ECOGRAPHY

Research

Trait–environment relationships could alter the spatial and temporal characteristics of aquatic insect subsidies at the macrospatial scale

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Ecography
43: 1–12, 2020
doi: 10.1111/ecog.05298

Subject Editor: Jani Heino
Editor-in-Chief: Miguel Araújo
Accepted 9 November 2020

Ecological flows across ecosystem boundaries are typically studied at spatial scales that limit our understanding of broad geographical patterns in ecosystem linkages. Aquatic insects that metamorphose into terrestrial adults are important resource subsidies for terrestrial ecosystems. Traits related to their development and dispersal should determine their availability to terrestrial consumers. Here, we synthesize geospatial, aquatic biomonitoring and biological traits data to quantify the relative importance of several environmental gradients on the potential spatial and temporal characteristics of aquatic insect subsidies across the contiguous United States. We found the trait composition of benthic macroinvertebrate communities varies among hydrologic regions and could affect how aquatic insects transport subsidies as adults. Further, several trait–environment relationships were underpinned by hydrology. Large bodied taxa that could disperse further from the stream were associated with hydrologically stable conditions. Alternatively, hydrologically variable conditions were associated with multivoltine taxa that could extend the duration of subsidies with periodic emergence events throughout the year. We also found that anthropogenic impacts decrease the frequency of individuals with adult flight but potentially extend the distance subsidies travel into the terrestrial ecosystem. Collectively, these results suggest that natural and anthropogenic gradients could affect aquatic insect subsidies by changing the trait composition of benthic macroinvertebrate communities. The conceptual framework and trait–environment relationships we present shows promise for understanding broad geographical patterns in linkages between ecosystems.

Keywords: aquatic–terrestrial linkages, biovectors, insect traits, macroecology, resource subsidies, stream ecology

Introduction

Material and energy fluxes across ecosystem boundaries, termed ‘resource subsidies’, couple adjacent ecosystems (Polis et al. 1997, Loreau et al. 2003, Holt 2004). Resource subsidies are globally common (Polis et al. 1997, Allen and Wesner 2016, Gounand et al. 2018) and play critical roles in controlling food webs and ecosystem production

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(Leroux and Loreau 2008, Yu et al. 2015, Gratton et al. 2017). The effect of resource subsidies is typically studied at local scales, which limits our understanding of large scale geographical variation in ecosystem linkages (Marcarelli et al. 2011, Subalusky and Post 2018, Lafage et al. 2019). When subsidies are transported by animals, their dispersal and development traits should influence the recipient ecosystem, determining the spatial extent of resource subsidies (i.e. the distance they travel form the donor ecosystem) and the period of time they are available to consumers (Yang et al. 2010, Muehlbauer et al. 2014, Gratton et al. 2017, Subalusky and Post 2018). If the presence of traits varies predictably with environmental conditions, trait distributions could underpin macroscale patterns in ecosystem linkages (Montagano et al. 2018, Lafage et al. 2019).

Aquatic insects that metamorphose into winged, terrestrial adults are important resources in terrestrial ecosystems (Baxter et al. 2005, Richardson et al. 2010, Schindler and Smits 2017). Traits related to their emergence and potential dispersal as adults should influence the duration and magnitude of their effect on terrestrial ecosystems. Terrestrial consumers respond to the quantity of aquatic insect subsidies (Nakano and Murakami 2001, Messan et al. 2018, Recalde et al. 2020) which, in turn, should be related to the proportion of individuals with adult flight stages in aquatic invertebrate communities (Gratton and Vander Zanden 2009, Greenwood and Booker 2016, McKie et al. 2018). Juvenile development speed and adult emergence patterns should determine when, and for how long, aquatic insects are present in terrestrial ecosystems. More frequent emergence events associated with faster development or shorter generation times should prolong the duration of aquatic insect subsidies in terrestrial ecosystems (Anderson et al. 2008, Gratton et al. 2017, McKie et al. 2018). The distance adult aquatic insects travel from the stream determines whether they are accessible to terrestrial consumers living further from the water's edge (Carlson et al. 2016). Dispersal distance should be related to an individual's flight strength, adult life span, and/or body size (Muehlbauer et al. 2014, McKie et al. 2018, Lancaster et al. 2020).

