentic area), we simply applied the geometric mean value of P from our literature compilation ($2.07 \text{ gC m}^{-2} \text{y}^{-1}$, see supplementary material: Appendix A), which was

appropriate because Secchi depth was independent of lake area (Log_{10} Secchi versus Log_{10} (Area), $r^2 = -0.001$, $P = 0.6283$). Bias correction of back transformed values was performed according to Rothery (1988).

Estimation of Insect Production for Lotic Systems

The same general procedure was used to develop a relationship between environmental variables and mean annual insect production for lotic waterbodies (36 lotic systems mostly located in temperate regions, see supplementary material: Appendix B). Latitude, longitude, mean annual water temperature ($^{\circ}\text{C}$), mean annual air temperature ($^{\circ}\text{C}$), discharge ($\text{m}^3 \text{y}^{-1}$), and stream width (m) were evaluated as independent variables. Mean annual water temperature ($^{\circ}\text{C}$) was the best explanatory variable for lotic P ($r^2 = 0.62$, $P < 0.001$, $\text{MSE} = 0.14$):

$$\text{Log}_{10}P = 0.10 \times \text{mean annual water temperature} - 0.45 \quad (2)$$

Thus, the calculation of the benthic P for lotic waterbodies in Wisconsin requires estimates of mean annual water temperature for each waterbody. In Wisconsin, mean annual water temperature is dependent on latitude and stream size, which can be approximated by drainage area (Lyons and others 2009). Lotic water temperature data recorded at 38 US Geological Survey (USGS) stream monitoring stations in Wisconsin (monitored continuously for at least 2 years between 2000 and 2010) were obtained from the USGS National Water Information System (NWIS; <http://waterdata.usgs.gov/nwis>). Mean annual stream temperature was calculated as the mean of daily stream temperatures. Upstream drainage areas for each lotic waterbody were obtained from the Great Lakes Aquatic GAP database (Brenden and others 2006). Mean annual stream temperature, \bar{T} (in $^{\circ}\text{C}$), was modeled as $\bar{T} = 52 + 0.67 \log_{10}DA - 0.97 \text{Lat}$, where DA is drainage area in km^2 , and Lat is latitude in decimal degrees ($r^2 = 0.49$, $P < 0.001$, $\text{MSE} = 0.77$). This equation was used to estimate mean annual stream temperature for all lotic waterbodies in the WDNR 1:24,000-scale hydrography dataset (WDNR 2011). Benthic insect production, P , was estimated from mean annual water temperature using Eq. 2.

Insect Emergence from Lentic and Lotic Systems

Insect emergence (E , $\text{gC m}^{-2} \text{y}^{-1}$) for each waterbody was calculated by multiplying estimated

benthic insect production (P , $\text{gC m}^{-2} \text{y}^{-1}$) by an estimate of the fraction of insect emerging from the aquatic ecosystem. We used previously published values of emerging fraction of 0.3 for lentic and 0.19 for lotic systems (Gratton and Vander Zanden 2009). For each waterbody, insect emergence, E , was multiplied by waterbody area ($A_{\text{waterbody}}$, m^2 , see below) to estimate the total amount of insect emergence (Table 1, $E_{\text{waterbody}}$, gC y^{-1}).

Lentic and lotic surface areas were calculated in ArcGIS 10 (ESRI 2011). Surface areas of lentic systems were calculated directly from polygons in 1:24,000-scale digital hydrography (WDNR; <http://dnr.wi.gov/maps/gis/datahydro.html>). For Lake Michigan and Lake Superior, we only included the adjacent littoral zone, defined as the depth of 1% surface irradiance, because at greater depth little or no net benthic primary production occurs. Larger lotic features are represented as polygons in the 1:24,000-scale hydrography layer, and surface areas were calculated directly from polygons. To estimate width of smaller streams, we developed regional (Level III ecoregions, Omernik 1987) hydraulic geometry equations from wetted width measurements for 240 lotic systems in Wisconsin (Robertson and others 2006). The equations are: $\text{Log}_{10}W = -0.03 + 0.47\text{Log}_{10}DA$ (Driftless Area, $r^2 = 0.81$, $P < 0.001$, $\text{MSE} = 0.01$), $\text{Log}_{10}W = -0.03 + 0.49\text{Log}_{10}DA$ (North Central Hardwood Forests, $r^2 = 0.93$, $P < 0.001$, $\text{MSE} = 0.01$), $\text{Log}_{10}W = 0.15 + 0.43\text{Log}_{10}DA$ (Northern Lakes and Forests, $r^2 = 0.78$, $P < 0.001$, $\text{MSE} = 0.03$), and $\text{Log}_{10}W = -0.15 + 0.53\text{Log}_{10}DA$ (Southeastern Wisconsin Till Plains, $r^2 = 0.82$, $P < 0.001$, $\text{MSE} = 0.02$), where W is wetted width (m) and DA is drainage area (km^2). Bias in log-transformed allometric equations was corrected according to Newman (1993). These equations were used to estimate stream width for all lotic waterbodies not represented as polygons in 1:24,000-scale hydrography. Surface areas of these lotic systems were then calculated by multiplying length and estimated width.

