

Stream network geometry and the spatial influence of aquatic insect subsidies across the contiguous United States

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Abstract. Emergent aquatic insects transport aquatic-derived resources into terrestrial ecosystems but are rarely studied at landscape or regional scales. Here, we investigate how stream network geometry constrains the spatial influence of aquatic insect subsidies in terrestrial ecosystems. We also explore potential factors (i.e., climate, topography, soils, and vegetation) that could produce variation in stream network geometry and thus change the extent of aquatic insect subsidies from one region to another. The stream signature is the percentage of aquatic insect subsidies traveling a given distance into the terrestrial ecosystem, relative to what comes out of the stream. We use this concept to model the spatial extent (area) and distribution (spatial patterning) of aquatic subsidies in terrestrial ecosystems across the contiguous United States. Our findings suggest that at least 8% of the subsidies measured at the aquatic–terrestrial boundary (i.e., the 8% stream signature) are typically transferred throughout the entire watershed and that variation in this spatial extent is largely influenced by the drainage density of the stream network. Moreover, we found stream signatures from individual stream reaches overlap such that the spatial extent of the 8% stream signature often includes inputs from multiple stream reaches. Landscape-scale stream network characteristics increased the area of overlapping stream signatures more than reach-scale channel properties. Finally, we found runoff was an important factor influencing stream network geometry suggesting a potential effect of climate on aquatic-to-terrestrial linkages that have been understudied.

Key words: Aquatic insects; confluences; meanders; resource subsidy; spatial patterns; stream networks; subbasins.

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INTRODUCTION

Aquatic and terrestrial ecosystems comprise a meta-ecosystem (Loreau et al. 2003), where the aquatic and terrestrial components are reciprocally linked by flows of material and energy across their boundaries (i.e., spatial subsidies or resource subsidies; Polis et al. 1997, Richardson et al. 2010, Allen and Wesner 2016, Gounand et al. 2018). Emergent aquatic insects are aquatic-derived energy and nutrient subsidies transported to terrestrial ecosystems (Baxter et al.

2005, Schindler and Smits 2017) and counteract gradational forces commonly associated with cross-ecosystem subsidies (Loreau et al. 2003, Leroux and Loreau 2008, Subalusky and Post 2018). These insects, largely members of the orders Diptera (Chironomidae), Ephemeroptera, Plecoptera, Trichoptera, and Odonata (Baxter et al. 2005), begin life as aquatic larva and metamorphose into winged, terrestrial adults. Meta-analysis has demonstrated the effects of these aquatic insect subsidies in terrestrial ecosystems can be large (Marczak et al. 2007, Allen and

Wesner 2016, Montagano et al. 2018), but they are typically studied along individual stream reaches (Sabo and Hagen 2012, Muehlbauer et al. 2014). Accordingly, the factors that govern the spatial influence of aquatic subsidies at larger spatial scales (i.e., within and between watersheds) are not well known.

At landscape scales, multiple stream reaches form dendritic networks (Wiens 2002, Benda et al. 2004, Campbell Grant et al. 2007) that enhance the amount of physical contact between aquatic and terrestrial systems (Turner 1989, Polis et al. 1997, Gratton and Vander Zanden 2009). The degree a watershed is dissected by streams relates to the amount of terrestrial habitat in proximity to the water's edge (Baker et al. 2007) and therefore determines the spatial extent (i.e., footprint) of aquatic insect subsidies within the catchment surrounding the river network (Sabo and Hagen 2012). Stream networks can also have implications for how aquatic insect subsidies are distributed within the spatial extent. For example, aquatic insects emerge from multiple locations within a river network such that locations near confluence junctions, sub-basin divides, and meander bends may receive elevated subsidy levels (Sabo and Hagen 2012). These locations can form discrete resource patches for terrestrial consumers (Power and Rainey 2000) that have elevated and/or more stable subsidy inputs (Moore et al. 2015). Indeed, Sabo and Hagen (2012) theoretically demonstrated the importance of stream network configuration and channel planform in defining the extent and distribution of aquatic insect subsidies, but this theory remains to be studied in real stream networks (but see Gratton and Vander Zanden 2009, Bartrons et al. 2013).

The degree stream network geometry drives the spatial patterning of aquatic insect subsidies is contingent on the distance they travel from the stream. The stream signature concept defines an ecological stream width as the percentage of aquatic subsidies measured adjacent to the stream, reaching a lateral distance into watersheds (Muehlbauer et al. 2014). For example, an 8% stream signature refers to the distance 8% of the subsidies measured at the water's edge travels laterally into the terrestrial environment. The distance–decay relationship is derived from a meta-analysis and modeled as an inverse power

function that reflects empirical observations (Muehlbauer et al. 2014). The majority of aquatic insect subsidies remain close to the stream (Gratton and Vander Zanden 2009), but some species are strong fliers (Macneale et al. 2005, Sabo and Hagen 2012) and weak fliers are subject to transport by wind (Power and Rainey 2000). Importantly, this model produces distance estimates that can be used to create boundaries around individual streams within a network which collectively represent the spatial extent of subsidies within a watershed without directly quantifying emergence.

Following the theoretical work of Sabo and Hagen (2012), we expect that the spatial extent of aquatic insect subsidies is related to drainage density and that the number of confluences, sub-basin width, and channel sinuosity influences how they are distributed in watersheds. Further, we suspect climate, hydrology, soils, topography, and vegetation are related to stream network geometry (Moglen et al. 1998, Smith et al. 2013, Sangireddy et al. 2016) and could underlie regional differences in the spatial influence of aquatic insect subsidies. Disentangling relative role of basin features (i.e., climate, hydrology, soils, topography, and vegetation) could highlight macroscale constraints on aquatic–terrestrial resource exchange (Heffernan et al. 2014, Larsen et al. 2016).

Here, we explore the statistical relationships between the spatial extent and distribution of aquatic subsidies and the components of stream network geometry used in Sabo and Hagen (2012). Then, we assess the role of basin features in predicting these geometric components of stream networks using large-scale geospatial data. We use the term spatial extent to describe the area of the stream signature (i.e., footprint) relative to the area of the watershed (Sabo and Hagen 2012) and spatial distribution to describe the spatial heterogeneity of aquatic insect subsidies in the terrestrial landscape caused by overlapping stream signature buffers. We hypothesize that (1) stream network geometry controls the spatial extent and distribution of aquatic subsidies in terrestrial ecosystems and (2) regional constraints on these aquatic–terrestrial interactions imposed by stream network geometry result from regional differences in climate, hydrology, topography, soils, and vegetation.