Environmental gradients should constrain the spatial and temporal characteristics of aquatic insect subsidies by altering trait composition (Statzner et al. 2004, Heino et al. 2013, Dodds et al. 2015). For example, traits for faster development and greater dispersal abilities typically persist in unpredictable environments because they promote avoidance of, and/or recolonization after, floods and droughts (Townsend and Hildrew 1994, Poff et al. 2010, 2018). Similarly, agriculture and urbanization impairs water quality, favoring pollutant tolerant taxa with smaller body size and shorter generation times (Allan 2004, McKie et al. 2018). At larger spatial scales trait composition may depend on environmental legacies (e.g. past glaciation; Ribera and Vogler 2004) or the regional species pool (Heino et al. 2013). Thus, evaluating trait–environment relationships for in-stream macroinvertebrate communities should be useful for anticipating how spatial and temporal subsidy characteristics might be impacted by global change (Larsen et al. 2016).

Here, we evaluate nine univariate trait–environment relationships for traits that could regulate the supply, extent and duration of aquatic insect subsidies in terrestrial ecosystems (Table 1). Our primary objectives were to: 1) develop a framework to assess large-scale geographic variation in the potential spatial and temporal characteristics of aquatic insect subsidies and 2) evaluate the relative importance of environmental (natural and anthropogenic) and geographical gradients in driving variation in trait composition of benthic macroinvertebrate communities (Supporting information). Because traits reflect an organism's adaptation to their environment, trait composition should covary with geographic variation in environmental and anthropogenic land use gradients. By synthesizing a national survey of benthic macroinvertebrate communities with a biological traits database, our results can be used to develop hypotheses about the spatial and temporal heterogeneity of aquatic insect subsidies and the potential connectivity between ecosystems.

Methods

Supply, extent and duration of subsidies

We used the National Rivers and Streams Assessment (NRSA; U.S. EPA 2016a) benthic macroinvertebrate surveys to generate nine metrics related to the supply, extent and duration of aquatic insect subsidies (Table 1). The primary goal of the NRSA is to conduct biological assessments of flowing waters in the US (U.S. EPA 2016a). As part of this national effort, NRSA collected composite benthic macroinvertebrate samples and physical habitat data (described below) from 1924 stream reaches throughout the contiguous US between May and September 2008–2009 (Supporting information). Benthic macroinvertebrates samples containing > 300 individuals were subsampled to a fixed number of individuals (typically 300; U.S. EPA 2016a) and identified to lowest possible taxonomic level (usually genus).

We calculated the proportion of taxonomic orders with flying adult life stages (i.e. Ephemeroptera, Plecoptera, Trichoptera, Diptera and Odonata; Baxter et al. 2005) relative to other members of the community as an indicator of the supply of aquatic insect subsidies. We estimated the spatial extent of aquatic insect subsidies using the 'stream signature' concept, where the stream signature is the distance a given proportion of insect subsidies measured at the water's edge travels perpendicular from the stream (Muehlbauer et al. 2014). We calculated the distance that 25% of the subsidies emerging from the stream travel away from the water (i.e. '25% stream signature') using regression coefficients from a negative power function parameterized via meta-analysis of 109 studies given in Appendix B of Muehlbauer et al. (2014). Major taxonomic groups of flying aquatic insects (i.e. Ephemeroptera, Plecoptera, Trichoptera and Chironomidae [Diptera]) have different regression coefficients so we weighted the 25% stream signature by the relative abundance of each taxon for each site. We excluded members of Odonata

Table 1. Description of trait-states potentially effecting the spatial and temporal characteristics of aquatic insect subsidies in terrestrial ecosystems. Modified from McKie et al (2018) and The Freshwater Traits Database (U.S. EPA 2012).