Insect Inputs from Lentic and Lotic System to Adjacent Land

We created a 100 m buffer around each lentic and lotic waterbody in ArcGIS 10 (ESRI 2011) as an approximation of the land area likely to receive aquatic insects. One hundred meters was previously estimated to represent 73–100% of total insect inputs to land (Gratton and Vander Zanden

2009). For each waterbody, we divided total emergence ($E_{\text{waterbody}}$, gC y^{-1}) by the 100 m buffer area (A_{buffer}), which yields the average insect input per square meter of land within the 100 m buffer (Dep_{buffer} , gC y^{-1}) (Table 1). Applying distance-decay functions (Gratton and Vander Zanden 2009) had no impact on our findings because our estimates of insect deposition are aggregated at the level of relatively large watersheds (hundreds of km^2 , and each containing large number of lotic/lentic systems). Also, we did not adjust our calculations to account for emergent insects that return directly back to the water surface. This phenomenon undoubtedly reduces the input to terrestrial systems, but we simply do not know what fraction of insect emergence returns directly back to the water, how much this varies among taxa, and whether it varies with stream/lake attributes such as waterbody size or presence of top predators like fish. As such, our results should be viewed as the overall potential inputs of aquatic insects to terrestrial systems.

We expressed deposition at the watershed level in two ways designed to allow us to distinguish between localized and aggregate effects of insect deposition. First, we divided lentic and lotic insect emergence ($E_{\text{watershed}}$, gC y^{-1}) by the total buffer zone area ($A_{\text{buffer-watershed}}$) for each watershed, which provides a measure of the intensity of insect inputs directly adjacent to aquatic systems ($Dep_{\text{buffer-watershed}}$, $\text{gC m}^{-2} \text{y}^{-1}$). $Dep_{\text{buffer-watershed}}$ identifies watersheds with highly concentrated insect deposition on the landscape, and is high where water surface area:buffer area tends to be high, such as near large lakes. Second, for each watershed we divided lotic and lentic insect emergence ($E_{\text{watershed}}$, gC y^{-1}) by total watershed area ($A_{\text{total-watershed}}$), which we call $Dep_{\text{total-watershed}}$. This metric provides an integrated (“bulk”) measure of insect deposition for each watershed. Estimates for individual lotic and lentic systems were aggregated within USGS 10-digit Hydrologic Unit Code (HUC)

watershed units (a total of 374 HUC-10 watersheds in Wisconsin).

RESULTS

Aquatic Insect Emergence in Wisconsin

Differences in the geometry of lotic and lentic systems on the landscape had consequences for potential emergent insect inputs to land. Statewide, lentic systems had 7× more surface area, 5× less perimeter, and 4× less land area within the 100 m buffer compared to lotic systems (Table 2). Statewide, 79% of the total estimated insect emergence was from lentic systems (Table 2). We estimate that 6,800 metric tons of carbon emerges from Wisconsin’s lotic and lentic systems annually.

Spatial Patterns of Aquatic–Terrestrial Linkages

Estimated aquatic insect input to land varied spatially (Figure 2). Insect input to land for lotic systems was lower (Dep_{buffer} : geometric mean: 0.005, range: 0.000007–9 $\text{gC m}^{-2} \text{y}^{-1}$) than for lentic systems (Dep_{buffer} : geometric mean: 0.03, range: 0.0007–52.5 $\text{gC m}^{-2} \text{y}^{-1}$). Insect input to land was concentrated around large waterbodies (for example, Lake Michigan, Superior and Winnebago, Figure 2A), as well as in regions with a high density of lentic systems (for example, northeastern Wisconsin). Aquatic insect inputs from lentic systems were more spatially heterogeneous than for lotic systems (Figure 2A vs. B).