METHODS

Stream networks

The National Hydrography Dataset Plus Version 2 (NHDPlusV2) integrates features from the Medium Resolution (1:100K) National Hydrography Dataset (NHD), National Elevation Dataset (NED), and Watershed Boundary Dataset (WBD) to produce digital stream networks (flow lines) for the contiguous United States (<http://www.horizon-systems.com/nhdplus>; McKay et al. 2012, Moore and Dewald 2016). In essence, this dataset creates a suitable spatial framework to assess macroscale processes in aquatic ecology. The geographic units (i.e., vector processing units; VPU) of NHDPlusV2 generally follow major drainage areas (i.e., hydrologic regions) of the United States (McKay et al. 2012) which harbor differences in climate, topography, soils, and vegetation characteristics. We randomly selected 35 fourth-order stream networks from each of the 21 hydrologic regions ($N = 735$; Fig. 1) for our analysis.

Spatial influence of aquatic insect subsidies

We define the spatial extent of aquatic insect subsidies as the proportional area of the stream signature buffer relative to the watershed area (Fig. 2A), which has a minimum value of zero but can be larger than 1 if the stream signature buffer area is larger than the watershed area. We define the spatial distribution of aquatic insect subsidies as the spatial heterogeneity of overlapping stream signatures within a watershed that can be produced by different mechanisms at two spatial scales. At the landscape scale, overlapping stream signatures can arise from stream network configurations that bring streams close to each other at confluences and subbasin divides (Fig. 2B). At the reach scale, the channel planform can produce overlapping stream signatures when channel sinuosity is high (Fig. 2C; Sabo and Hagen 2012).

We quantified the effects of network configuration (subbasin divides and confluence) and channel planform (sinuosity) on the spatial distribution

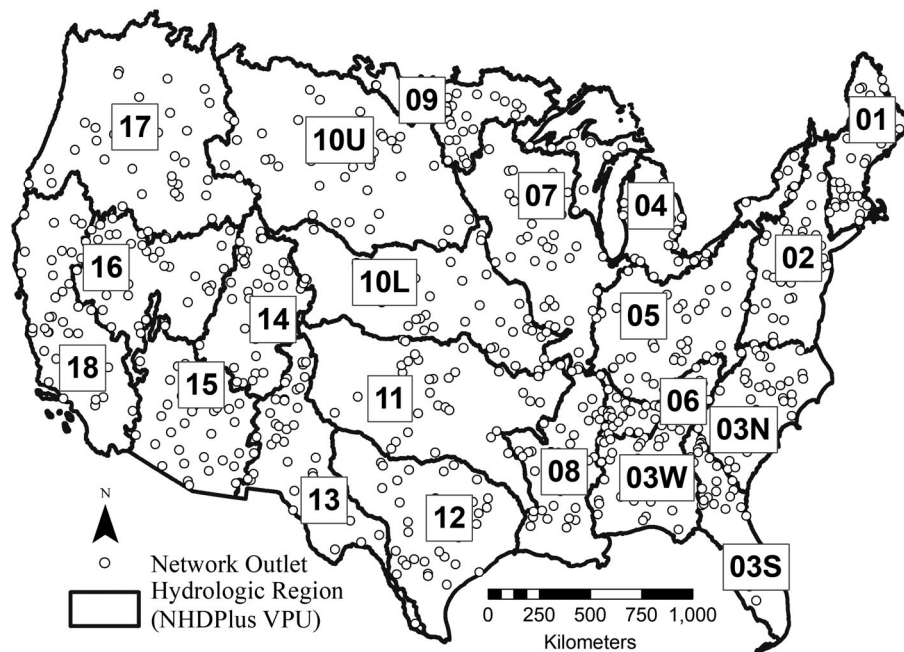


Fig. 1. NHDPlusV2 vector processing units (e.g., hydrologic regions) for the contiguous United States. 01 = Northeast; 02 = Mid-Atlantic; 03N = South Atlantic North, 03S = South Atlantic South, and 03W = South Atlantic West; 04 = Great Lakes; 05 = Ohio; 06 = Tennessee; 07 = Upper Mississippi; 08 = Lower Mississippi; 09 = Souris–Red–Rainy; 10U = Upper Missouri and 10L = Lower Missouri; 11 = Arkansas’ Red-White; 12 = Texas; 13 = Rio Grande; 14 = Upper Colorado; 15 = Lower Colorado; 16 = Great Basin; 17 = Pacific Northwest; and 18 = California. Points are randomly selected fourth-order river network outlets ($N = 735$).