Trait-state	Name	Description	Assumed function
Winged adult life stage	Flying	Proportion of flying individuals (Diptera, Ephemeroptera, Plecoptera, Odonta and Trichoptera) in benthic communities	Individuals with flying adult life stages can exit the aquatic ecosystem, while non-flying individuals cannot
Stream signature distance	SS25	Community weighted 25% stream signature distance (m)	Stream signature could reflect the lateral distance aquatic insects could travel from the stream
Body size (large)	BSL	Large body size. Proportion of flying individuals having a maximal body size > 9 mm	Large body size could correspond to more energy reserves that allow individuals to disperse further from the stream
Life span (long)	LSL	Long life span. Proportion of flying individuals having an adult life span > 1 week	Long adult life span could correspond to individuals that have more time in the terrestrial environment to disperse further from the stream
Flight strength (strong)	FSS	Proportion of flying individuals that can fly into a light breeze	Strong flight strength could correspond to individuals that have innate abilities (e.g. wing morphologies) that allow them to disperse further from the stream
Female dispersal (high)	FDH	Proportion of flying individuals having females capable of flying > 1 km before laying eggs	High female dispersal could correspond to females that disperse further from the stream in search of a suitable oviposition sites
Development speed (fast)	DSF	Proportion of flying individuals having fast development occurring over spring/summer	Fast development could correspond to taxa that have multiple emergence events throughout the season and extend the duration of subsidies
Emergence synchrony (poor)	ESP	Proportion of flying individuals having poorly synchronized emergence	Poorly synchronized emergence could correspond to individuals that emerge from the stream at different times and extend the duration of subsidies
Voltinism (multi)	VOM	Proportion of flying individuals having > 1 generation per year	Multivoltinism could correspond to taxa that reach adult life stages and emerge from the stream multiple times during the year and extend the duration of subsidies

and non-chironomid Diptera because stream signature coefficients were unavailable for these taxa and used the same 'productivity' coefficient for all sites (Muehlbauer et al. 2014).

We derived seven additional metrics of dispersal and development traits using the Freshwater Biological Traits Database (Table 1; U.S. EPA 2012, McKie et al. 2018). Traits were assigned to flying genera collected by the NRSA survey and allowed us to explore potential variation in spatial and temporal subsidy characteristics at a finer taxonomic resolution than the stream signature. Prior to assigning 'trait-states' for dispersal and development traits (Table 1; Vieira et al. 2006), we harmonized genus names between the two datasets using the integrated taxonomic information system (<www.itis.gov/taxmatch.html>). We then quantified trait composition as the proportion of individuals expressing a trait-state that could increase the spatial extent or duration of subsidies relative to the total number of flying individuals with trait information (Table 1; McKie et al. 2018).

Environmental gradients and anthropogenic disturbance class

We used a combination of field and GIS data to characterize physical and hydrological conditions and anthropogenic disturbances at each site (Table 2). Mean depth and wetted width of the stream, percent embeddedness and substrate < 16 mm in diameter were collected by the NRSA (U.S. EPA 2016a). We obtained catchment area (km^2), elevation (m), slope (%), discharge (m^3 s^{-1}) and land cover (% agricultural or urban) from the National Hydrography Dataset Plus, ver. 2 (NHDPlusV2; McKay et al. 2012). We extracted temperature and hydrologic data at each site from McManamay and Derolph (2019). Briefly, McManamay and Derolph (2019) predicted mean summer water temperature at 1764 reference locations and classified hydrological conditions at 2600 USGS stream gages into 15 different classes. Temperature and hydrologic classes were extrapolated to ungaged locations across the entire NHDPlusV2 using a suite of environmental variables (McManamay and Derolph 2019).

The NRSA also classified anthropogenic impacts at each site as 'good' (least disturbed), 'fair' (moderately disturbed) or 'poor' (most disturbed) based on a multi-metric index (MMI) (U.S. EPA 2016a). The MMI combines multiple attributes of the biological community (e.g. composition, tolerance to disturbance and habitat preference) into a single index (Stoddard et al. 2008, U.S. EPA 2016a, Hill et al. 2017). Condition class of a site is assigned using percentiles of MMI scores calculated at minimally impacted sites (Herlihy et al. 2008, Hill et al. 2017). We present analyses linking MMI to traits that could reflect the spatial and temporal characteristics of subsidies to place our results in a general bioassessment context, although we acknowledge that MMI and some trait-states may be correlated.

Data analysis

Of the 1924 NRSA sites surveyed for benthic macroinvertebrates, 36 samples were lost during processing and 29 sites

Table 2. Predictor variable used in our analysis and their descriptions.