Insect Deposition at the Watershed Scale

Aggregating insect emergence at the watershed level further highlighted spatial patterns. Expressing total insect emergence relative to total buffer area ($Dep_{\text{buffer-watershed}}$, Figure 3A–C) in each watershed is reflective of the intensity of insect emergence in areas adjacent to waterbodies.

Table 2. Key Descriptive Statistics for Lentic and Lotic Ecosystems for the State of Wisconsin (USA), and the Lentic to Lotic Ratio

	Lentic	Lotic	Lentic/lotic
Total number of waterbodies	87,400	117,935	0.7
Total area ($\Sigma A_{\text{waterbody}}$, ha)	961,327	133,691	7
Total perimeter (km)	51,995	260,360	0.2
Total land area in buffer (ΣA_{buffer} , ha)	687,342	2,832,403	0.25
Geometric mean of insect emergence (E , $\text{gC m}^{-2} \text{y}^{-1}$)	0.6	0.6	1
Geometric mean of inputs to buffer (Dep_{buffer} , $\text{gC m}^{-2} \text{y}^{-1}$)	0.03	0.004	7
Total emergence in Wisconsin (E_{state} , gC y^{-1})	5.4×10^9	1.4×10^9	3

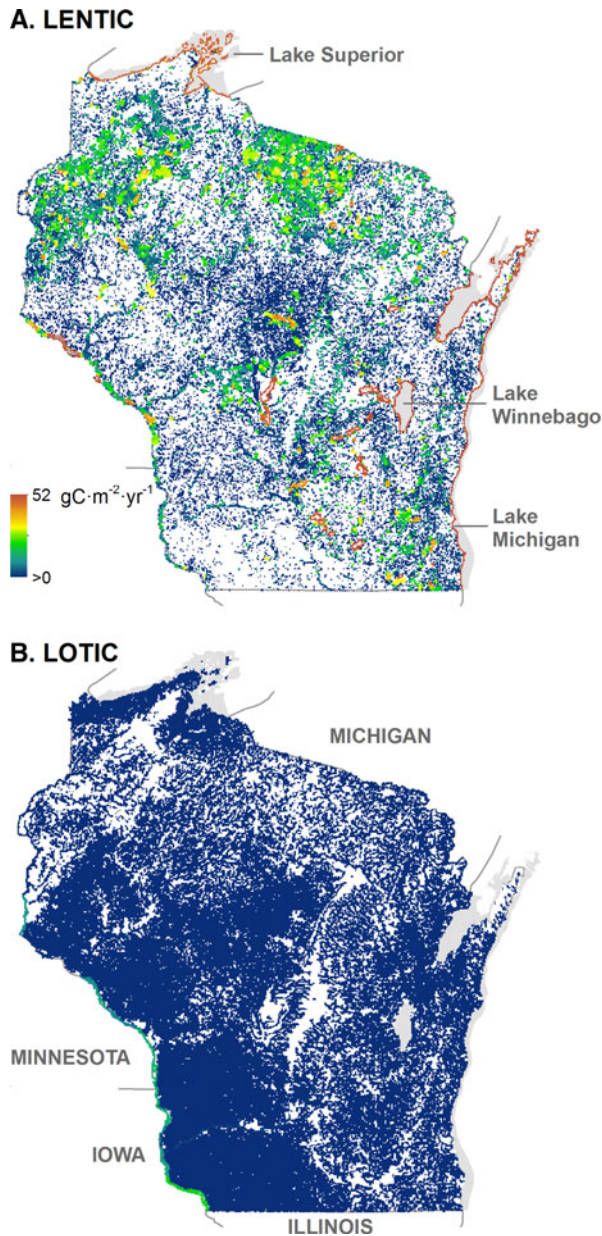


Figure 2. Spatial distribution of insect inputs ($\text{gC m}^{-2} \text{yr}^{-1}$) from for lentic (A), lotic (B) waterbodies to the adjacent land in Wisconsin, USA. Values are aggregated at 1 km^2 pixels for better visual resolution.