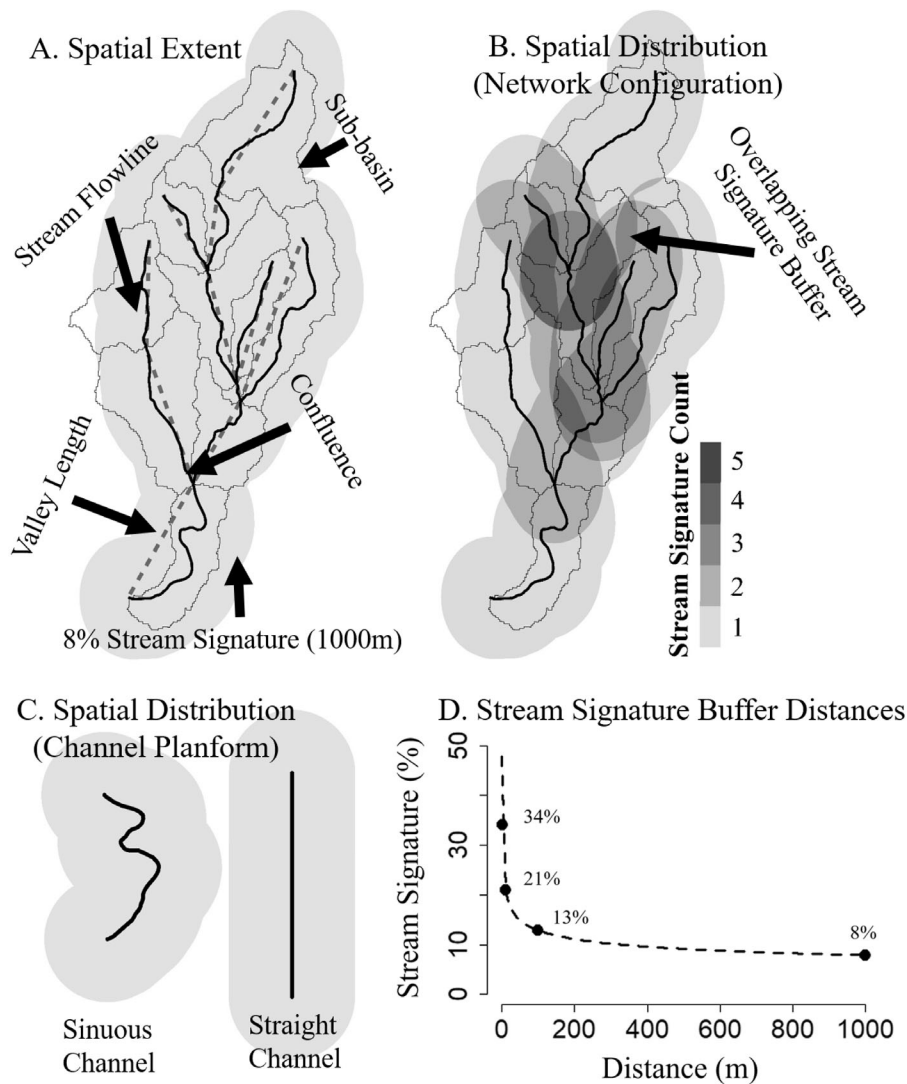


Fig. 2. (A) The spatial extent of an 8% stream signature and components of stream network geometry. (B) The spatial distribution (i.e., increasing shading intensity indicates overlapping stream signature values = 1–5) resulting from stream network configuration within an 8% stream signature (1000 m) buffer. (C) Channel planform (reach scale) overlap example. The difference in area between a stream signature buffer created around the reach (left) and one created around a straight channel of equal length (right) is the area of overlapping stream signature. (D) Inverse power function from Muehlbauer et al. (2014) used to calculate 34%, 21%, 13%, and 8% stream signatures. The figure shows a third-order stream network for clarity, while our analysis focused on fourth-order systems.

of insect subsidies separately as proportions of the spatial extent. For network configuration, we quantified the total area of overlapping stream signature buffers within the spatial extent (Fig. 2B), and for channel planform, we took the difference in area between a stream signature

buffer created around a straight channel (i.e., no overlap) and the same buffer created around the actual NHDPlusV2 flow line (Fig. 2C). It was not possible to directly count the number of overlapping stream signatures resulting from channel planform, so comparisons are made based on area

receiving multiple (i.e., >1 stream signature) signatures. Additionally, we used an area-weighted average of the overlapping stream signatures resulting from confluences and subbasins, as it was possible to directly count the overlapping stream signatures (Fig. 2B), to derive a mean stream signature for the network.

We created four stream signature distances buffers representing different levels of aquatic insect subsidies (i.e., 34%, 21%, 13%, and 8% stream signatures) at different distances (i.e., 1, 10, 100, and 1000 m; Fig. 2D; Muehlbauer et al. 2014) in ArcGIS (Version 10.4; ESRI, Redlands, California, USA). Specifically, we used the inverse power function derived from a meta-analysis of 109 studies and chose coefficients for all organisms (i.e., caddisflies, mayflies, stoneflies, and midges) dispersing from an ecosystem and with “medium productivity” to reflect average conditions (Muehlbauer et al. 2014). Although stream signature distance is likely influenced by the identity of the subsidy (Muehlbauer et al. 2014) and boundary conditions (Greenwood and Booker 2016), these data were unavailable at our study sites; thus, we assume no variation in mean flight strength among communities and completely permeable boundaries. Further, decay curves do not produce sharp breaks where subsidies reach zero. Indeed, using break points neglects uncertainty driven by the ecology of the system, but establishing breaks in continuous functions are necessary (Gratton and Vander Zanden 2009, Bartrons et al. 2013, Muehlbauer et al. 2014) and our main objective was to evaluate the effects of stream network geomorphology. Uniform buffers were chosen deliberately to isolate the effects of stream networks from the biology.

Characterizing stream network geometry

For each of our networks, we characterized the same components of stream network geometry that have been theoretically shown to influence the spatial extent and distribution of aquatic subsidies in terrestrial ecosystems (Fig. 2A) by Sabo and Hagen (2012). Drainage density (D_d) is the total length of stream within a network divided by the catchment area (Horton 1945) and expresses how well an area is dissected by rivers; sinuosity (λ) is defined as the length of the NHDPlusV2 flow line divided by the valley

length (i.e., straight-line length) and captures the curvature of a stream channel; subbasin width (W_b) is calculated as the length of the subbasin divided by the subbasin area and captures the distance separating adjacent tributaries; and confluences (C) occur when two stream reaches merge. We derived network-scale equivalents of λ and W_b as a channel length-weighted mean and median, respectively. All variables were calculated in Program R (Version 3.4) with the StreamNetworkTools Package (https://github.com/dkopp3/StreamNetworkTools_git), such that these and other variables can be calculated for all stream networks within the contiguous United States.

Characterizing climate, topography, soil, and vegetation

To investigate indirect factors that may contribute to spatial influences of aquatic subsidies, we evaluated relationships between stream network geometry variables and biophysical basin features that reflect climate, topography, soil, and vegetation conditions (cf. Moglen et al. 1998). Cumulative mean annual runoff (R) is the sum of the 1971–2000 runoff grids derived by McCabe and Wolock (2011) within the NHDPlusV2 catchment (McKay et al. 2012). We divided R by catchment area such that units are mm/km^2 . Slope estimates are nonnegative and unitless and derived from an elevation smoothing technique to ensure a smooth transition between headwater/confluence and outlet (McKay et al. 2012). We aggregated these values to the network scale using a length-weighted mean of reaches that had identifiable slopes. As an artifact of the elevation smoothing technique, the lowest slope for a reach that could be obtained was 0.0001. Reaches with unattainable slopes typically made up less than 1% of all networks within the hydrological regions. Percent bare ground was quantified from the National Land Cover Database (Homer et al. 2015; <https://www.mrlc.gov/>) supplied with NHDPlusV2.