Gradient	Abrev.	Description	Data source
Region	REGION	Major hydrologic region	NHDPlusV2
Habitat	EMBED	Embeddedness (%)	NRSA
	FINES	Substrate < 16 mm in diameter (%)	NRSA
	SLOPE	Slope of channel (%)	NHDPlusV2
Network positon	ELEV	Elevation (m)	NHDPlusV2
	AREA	Log of catchment area (km^2)	NHDPlusV2
Land use	AGRI	Agricultural land cover (%)	NHDPlusV2
	URBAN	Urban land cover (%)	NHDPlusV2
Hydro-climate	PRECIP	Mean annual precipitation (mm)	NHDPlusV2
	TEMP_MA	Mean annual temperature (°C)	NHDPlusV2
	TEMP_JA	Mean July August temperature (°C)	McManamay and Derolph (2019)
	TEMP_CoV	Mean monthly temperature coefficient of variation	NHDPlusV2
	PRECIP_CoV	Mean monthly precipitation coefficient of variation	NHDPlusV2
	WIDTH	Mean channel width (m)	NRSA
	DEPTH	Mean thawleg depth (cm)	NRSA
	DISCHARGE	Mean annual discharge (m^3 s^{-1})	NHDPlusV2
	HYDROCLASS	Hydrological class	McManamay and Derolph (2019)

lacked sufficient environmental data. We discarded an additional 7 sites because it was not possible to estimate a stream signature for sites with only Odonata and/or non-chironomid Diptera as flying taxa, leaving us with 1852 sites for this study (Supporting information). Due to data availability, we restricted the trait analysis to sites that had trait assignments for > 50% of the flying individuals (n = 574, Supporting information) and calculated the frequency of a given trait-state using only individuals with trait data. We chose this threshold to achieve a minimum sample size for each hydrologic region (n ≥ 3, Supporting information) but found similar results for more conservative thresholds (i.e. > 60, > 70 and > 80%; Supporting information). Further, trait data were only available for 232 genera (46% of flying genera) and were unequally represented among the taxonomic groups collected during the NRSA survey (i.e. 14% Diptera, 75% Ephemeroptera, 67% Odonata, 88% Plecoptera, 68% Tricoptera; Supporting information). Given the relatively low representation of Diptera in the traits database, sites dominated by these taxa may have been excluded from our analysis (Supporting information).

We used random forest regression models to predict each of the nine response variables from 15 environmental predictor variables (Breiman 2001, Table 2). Random forest is a machine learning algorithm that combines predictions from multiple independent decision trees and is now common in ecology (Fox et al. 2017, Hill et al. 2017). Prior to model fitting we randomly selected and withheld 20% of sites for validation. We removed strongly correlated variables (r > 0.7; DISCHARGE, WIDTH and DEPTH and JA_TEMP) to avoid potentially misleading estimates of variable importance (Gregorutti et al. 2017). The remaining variables were mean-centered and standardized.

Models were fit using the 'randomForest' R-package (Liaw and Wiener 2002). Random forest models have two tuning parameters that specify the number of variables randomly selected at each node (mtry) and the number of trees used to build the model (ntree). We conducted a sensitivity analysis to evaluate different parameter values for each model (Supporting information; Fox et al. 2017, Brieuc et al. 2018). Consistent with Fox et al. (2017), we found the optimal mtry value offered little improvement over the default (mtry = 4) for many of the models (Supporting information), but increasing the number of trees enhanced the reproducibility (Supporting information). We specified mtry = 4 and ntree = 3000 for all models except FSS (mtry = 1, ntree = 3000). We evaluated model performance with Nash–Sutcliffe efficiency (NSE), mean absolute error (MAE), the ratio of the root mean square error to the standard deviation of observed data (RSR) and Out-of-Bag R^2 (Moriasi et al. 2007, Greenwood and Booker 2016).

We used mean decrease in accuracy (MDA) and marginal effects to assess the relative importance and direction of each trait–environment relationship. MDA is the change in mean squared error after permutating a single predictor variable, averaged and scaled by the standard deviation of all trees in the random forest (Liaw and Wiener 2002). Larger MDA values indicate more important variables because permutation increased the mean squared error (Liaw and Wiener 2002). Marginal effects show how a response variable changes with a single independent variable while holding all other variables constant (Elith et al. 2008). We created partial dependence plots to illustrate the marginal effects for the five most important predictor variables for each trait–environmental relationship. When hydrologic region was among the most important predictor variables, we mapped the marginal effects for hydrologic region to visualize geographic differences. The 'importance' and 'partialPlot' functions were used to calculate MDA and marginal effects, respectively (Liaw and Wiener 2002).