Aggregating at this scale revealed much higher and more spatially variable emergence from lentic systems (Figure 3A) relative to lotic systems (Figure 3B, C). This pattern is driven largely by the fact that lakes tend to have relatively more surface area (Figure 4A), less perimeter (Figure 4B), and thus less buffer zone area (Figure 4C) compared to streams. This comparison revealed low insect inputs in southwestern Wisconsin, which is dominated by streams. In contrast, parts of northern

Wisconsin that are dominated by lakes had a high intensity of inputs (Figure 3A, B).

Insect emergence was also expressed relative to total watershed area ($Dep_{\text{total-watershed}}$, Figure 3D–F), which provides a more integrative (rather than localized) measure of insect emergence. Expressing emergence this way reveals less stark contrasts between lotic and lentic emergence, though the same general patterns are still apparent. Emergence from lotic systems is less spatially heterogeneous than for lentic systems. Overall emergence tends to be dominated by lentic systems (Figure 3D–F).

The ratio of lentic to lotic insect emergence ($E_{\text{watershed(lentic)}}/E_{\text{watershed(lotic)}}$) for watersheds varied widely (Figure 5A). Lentic exceeded lotic insect emergence (that is, ratio >1) in 60% of watersheds, and in some watersheds by 1,000-fold or more. The spatial pattern of lentic:lotic inputs revealed the importance of lotic systems in southwestern Wisconsin (Figure 5B). This part of the state (called the Driftless Area) was not covered with glaciers and thus lacks natural lakes of glacial origin. Within this unglaciated area, 69% of total insect emergence is lotic. In contrast, lotic systems are relatively minor contributors to total insect emergence in the formerly glaciated parts of the state, comprising 14% of total insect emergence (Figure 5B).

DISCUSSION

Although many studies have examined the movement of energy and nutrients across habitat boundaries and their implications for recipient food webs and ecosystems, they have largely been conducted at the site level. Many of these studies illustrate the potentially important role of aquatic–terrestrial linkages for food web dynamics (Ballinger and Lake 2006; Milner and others 2007; Gladyshev and others 2009; Jonsson and Wardle 2009; Macdade and others 2011; Dreyer and others 2012; Greig and others 2012). Yet there is a need to consider these site-specific studies within a broader landscape context. For example, how important are such linkages at regional scales, and what are the dominant drivers? By combining the model of Gratton and Vander Zanden (2009) and empirical data within a GIS framework, we estimated aquatic-to-terrestrial linkages for a real landscape—a first attempt to quantify the magnitude and spatial pattern of this cross-habitat linkage beyond the scale of an individual study site. We estimated that Wisconsin’s lotic and lentic ecosystems yield over 6,800 metric tons of carbon in the form of aquatic insects each year. Statewide, lentic systems (lakes