The whole soil erodibility factor quantifies the susceptibility of soil particles to detachment and movement by water while accounting for rock fragments. We derived an area-weighted mean erodibility factor (K_w) from State Soils Geographic Dataset (STATSGO2; <https://websoilsurvey.nrcs.usda.gov/>). First, we obtained a K_w factor for each STATSGO2 map unit using the

soil component percentages as a weighting factor. Second, we conducted an intersection in ArcGIS (10.4.1; ESRI) between the STATSGO2 map unit polygons and NHDPlusV2 catchments to weight each map unit value by their shared area. STATSGO2 components with unavailable K_w factors (e.g., rocky outcrop and urban areas) were assigned a value of zero (i.e., low erodibility potential).

Analysis

Statistical analysis proceeded in three parts (Appendix S1: Fig. S1). First, we used a simple Bayesian regression model to (1) establish a quantitative relationship between the stream network geometry variables (predictors) and the spatial extent or mean signatures (responses) and (2) evaluate how these relationships change with different stream signature buffers (34%, 21%, 13%, and 8%). We chose a normal likelihood and minimally informative priors for these models (Appendix S1). Although spatial extent is expressed as a proportion, we chose the normal likelihood because values can be greater than 1 if the stream signature buffer area exceeds the catchment area. We also compared the effects of channel planform (i.e., sinuosity) vs. network configuration (i.e., overlap at confluences and subbasin divides) on the mean proportion of the spatial extent receiving elevated aquatic insect subsidies using an intercept-only model with a beta likelihood. Next, we used mixed-effects Bayesian models, to assess regional differences in stream network geometry and the relative importance of the basin features in predicting them. These models included vector processing unit (VPU) as a random effect, stream network basin features (i.e., runoff, erodibility, slope, and vegetation) as fixed effects, and stream network geometry variables as responses. We used a backward stepwise approach followed by model selection to find the best performing model for each response. Last, we modeled the relationship between runoff and drainage density as a random effect to assess regional variability in this relationship. For each set of models, we centered and standardized variables to make comparisons of parameter values across different stream signature buffers and regions. We provide a more detailed description of our modeling approach in Appendix S1.

The spatial extent models were fit using maximum a posteriori fitting due to their simplicity (McElreath 2016). The remaining, more complex models were estimated using Hamiltonian Monte Carlo (HMC). We fit all models in program R (Version 3.5), using the map or map2stan (HMC) functions in rethinking package (McElreath 2016) or the stan_betareg function in rstanarm package (Goodrich et al. 2018). For each model, we sampled from 4 independent chains using 10,000 sampling iterations with a 5000-iteration warm-up. We visually observed trace plots for convergence of the chains and used the mean observed vs. expected ratio and R^2 to assess goodness of fit.

RESULTS

Aquatic insect subsidies and stream network geometry

The spatial extent of the 8% stream signature on average covered 100% of the watershed (Table 1), while higher stream signatures (i.e., 13%, 21%, and 34%) remained closer to stream channels and covered smaller proportions of the watershed (i.e., 15%, 1%, and 0.2%, respectively; Table 1). Drainage density was consistently the most important variable predicting the spatial extent of all stream signatures, and the number of confluences, mean sinuosity, and median subbasin width had little explanatory power (i.e., coefficient $> |0.001|$) except at the lowest stream signatures (i.e., 8% and 13%). Stream signatures from different reaches within the same network overlapped as many as 37 (mean \pm SD = 9.04 ± 2.8) and 8 (4.06 ± 0.87) times for the 8% and 13% signatures and 4 times for both 21% and 34% stream signatures (3.11 ± 0.32 and 3.10 ± 0.31 , respectively). Using an area-weighted mean demonstrated these areas of overlap can be considerably small relative to the spatial extent for stream signatures $>8\%$ (mean ≈ 1.0 ; Table 1). Alternatively, at the 8% stream signature we found a national mean 2.22 (CoV = 0.24) suggesting the entire spatial extent receives 8% of the aquatic subsidies originating from at least two different stream reaches within the network. Of the stream network geometry characteristics, subbasin width was typically the most important for predicting the mean overlap at the higher stream signature percentages (coefficient values >0.50 ; Table 1). By indirectly

quantifying instances of stream signature overlap resulting from channel sinuosity, we determined network configuration (subbasin width and confluences) could contribute more to the area receiving elevated amounts of aquatic insect subsidies (Fig. 3).

Regional patterning was present in the spatial extent of aquatic insect subsidies and overlapping stream signatures throughout the contiguous United States (Fig. 4). At the 13% (100 m) stream signature, we found the Lower Mississippi hydrological region (VPU08) to have the highest spatial extent of aquatic insect subsidies (i.e., 95% CrI = 20, 22% of the watershed; Fig. 4A) and among the highest average overlap between stream signatures (95% CrI = 1.08, 1.09; Fig. 4B). Alternatively, the Texas and the Souris–Red–Rainy hydrological regions (VPU12 and 09, respectively) had the lowest spatial extent (95% CrI = 0.09, 0.11; Fig. 4A) and number of overlapping stream signatures (95% CrI = 1.03, 1.04 and 1.04, 1.04, respectively; Fig. 4B). We also found the effects of network configuration (i.e., subbasin width and confluences; Fig. 4C) and channel sinuosity (Fig. 4D) varied regionally with the latter being most prevalent in the midwestern United States.

Stream network geometry and basin features

Intercept estimates for the Bayesian mixed-effects models indicate differences in stream network geometry components among hydrologic regions (Fig. 5A–D; Appendix S1: Table S1).