We used Bayesian regression models to evaluate the effect of anthropogenic activities on aquatic insect subsidies. Each model included only NRSA condition class as a grouping term (e.g. 'random effect' or 'intercept only model'; Wesner et al. 2019) and had either a beta-binominal likelihood with logit link function (i.e. proportional responses) or a normal likelihood (i.e. stream signature distance). We obtained a mean and standard deviation from Muehlbauer et al. (2014) and McKie et al. (2018) to specify the prior for the 25% stream signature and each trait model, respectively (Supporting information). All models were fit using the 'Rethinking' R package (McElreath 2016) with 4 chains and 10 000 iterations (first 2000 discarded as warmup). The large number of iterations allowed us to estimate the probability that the posterior distributions of two condition classes overlapped.

Results

Random forest models explained approximately 31% of the variation in the proportion of flying individuals and 18% of the variation in the stream signature distance (mean absolute error [MAE] = 0.17 and 8.79, respectively; Supporting information). Elevation, agricultural land use, catchment area and region were among the most important variables in both models (Fig. 1A–B). Elevation was associated with an increase in the proportion of flying taxa but a decrease in stream signature distance. Conversely, agriculture had the opposite association. Catchment area had a negative relationship with the proportion of flying taxa and the stream signature distance.

Random forest models explained > 10% of the variation in all trait-states except strong flight strength (min MAE = 0.15, max MAE = 0.23, Supporting information). Hydrologic class was the most important variable trait states related to emergence duration (Fig. 1C–E) and for large body size (Fig. 1F). The 'intermittent flashy' hydrologic class appeared to have the lowest proportion of individuals with poorly synchronized emergence and fast development but high multivoltinism while the 'stable' hydrologic classes had higher proportions of large body size (Fig. 1F). Catchment area was most important for high female dispersal (Fig. 1G) and the proportion of individuals with long life span declined with the percent of fine substrate (Fig. 1H).

Hydrologic region was an important variable in all random forest models except strong flight strength (Fig. 2). The California (hydrologic unit code [HUC] 18), Rio Grande (HUC13) and Upper Colorado (HUC 14) had the highest proportion of flying individuals and the Upper Mississippi (HUC 07), Ohio (HUC 05) and South Atlantic (HUC 03N and 03S) had the largest stream signature distance (Fig. 2B–C). The proportion of poorly synchronized emergence, multivoltinism and fast developing individuals were highest in the Lower Colorado (HUC 14), and Rio Grande (HUC 13) hydrologic regions (Fig. 2D–F). Large body size, long life span and high female dispersal were most prevalent in the California (HUC 18) hydrologic region but were generally variable among hydrologic regions (Fig. 2G–I).

The habitat condition class affected the potential spatial and temporal characteristics of aquatic insect subsidies (Fig. 3). The least disturbed sites had the greatest proportion of flying individuals (mean, [95% credible interval]: 0.71, [0.68, 0.74]; Fig. 3A) but the lowest 25% stream signature distance (27.17, [25.65, 28.69]; Fig. 3B). In both instances, the probability of overlap between the posterior distributions of the least and most disturbed condition (hereafter 'Pr') was < 0.0001. Poorly synchronized emergence and fast development were higher at the least disturbed sites (Pr = 0.11 and 0.02, respectively; Fig. 3C, E) but multivoltinism was higher at the most disturbed sites (Pr < 0.01, Fig. 3D). Large body size and long life span were more prevalent in the least disturbed condition (Pr = 0.04 and 0.03, respectively; Fig. 3F, H) and the proportion of high female dispersal and strong flying strength was higher in the most disturbed condition (Pr = 0.03 and 0.11, respectively; Fig. 3G, I).

Discussion

Understanding how ecosystems are linked is a focal area of ecological research (Allen and Wesner 2016, Tanentzap et al. 2017, Gounand et al. 2018) but understanding how these linkages vary across large spatial scales remains unclear. We developed a conceptual framework centered on hydroclimatic and physiographic variables that generate geographical variation in species traits that could influence spatial and temporal characteristics of animal-mediated resource subsidies in recipient ecosystems. Using aquatic insects as a focal organism, we tested this framework and found that a combination of watershed and land use variables could influence the supply, duration and distance of aquatic insect subsidy transport to terrestrial ecosystems.