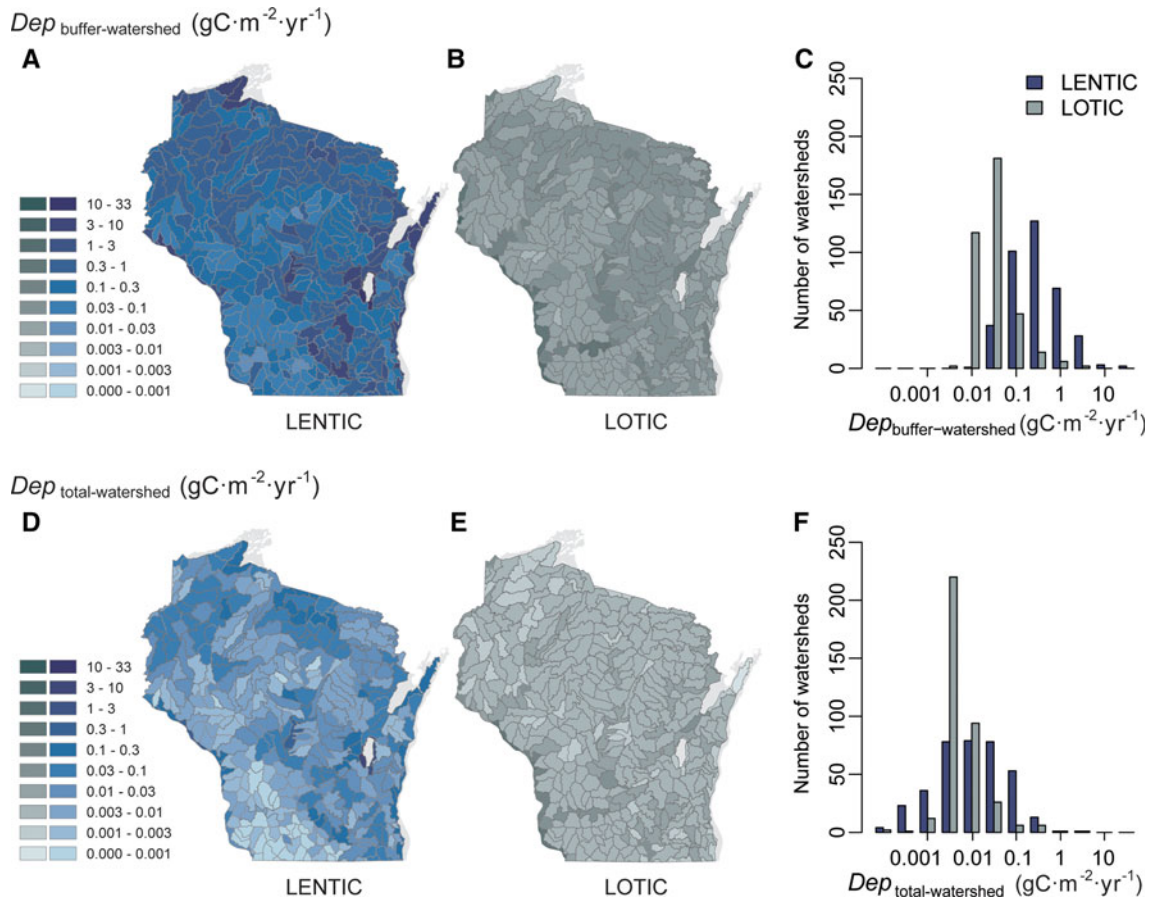


Figure 3. Aggregating insect emergence at the watershed scale. Spatial distribution of insect inputs to land, expressed as per square meter of buffer within a watershed (**A–C**, $Dep_{buffer-watershed}$, $gC\ m^{-2}\ yr^{-1}$). Insect inputs to land, per square meter of watershed (**D–F**, $Dep_{total-watershed}$, $gC\ m^{-2}\ yr^{-1}$) for lentic (*blue* **A**, **D**) and lotic (*gray* **B**, **E**) systems in Wisconsin. **C**, **E** show the frequency distribution of $Dep_{buffer-watershed}$ ($gC\ m^{-2}\ yr^{-1}$) and $Dep_{total-watershed}$ ($gC\ m^{-2}\ yr^{-1}$) for watersheds, shown separately for lentic and lotic systems.

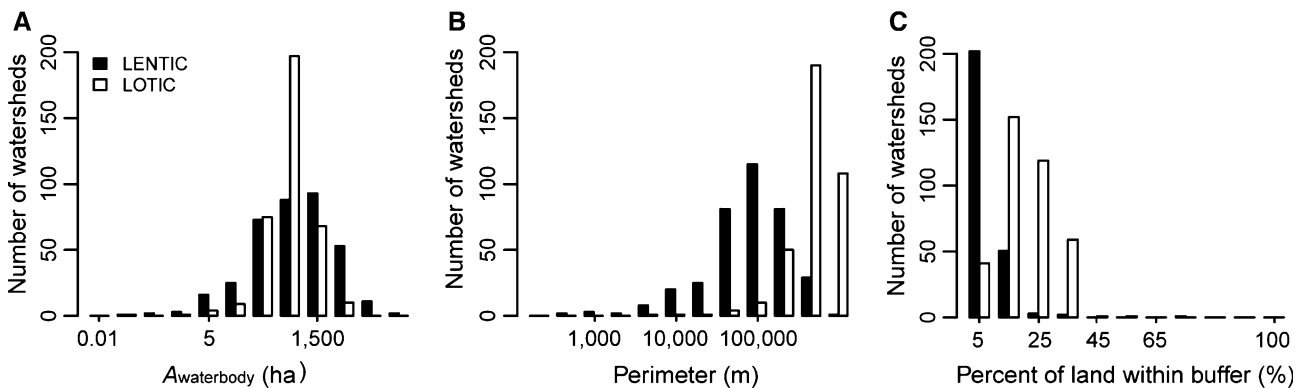


Figure 4. Frequency distributions of several key metrics, aggregated at the watershed level. **A** Total waterbody surface area (km^2). **B** Total waterbody perimeter (km). **C** Percent of total land area within 100 m buffer zone. Estimates are shown separately for lentic (*black*) and lotic (*white*) systems.

and ponds) accounted for 79% of the overall inputs of insects from aquatic systems.