Specifically, the Lower Mississippi hydrologic region (VPU 08) was among the highest values for both drainage density ($D_d = 0.94$ [0.87, 1.02], mean [90% CrI]; Fig. 5A), and the number of confluences ($C = 164.25$ [136.44, 198.52]; Fig. 5C) and among the lowest for median effective basin width ($W_b = 509.4110$ [462.80, 561.20]; Fig. 5B). This is consistent with the large spatial extent and relatively high degree of overlapping stream signatures. Alternatively, the Texas hydrologic

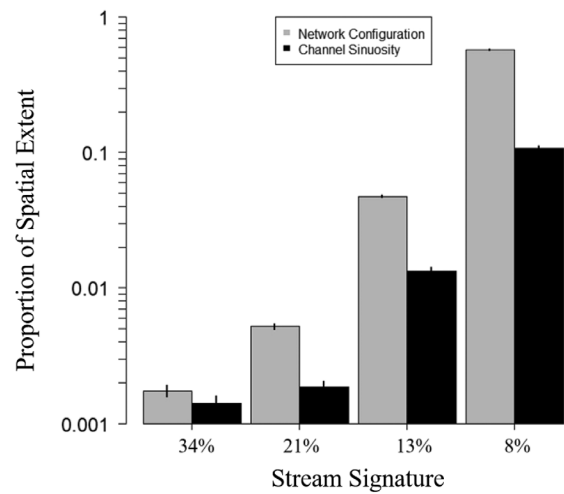


Fig. 3. The proportion of the spatial extent consisting of overlapping stream signatures resulting from channel sinuosity (black) or network configuration (gray) at different stream signature distances. 95% credible intervals are displayed over bars.

Table 1. Spatial extent and mean stream signature with mean parameter estimates (90% credible intervals) for network geometry components

Stream signature buffer (distance)	National mean (CoV)	Parameter estimates				R^2
		D_d (90% CrI)	C (90% CrI)	W_b (90% CrI)	λ (90% CrI)	
Extent of stream signature						
8% (1000 m)	1.007 (0.229)	0.947 (0.920, 0.978)	-0.126 (-0.149, -0.102)	0.154 (0.124, 0.183)	-0.165 (-0.189, -0.141)	0.85
13% (100 m)	0.159 (0.325)	1.000 (0.995, 1.006)	-0.005 (-0.01, 0.000)	0.02 (0.014, 0.026)	-0.039 (-0.044, -0.034)	0.99
21% (10 m)	0.010 (0.331)	1.000 (1.000, 1.003)	0.000 (-0.001, 0.000)	0.001 (0.001, 0.001)	-0.001 (-0.001, -0.001)	1.00
34% (1 m)	0.002 (0.332)	1.000 (1.000, 1.000)	0.000 (0.000, 0.000)	0.000 (0.000, 0.000)	0.0000 (0.000, 0.000)	1.00
Mean stream signatures						
8% (1000 m)	2.219 (0.237)	0.682 (0.652, 0.713)	0.091 (0.066, 0.116)	-0.323 (-0.353, -0.292)		0.83
13% (100 m)	1.060 (0.025)	0.255 (0.200, 0.310)	0.012 (-0.033, 0.056)	-0.506 (-0.561, -0.452)		0.47
21% (10 m)	1.005 (0.002)	0.247 (0.195, 0.298)	-0.007 (-0.048, 0.0349)	-0.559 (-0.610, -0.508)		0.53
34% (1 m)	1.000 (0.000)	0.245 (0.194, 0.296)	-0.006 (-0.0481, 0.035)	-0.510 (-0.611, -0.508)		0.53

Notes: CoV, coefficient of variation; D_d , drainage density; C , number of confluences; W_b , median subbasin width; λ , mean sinuosity.

region (VPU12) had relatively low drainage density ($D_d = 0.64$ [0.59, 0.7]; Fig. 5A), and high values of median effective basin width ($W_b = 980.95$ [907.57, 1057.27]; Fig. 5B), indicating the region is generally not well-drained and adjacent stream reaches are further apart. Estimates for the intercepts and 90% CrI for other regions are provided in Appendix S1: Table S2.

Runoff and basin slope were included in the best performing model for each of the stream

network geometry components (Table 2) and therefore could have an indirect effect on aquatic insect subsidies (see Appendix S1: Table S2 for model selection results). The drainage density (D_d) model included all four basin features ($R^2 = 0.44$) and was most strongly influenced by mean annual runoff ($\beta_R = 0.22$ [0.17, 0.26]), while the effective basin width model (W_b) included three basin features ($R^2 = 0.26$) and was most strongly influenced by basin slope