Stream signatures and the potential supply of insect subsidies

The proportion of flying individuals and the 25% stream signature was largely influenced by network position (i.e. catchment area and elevation; Tonkin et al. 2016). Larger proportions of flying individuals at higher elevations and in smaller catchments could result from environmental filters common to these habitats. For example, cooler water temperatures in headwater systems could preclude warm-adapted, non-flying taxa such as many snails (Nelson et al. 2017). Alternatively, the enhanced dispersal abilities of flying taxa could enable them to colonize headwaters as isolated termini of stream networks (Clarke et al. 2008, Finn et al. 2011). Stream signature distance, however, was negatively related to both catchment area and elevation which may be due to the taxa that are most associated with headwaters. Muehlbauer et al. (2014) found that the stream signature decays quickest for Ephemeroptera and Plecoptera (i.e. these orders have the shortest stream signature). Indeed, some Ephemeroptera develop as larva in mainstem river sections (Uno and Power 2015), and cooler water temperatures at higher elevations could favor

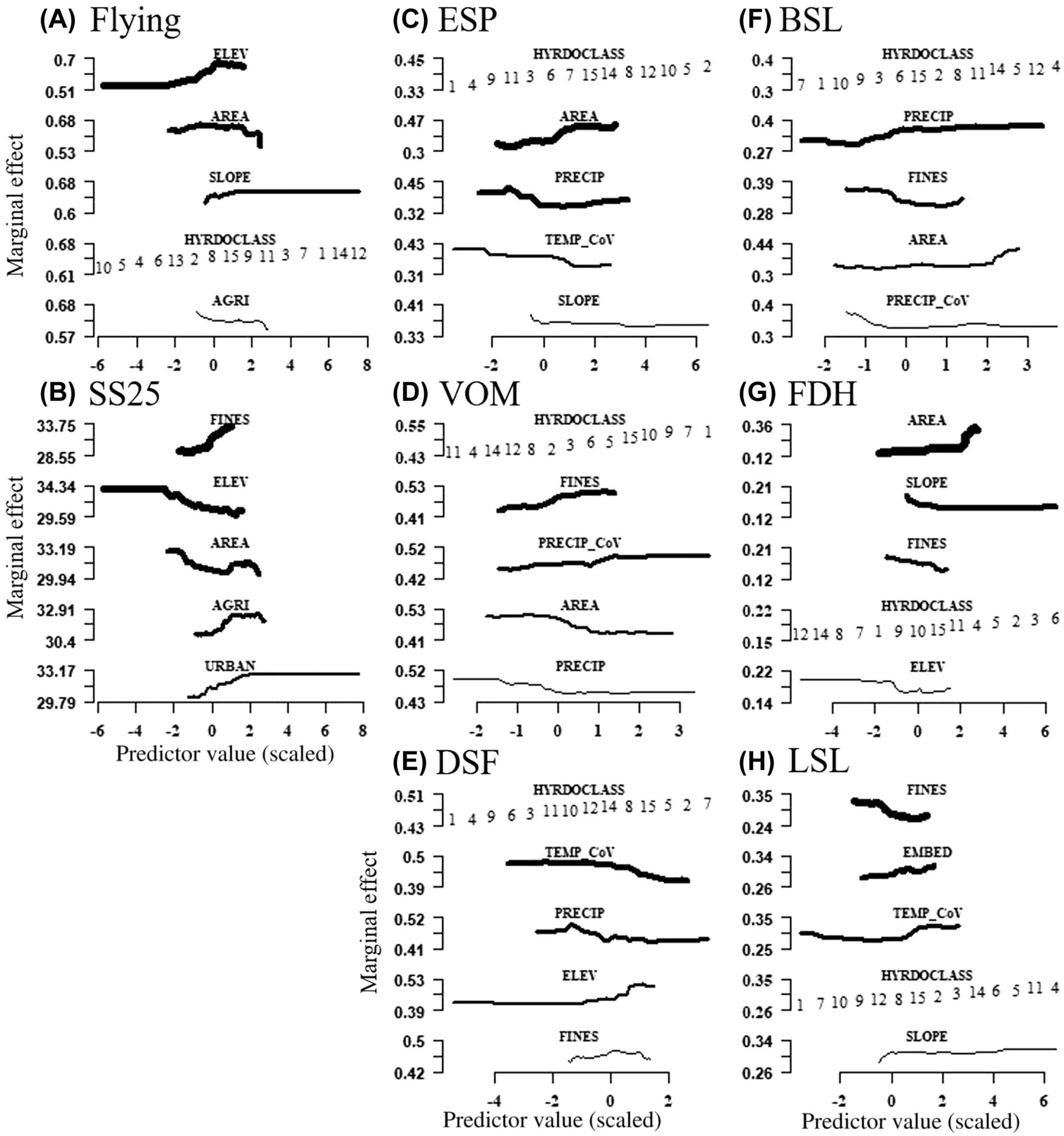