Aquatic insect inputs to land were spatially heterogeneous (Figure 2). For lentic systems, there

was dramatic spatial contrast in aquatic insect inputs, including some locations where aquatic insect inputs were estimated to be exceptionally high (hotspots). In contrast, lotic systems produced a less

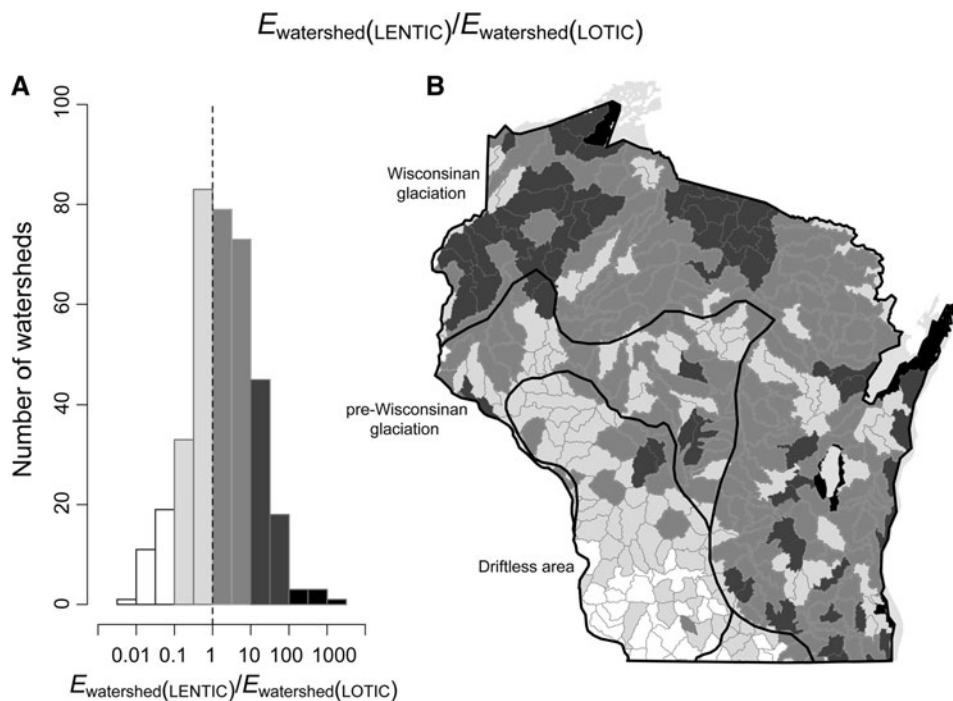


Figure 5. The ratio of lentic to lotic insect emergence (gC y^{-1}) for watersheds of Wisconsin. **A** Frequency distribution of lentic/lotic emergence. Values below 1 (*light*) are dominated by lotic emergence, values above 1 (*dark*) are dominated by lentic emergence. **B** The spatial pattern of the lentic to lotic ratio. *Black lines* show the boundary limits of Wisconsinan glaciation, pre-Wisconsinan glaciation, and the unglaciated (Driftless) Area.

concentrated, but more extensive blanketing of the landscape, with relative few locations (for example, along the Mississippi River) that would be considered hotspots (Figure 2).

These broad patterns are driven by the fundamental landscape geometry of lotic and lentic systems (Table 2; Gratton and Vander Zanden 2009). We aggregated insect inputs to land in two ways: relative to the buffer area within a watershed ($Dep_{\text{buffer-watershed}}$, Figure 3A–C), and relative to the total area of the watershed ($Dep_{\text{total-watershed}}$, Figure 3D–F). Expressing emergence relative to buffer area highlights the intensity of insect inputs at those locations receiving inputs (that is, within the buffer). This pattern is largely driven by lakes because individual lakes tend to be large in surface area compared to streams. As a result, lakes have a high ratio of surface area to perimeter, and thus produce highly concentrated inputs to the buffer (Figure 4C). In contrast, streams tend to be small, and thus have a low ratio of aquatic surface area to perimeter. The consequence is less concentrated inputs, though inputs tend to be spread out across a broader area. This is readily apparent when examined at the statewide scale: the surface area of lentic systems in Wisconsin is estimated to be $7\times$ higher than for lotic systems. Yet, for lotic systems, there is about $4\times$ more land area within the 100 m buffer zone compared to lentic systems (16.7% lotic vs. 4% lentic, Figure 4C). The result is that emergence from lakes produces highly concentrated local