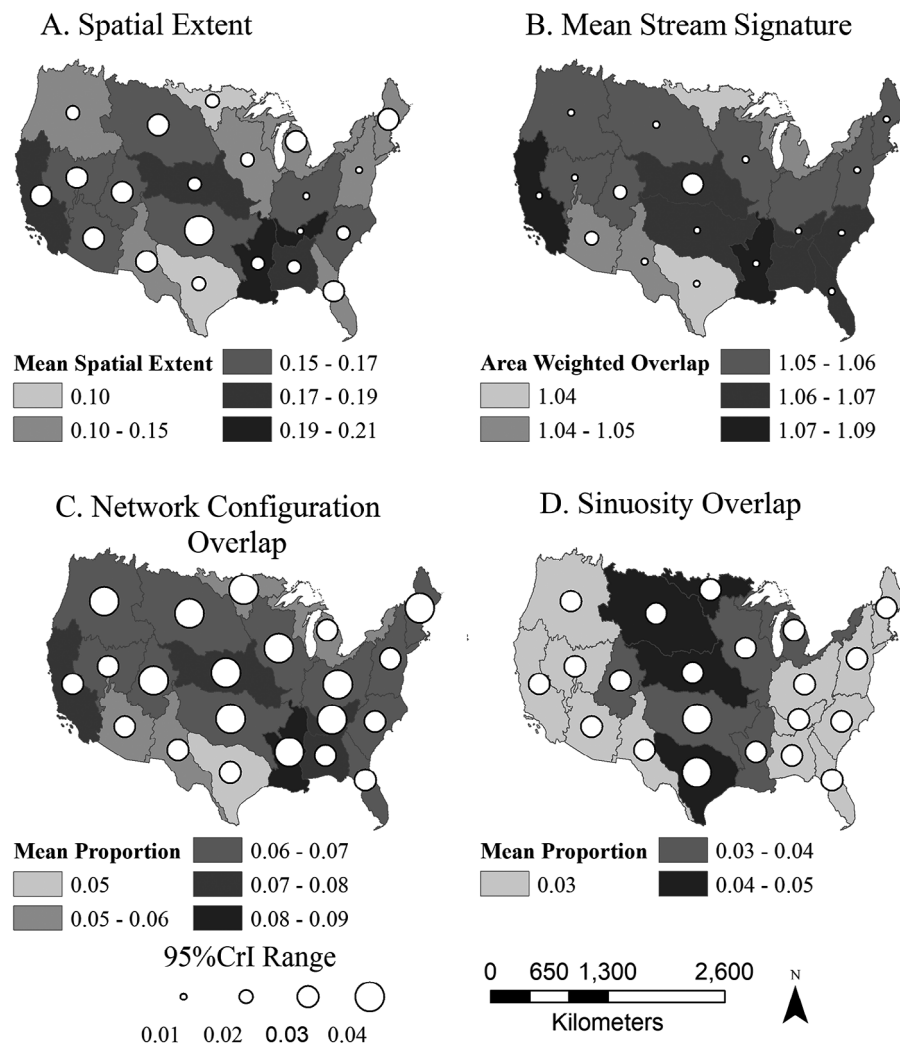


Fig. 4. (A) Regional variability in the mean spatial extent and (B) area-weighted stream signature and the proportion of extent consisting of multiple stream signatures resulting from network configuration (C) and channel planform (D) at the 13% stream signature (100 m). Circles represent the range of 95% credible intervals capturing the mean estimate for the hydrological region indicated by shading intensity.

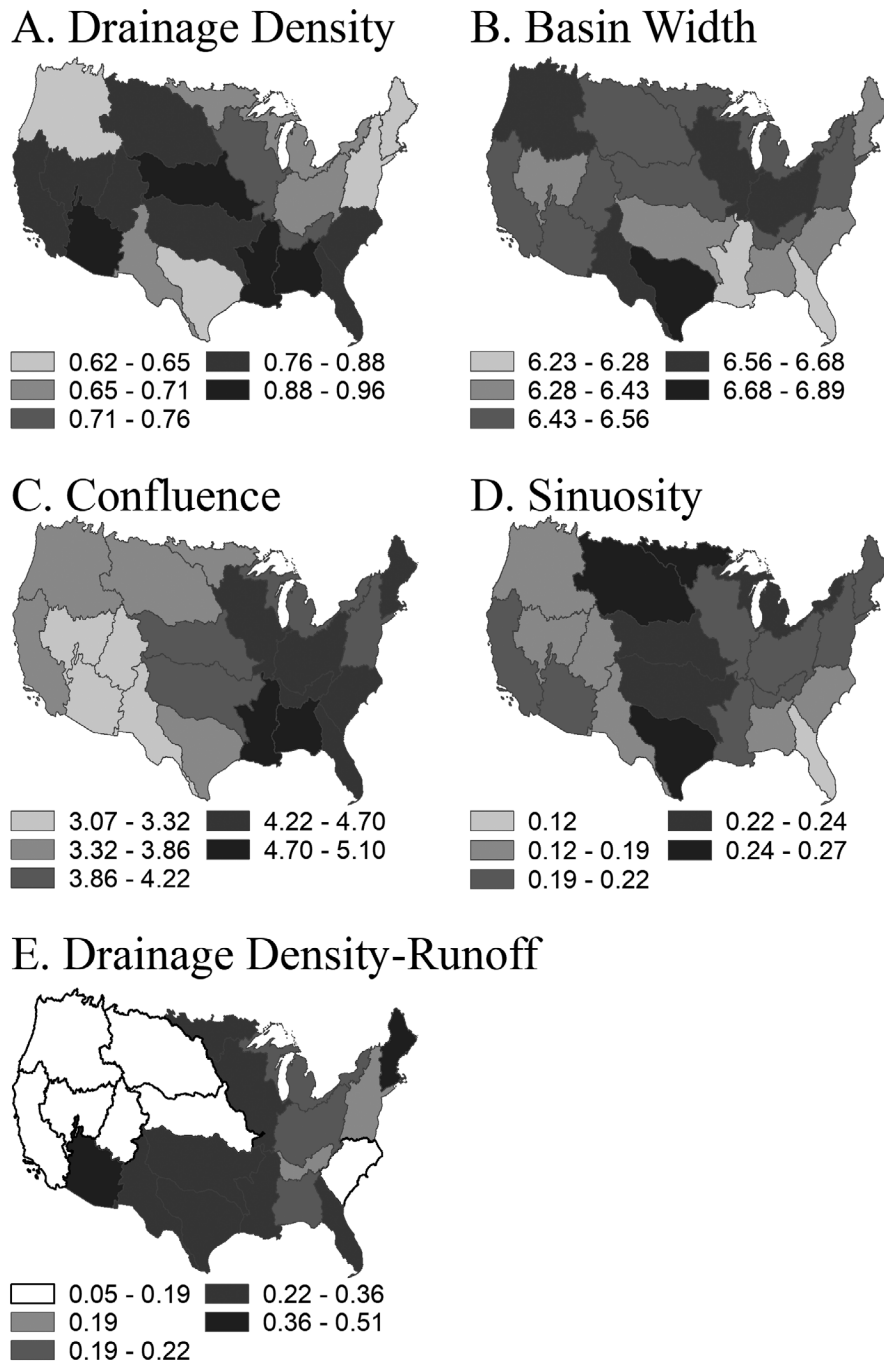


Fig. 5. Mean intercept estimates from representing regional variability in components of stream network geometry (A–D) and slope estimates between drainage density and runoff (E). Estimates in panels B, C, and D were natural log-transformed. In panel E, unshaded VPUs indicate 90% credible intervals overlap with zero.

($\beta_5 = -0.07 [-0.09, -0.04]$). Lastly, confluence number (C) and sinuosity (λ) models both included two variables ($R^2 = 0.37$ and 0.45 ,

respectively) and indicated runoff had a greater or equal influence on the response compared with basin slope.