Figure 1. Partial dependence plots for random forest models with > 10% proportion of variation explained. (A) Proportion of flying individuals, 'Flying'; (B) 25% stream signature distance, 'SS25'; (C) poorly synchronized emergence, 'ESP'; (D) multivoltinism, 'VOM'; (E) fast development speed, 'DSF'; (F) large body size, 'BSL'; (G) high female dispersal, 'FDH'; (H) long life span, 'LSL'. AREA = catchment area, ELEV = elevation, SLOPE = channel slope, FINES = percent fine substrate, EMBED = percent embeddedness, AGRI = percent agricultural land cover, URBAN = percent urban land cover, PRECIP = mean annual precipitation, TEMP_CoV = mean annual temperature coefficient of variation, PRECIP_CoV = mean annual precipitation coefficient of variation. For hydrological class, 'HYDROCLASS': 1 = 'intermittent flashy 1', 2 = 'late timing runoff', 3 = 'perennial runoff 1', 4 = 'perennial runoff 2', 5 = 'super stable groundwater', 6 = 'stable high baseflow', 7 = 'intermittent flashy SW', 8 = 'snowmelt 2', 9 = 'perennial flashy', 10 = 'intermittent flashy 2', 11 = 'western coastal runoff', 12 = 'stable high runoff', 13 = 'harsh intermittent', 14 = 'snowmelt 1', 15 = 'glacial high runoff' (McManamay and Derolph 2019). All predictor variables were mean-centered and scaled by their standard deviation prior to analysis. Line widths represent ranked importance of each variable.

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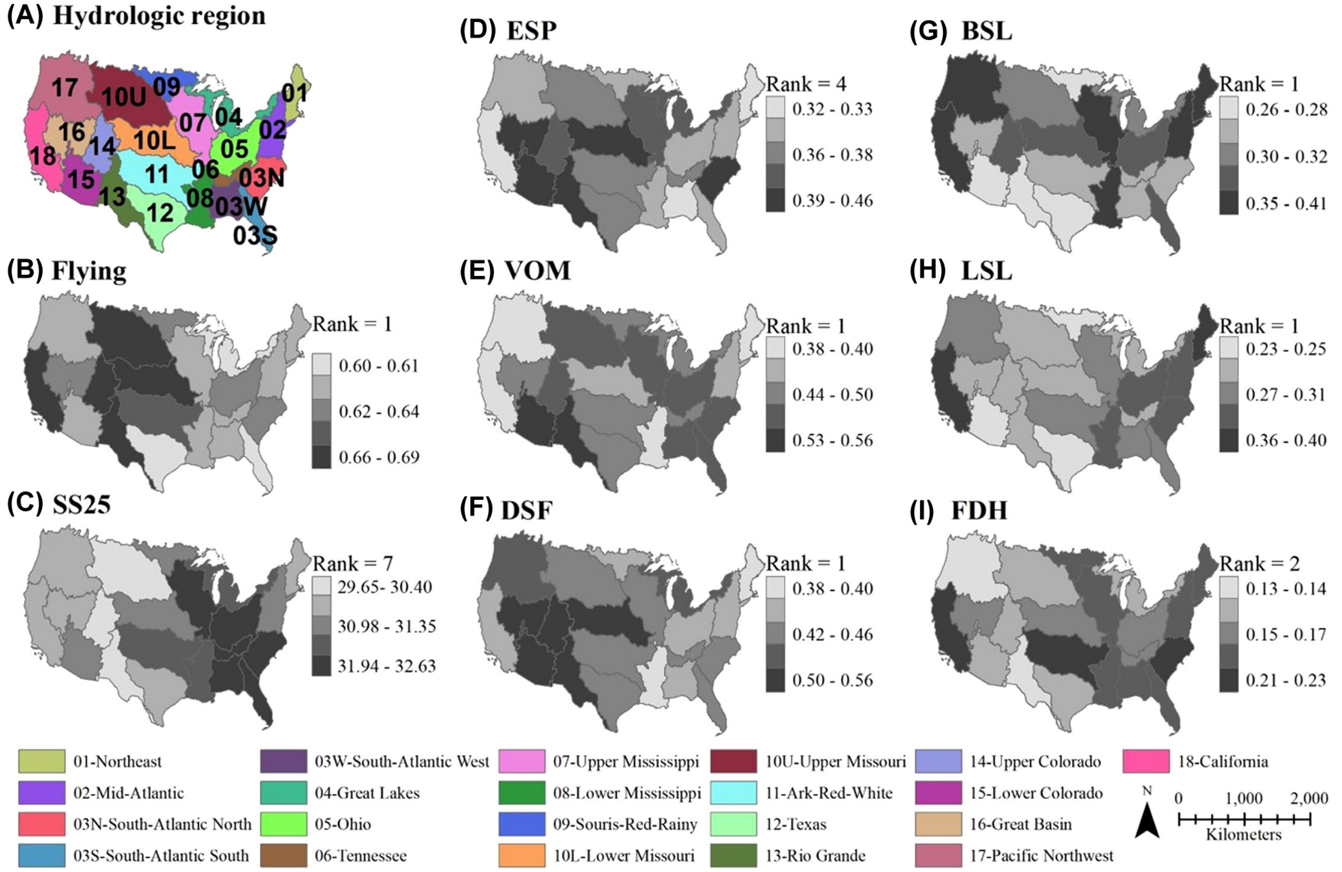