effects (Figure 3A) whereas emergence from lotic systems tends to be more diffuse (Figure 3B). Expressing insect deposition relative to the total watershed area is a measure of the overall importance of emergent insects at the watershed scale. This metric tends to increase the importance of streams (Figure 3D, E), which as noted above, produce less concentrated inputs to land, but can still be quite important in landscapes where a large fraction of land area falls within stream buffer zones.

Overall patterns of lentic and lotic insect deposition to land across the landscape were related to the post-glacial geography of Wisconsin (Figure 5). Much of southwestern Wisconsin (called the Driftless Area) was not impacted by glaciation during the Pleistocene and is characterized by a high density of streams and few natural lakes and ponds. This region has relatively low levels of aquatic insect inputs to land, and inputs are dominated by lotic systems. In contrast, the rest of Wisconsin was formerly glaciated, and tends to be dotted with lakes. Here, emergent aquatic insect inputs are high and dominated by lakes.

Terrestrial In Situ Secondary Production Versus Aquatic Inputs

The relative importance of aquatic inputs to terrestrial food webs will depend on how large aquatic inputs are relative to in situ terrestrial secondary

production in riparian zones. We estimated secondary production from estimates of primary production from remotely sensed data. MODIS (Moderate Resolution Imaging Spectroradiometer) satellite observations (<https://wist.echo.nasa.gov/>) are employed to produce global annual net primary productivity estimates (NPP, kg C m^{-2} , mean over a 10-year period) at 1 km spatial resolution (Running and others 2004). We used McNaughton and others (1989) equations to estimate net secondary production (for example, herbivorous insects) on land from estimated net primary production. Net terrestrial secondary production in aquatic buffer areas was estimated to range between 0.02 and $0.44 \text{ gC m}^{-2} \text{ y}^{-1}$, whereas aquatic inputs to these areas were much more variable, ranging from $0.000006\text{--}107 \text{ gC m}^{-2} \text{ y}^{-1}$. In 13% of all buffer areas aquatic insect inputs exceeded the estimated in situ terrestrial secondary production. In areas adjacent to large lakes, aquatic inputs exceeded estimated terrestrial secondary production by 100 times or more. The sum of aquatic inputs to all riparian (buffer) zones in Wisconsin (6,800 metric tons of C y^{-1}) exceeded the total estimated in situ terrestrial secondary production in those riparian zones (5,654 metric tons of C y^{-1}).

Sensitivity and Modeling Approach

Though our analysis relies on several simplifying assumptions (see supplementary material: Appendix C) and includes sources of potential variability in the input variables, we find that these assumptions have minor effects on our overall results. As an example, for lakes we compared $Dep_{\text{total-watershed}}$ calculated using: 1. Secchi depth where available and the geometric mean for the remaining lakes, and alternatively; 2. the geometric mean for all lakes (see supplementary material: Appendix C). In comparing individual lakes, as well as aggregating at the watershed level, estimates from the two approaches were closely correlated, with $r^2 > 0.9$ and slopes near 1 (see supplementary material: Appendix C). Notably, for the three largest lakes (Michigan, Superior, Winnebago), the Secchi model gave estimates of production that qualitatively matched known emergence, that is, low per-unit-area production in Michigan (Secchi = 12 m) and Superior (Secchi = 20 m), and high per-unit-area production in Winnebago (Secchi = 0.9 m). Method choice did have an effect on insect production estimates for these three lakes, and due to the large surface area of these lakes, method choice did affect our statewide emergence estimate: total lentic statewide emergence calculated using the

Secchi model was 9% lower than the estimate that assigned the geometric mean of insect production to all lentic waterbodies. Use of the Secchi model provided a better measure of emergence for these large lakes, which is why it was chosen over the simpler alternative.