Table 2. Parameter estimates (90% credible intervals) for mixed-effects models predicting stream network geometry components

Network geometry (Y_i)	Basin slope (β_s)	Runoff (β_R)	Erodibility (β_{K_e})	Bare ground (β_v)	Sigma (σ_i)	R^2	Mean (O/E)
(D_a)	0.08 (0.06, 0.11)	0.22 (0.17, 0.26)	0.07 (0.06, 0.09)	-0.02 (-0.03, -0.01)	0.21 (0.2, 0.22)	0.44	0.99
Log (λ)	-0.03 (-0.04, -0.02)	-0.03 (-0.04, -0.02)			0.55 (0.52, 0.57)	0.45	0.30
Log (C)	0.3 (0.24, 0.35)	-1.33 (-1.45, -1.22)			0.06 (0.06, 0.06)	0.37	0.63
Log (W_b)	-0.07 (-0.09, -0.04)	-0.05 (-0.11, 0.01)	-0.03 (-0.05, -0.01)		0.26 (0.25, 0.28)	0.26	0.84

Notes: Models are best performing (the lowest WAIC) of those generated from a backward stepwise procedure. Predictor variables were mean-centered and standardized such that direct comparisons can be made between parameters.

Runoff and drainage density

Drainage density was the most important variable predicting the extent and distribution of aquatic insects (Table 1), and runoff was an order of magnitude more important than the other variables we considered for predicting drainage density at the national scale (Table 2). Our Bayesian mixed-effects model revealed the relationship between drainage density and mean annual runoff varied across the United States (Fig. 5E) and was consistently positive. The Lower Colorado (VPU15; $\beta_R = 0.51[0.2, 0.82]$), Northeast (VPU 01; $\beta_R = 0.45 [0.30, 0.59]$), Rio Grande (VPU13; $\beta_R = 0.36 [0.01, 0.71]$), and Souris–Red–Rainy (VPU09; $\beta_R = 0.35 [0.02, 0.68]$) hydrological regions had the strongest relationship between drainage density and mean annual runoff. Regions without strictly positive 90% credible intervals did not have strong evidence for a relationship (positive or negative) between drainage density and runoff were generally found in western half of the country (unshaded in Fig. 5E).

DISCUSSION

In spite of many studies showing the importance of spatial flows of resources between aquatic and terrestrial ecosystems (Baxter et al. 2005, Richardson and Sato 2015, Ramey and Richardson 2017, Subalusky and Post 2018), few have done so in a spatially explicit manner (but see Sabo and Hagen 2012, Bartrons et al. 2013). Even fewer have studied resource exchanges at regional and larger scales to explore factors that constrain the effects of resource subsidies in recipient ecosystems (but see Montagano et al. 2018). In exploring how stream network geometry contributes to the spatial extent and distribution of

aquatic insect subsidies in terrestrial ecosystems, we found that a nontrivial portion of aquatic subsidies can be detected throughout the entire watershed because streams exist in a dendritic network. Moreover, we found aquatic inputs from multiple locations within the stream network overlap to create discrete areas elevated or more stable subsidy inputs, and that these hotspots are incredibly common in watersheds studied across the contiguous United States. We also found spatial patterns of aquatic insect subsidies were related to stream geomorphological features that differed regionally due to runoff, topographical, soil, and vegetation conditions. Collectively, these results are striking because they suggest that the spatial influence of aquatic insect subsidies on terrestrial ecosystems may be greater and more complex than previously acknowledged.

On average, the 8% stream signature covered the entire watershed meaning it may be possible to detect some level of aquatic insect subsidies throughout the entire terrestrial ecosystem. Whether this level of aquatic insect subsidies can elicit a detectable response in terrestrial communities is unclear. Likely, the magnitude of response depends on the quantity and quality of the subsidy leaving the donor system (Marczak et al. 2007, Marcarelli et al. 2011, Subalusky and Post 2018). Unfortunately, continental-scale estimates of emergent insect production are unavailable at present, so it was not possible to quantify the level of aquatic insects being deposited within the spatial extent of the stream signature. Other studies have estimated emergence as a fraction of benthic insect production (Gratton and Vander Zanden 2009, Bartrons et al. 2013) however, and recently, global predictions of aquatic secondary production have become available (Patrick et al. 2019). Thus, future studies could combine these

newly available secondary production estimates with the stream signature concept and our spatial extent estimates to quantify aquatic insect deposition across broad spatial scales. Even if the subsidy magnitude is small, aquatic insects have higher nutritional value than terrestrial prey for terrestrial predators, containing substantially more omega-3 fatty acids (Martin-Creuzburg et al. 2017, Popova et al. 2017, Twining et al. 2019). Consequently, aquatic insect subsidies could be used by terrestrial organisms disproportionately to their level of input and our study demonstrates this could have spatially extensive implications.

The dendritic nature of stream networks also causes adjacent stream reaches to come in close proximity to one another such that their stream signatures overlap at confluences, along ridgelines and, to a lesser extent, at adjacent meander bends (Fig. 3). Thus, these geomorphological features could represent areas of elevated (Sabo and Hagen 2012) or more stable (Moore et al. 2015) sources of aquatic insect subsidies, affecting habitat complexity (White et al. 2018), trophic interactions (Iwata et al. 2003), and spatial patterns of species diversity (Ramey and Richardson 2017). Stream networks are often investigated in the context of meta-populations and have been shown to confer stability in aquatic ecosystems through the aggregation of dynamics occurring at individual stream reaches (Yeakel et al. 2014, Moore et al. 2015). Here, our overlapping stream signatures could parallel these findings for terrestrial ecosystems whereby the variance in insect emergence at any single reach is dampened by the others (i.e., meta-stability; Wu and Loucks 1995). Interestingly, we found stream signatures from individual stream reaches could overlap as many as 37 times in some networks and recommend future research assess the degree of asynchrony in aquatic insect emergence among stream reaches within river networks, which can be generated by heterogeneity in stream water temperatures (Uno 2016).