Another methodological issue relates to the way in which aquatic insect production values are assigned to specific waterbodies, and whether model error associated with the productivity estimates influences the results. To examine how variability in production affects patterns of overall insect emergence and deposition to land, we estimated production using the empirical models for lentic and lotic systems (Eqs. 1, 2), and then randomly adjusted each waterbody-specific production estimate based on the observed regression model error. We then compared the “base” (the non-adjusted production estimate from the regression model) and the “error-adjusted” values (see supplementary material: Appendix C). This error adjustment created a substantial amount of scatter at the level of individual lakes or streams. However, this procedure had much less effect on watershed-scale or statewide estimates ($E_{\text{watershed}}$, $Dep_{\text{buffer-watershed}}$, $Dep_{\text{total-watershed}}$) because the variability introduced for individual waterbodies is averaged across the many lakes and streams within any given watershed (see supplementary material: Appendix C). Statewide, and compared to the “base” method, the error-adjusted method gives statewide emergence values that range from 10% lower to 20% higher for lentic systems. The relatively high variation across model iterations is driven by the overwhelmingly large influence of the three large lakes (Superior, Michigan, and Winnebago) on statewide insect emergence. For lotic systems, the error-adjusted method gave statewide emergence estimates that ranged from 5% lower to 1% higher (see supplementary material: Appendix C).

Although our efforts to scale up aquatic insect emergence to the regional level may be sensitive to how key input parameters are estimated and their sources of variability, our overall results were invariant to different approaches. A principal reason for the robustness of the model output is that the dominant driver of total emergence for any individual waterbody is its surface area, an idea that was previously explored in great detail, albeit in a more abstract context (Gratton and Vander Zanden 2009). Waterbody area varies by more than 10 orders of magnitude. In contrast, aquatic insect production (on a per-unit-area basis) varies by less than 2 orders of magnitude. The implications are clear: the differences that derive from the various

assumptions and methods regarding insect production and emergence are ultimately overwhelmed by the effect of waterbody area.

Summary

Emergent aquatic insects from lotic and lentic systems can be viewed as an allochthonous input of nutrient, organic matter, and prey to terrestrial habitats adjacent to aquatic systems (Gratton and Vander Zanden 2009). The magnitude of this input varies widely among waterbodies, depending on waterbody size, geometry, and per-unit-area insect productivity. Furthermore, these inputs can occur during relatively narrow time windows, often around the beginning of the plant growing season, when terrestrial productivity is low. Indeed, the timing of reciprocal resource pulses is a critical component that determines the cascading effects of spatial flows (Leroux and Loreau 2012). Takimoto and others (2002) showed how resource pulses that are out of phase with in situ resources tended to stabilize recipient consumer populations, highlighting the potential importance of asynchronies between resources.

The estimation of aquatic to terrestrial inputs at regional scales is a step towards a more complete understanding of how distinct habitats are linked on natural landscapes. When these linkages are strong, they have the potential to affect the adjacent terrestrial ecosystems by increasing nutrient inputs or altering consumer trophic dynamics within the recipient ecosystem (Baxter and others 2005; Ballinger and Lake 2006; Hoekman and others 2011; Macdade and others 2011; Dreyer and others 2012; Hoekman and others 2012). Anthropogenic perturbations, such as climate change, eutrophication, invasive species, pollution, and hydrological changes, could have dramatic effects on these aquatic-terrestrial ecosystem interactions. Greig and others (2012) found an amplification of subsidies between aquatic and terrestrial ecosystems due to warming, eutrophication, and changes in the abundance of top predators. Both Epachin and others (2010) and Benjamin and others (2011) described indirect effects of non-native aquatic species on recipient systems via a reduction in the strength of cross-habitat food web linkages. Paetzold and others (2011) observed a marked decline in web spider population density and a shift in spider community composition due to the effects of chronic stream pollution on lotic insect emergence.

The broader management and conservation implications of such cross-habitat linkages are poorly understood, though such linkages undoubtedly benefit many terrestrial consumers—this is a topic of

relevance for future research. Our study is the first to consider these aquatic-to-terrestrial food web and ecosystem linkages at the regional scale. Beyond the fact that these linkages affect a sizeable fraction of the total landscape (~20% of the total land area of Wisconsin falls within 100 m of a lotic or lentic waterbody), we also find that such inputs regularly exceed estimated terrestrial secondary production with riparian buffer areas. This result suggests a strong potential for localized ecological effects. Identifying the broader ecological implications of cross-habitat linkages at these “hotspot” locations represents an important next step, and will help bridge landscape and food web approaches to ecology.

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