A novelty of this research is using a statistical analysis of data from real stream networks to evaluate theory put forth by Sabo and Hagen (2012). Specifically, we confirmed drainage density is the most important component predicting the spatial extent of aquatic subsidies, while confluences, basin widths, and channel sinuosity

become more important at lower stream signature percentages (larger distances) as stream signatures begin to overlap. Drainage density essentially describes the amount of contact between aquatic and terrestrial ecosystems; thus, it is unsurprising that it was the best predictor. Coefficients for confluences, subbasin width, and channel sinuosity however begin to differ from 0 at the 21% stream signature (i.e., 100 m distance from the water's edge) meaning statistically these network characteristics did not affect the spatial extent of higher stream signature percentages because they remained closer to the stream channel. We propose overlap occurs between moderate levels (lower stream signatures) of aquatic insect subsidies. Contrary to Sabo and Hagen (2012), we found network configuration (i.e., confluences and subbasins) was more important for overlapping stream signatures than channel sinuosity (Fig. 3). This departure from theory could be driven by the irregularity of meanders in real stream networks—very rarely do they fit simplified version Sabo and Hagen (2012) needed to make the mathematics tractable—which reduces the interaction between adjacent meanders. This finding may be especially important because few if any studies have focused on aquatic insect deposition at confluences and/or subbasin divides.

Linking the spatial patterning of aquatic insect subsidies to the geomorphic template of the stream network allowed us to make predictions about the relative importance of aquatic insect subsidies at regional scales and explore the broad-scale factors that potentially drive differences among regions. For example, the Lower Mississippi (VPU08) hydrologic region is relatively well dissected by streams and has a high number of confluences and narrow subbasins. Accordingly, we might expect aquatic subsidies to play a more important role in terrestrial ecosystems in this region (i.e., cover a large spatial extent and to overlap more often). Alternatively, the Texas hydrologic (VPU13) region had relatively low drainage density and wide subbasins and thus could potentially have less extensive dependence on aquatic insect subsidies. Rarely have spatial subsidies been placed in a geographic context but as ecologists are tasked with addressing problems at increasingly large spatial scales, knowing where cross-ecosystems linkages are most

important could inform management interventions and study designs to better understand local ecosystem functions (Loreau et al. 2003, Turner and Chapin 2005, McCluney et al. 2014).

Beyond applying a theory of aquatic–terrestrial linkages to a large-scale geospatial dataset spanning the contiguous United States and evaluating it statistically, we also found relationships between runoff and stream network geometry which could indicate a potential indirect role of climate in moderating aquatic-to-terrestrial interactions. In particular, associations between runoff and drainage density and confluences have been detected elsewhere (Smith et al. 2013, Seybold et al. 2017) and we found evidence for geographical dependence of this relationship. Indeed, others have reported nonlinear relationships (i.e., shifting between positive and negative along continuous precipitation gradients) between drainage density and runoff (Moglen et al. 1998, Smith et al. 2013, Sangireddy et al. 2016) that are inconsistent with the positive parameter estimates reported here. Still, the credible intervals for some regions were not strictly positive or differing from zero and others were exceptionally large, indicating variation in the drainage density–runoff relationship within a hydrologic region. The Pacific Northwest (VPU17) for instance spans a precipitation gradient large enough to produce both positive and negative relationships observed in other studies (Sangireddy et al. 2016). Consequently, at the resolution of our analysis (i.e., hydrologic region), positive associations could mask negative ones when both exist across a large spatial scale. Though future efforts are needed to clarify the exact relationship between basin features and stream network geometry, the linkage we have uncovered here could highlight a potential understudied impact of climate change on aquatic-to-terrestrial resource exchange that could affect some regions more than others (Larsen et al. 2016).

Caveats and model assumptions

A uniform stream signature buffer was appropriate for assessing the spatial influence of aquatic subsidies and allowed us to isolate the effects of network geometry, but this approach greatly reduces the complexity experienced in nature and could potentially mask error propagation issues

resulting from combining models. Foremost, we parameterized the stream signature models with general values (i.e., all taxa and medium production) and sacrificed specific estimates of uncertainty driven by regional variation in these parameters (i.e., variation driven by the ecology of the systems). Specifically, the relative abundance of emergent taxa with different flight capabilities (Vieira et al. 2006) and the level of primary productivity (Marczak et al. 2007) should differ within and among stream networks and will change the stream signature decay curve (Muehlbauer et al. 2014). Moreover, we did not consider trophic relays (i.e., indirect transfers of aquatic subsidies through trophic interactions) in extending the stream signature within (Schindler and Smits 2017) nor integrate potential effects of land cover on the relative permeability of the aquatic–terrestrial boundary (Greenwood and Booker 2016). With respect to the latter, Muehlbauer et al. (2014) did not find an effect of terrestrial vegetation structure on stream signatures, but the data included in the meta-analysis were poorly quantified by the original source. Moving forward, we encourage future studies to use national-scale biological monitoring surveys (e.g., the U.S. Environmental Protection Agency’s National Aquatic Resource Survey) to assess continental-scale variation in flight traits, aquatic primary production, and boundary permeability to better parameterize stream signature models.

Our analysis relies on the NHDPlusV2 flow lines (McKay et al. 2012) for a spatial framework and is thus susceptible to issues caused by the spatial resolution (Benstead and Leigh 2012) and original digitization of USGS Quadrangle maps. More specifically, the medium resolution could underestimate drainage density and therefore affect our estimates of the extent of the aquatic insect subsidies. Also, planimetric 1:24K maps were generalized to fill in gaps in the 1:100K maps to create a seamless coverage at the time NHD was created and as a result produced some inconsistencies in drainage densities along township boundaries. Currently, there is not scale-based method to resolve this issue (NHDPlus Team, *personal communication*), but visual inspection of the entire NHDPlusV2 dataset did not reveal systematic inconsistencies between the hydrologic regions. Thus, we assume they are evenly distributed across the United States and did not bias our analysis.

Regardless of these limitations, establishing a link between stream network geometry and the spatial influence of aquatic insect subsidies provides a potential explanation of regional differences in the importance of subsidies and is a crucial step toward understanding ecosystem functioning at landscape scales. More generally, this study provides a framework for uniting meta-analyses with theory and large-scale geospatial datasets which could be used to generate novel insights into broadscale patterns in ecology. As ecologists are presented with problems occurring at larger spatial scales, this approach could become increasingly important.

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