Figure 2. Regional variability in benthic macroinvertebrate traits displayed as marginal effects of hydrologic region. (A) Hydrologic regions; (B) proportion of flying individuals, ‘Flying’; (C) 25% stream signature distance, ‘SS25’; (D) poorly synchronized emergence, ‘ESP’; (E) multivoltinism, ‘VOM’; (F) fast development speed, ‘DSF’; (G) large body size, ‘BSL’; (H) high female dispersal, ‘FDH’; (I) long life span, ‘LSL’. Trait definitions are provided in Table 1. Legend shows hydrologic region codes and ‘rank’ indicates the ranked importance of hydrologic region relative to other variables in the random forest models.

Plecoptera as cold water adapted taxa (Anderson et al. 2019). Importantly, these findings suggest that the potential supply and spatial extent of aquatic insect subsidies could vary along longitudinal gradients in streams as a result of differences in trait frequencies within benthic macroinvertebrate communities in headwaters versus mainstems.

Agricultural land use in the watershed was associated with a decrease in the proportion of flying insects but an increase in stream signature distance. Land use intensification can alter the trait composition of benthic macroinvertebrate communities by favoring pollution tolerant taxa (Allan 2004, Dolédec et al. 2006), such as Chironomidae (Diptera) (Serra et al. 2017, Raitif et al. 2019) or mollusks (Harding and Winterbourn 1995, Greenwood and Booker 2016). Chironomidae have the longest stream signature distance of all flying orders studied by Muehlbauer et al. (2014), and increasing their relative abundances could increase the spatial extent of aquatic insect subsidies. Consequently, anthropogenic impacts in the watershed may decrease the relative magnitude of aquatic insect subsidies in the terrestrial environment, but the spatial extent of that subsidy might be relatively greater.

The importance of hydrologic region for explaining the proportion of flying individuals and the 25% stream signature distance supports the notion that cross-ecosystem linkages can vary across broad spatial scales. For example, if we assume the entire larval community can metamorphose into winged adults, then the California (HUC 18) hydrologic region could export 10% more aquatic insect subsidies than the Southern Atlantic (HUC 03S), all else being equal. Similarly, aquatic insects may be expected to travel further from where they emerge in the Upper Mississippi (HUC 07) than the Upper Colorado (HUC 13) because of longer stream signature distances. These regional patterns in trait composition could reverberate throughout the landscape and drive differences in subsidy use among terrestrial consumers (Lafage et al. 2019).

Traits of flying individuals

Hydroclimatic features played an important role in structuring the presence and abundance of trait-states that should influence the spatio-temporal characteristics of aquatic insect subsidies. For example, flying individuals living in

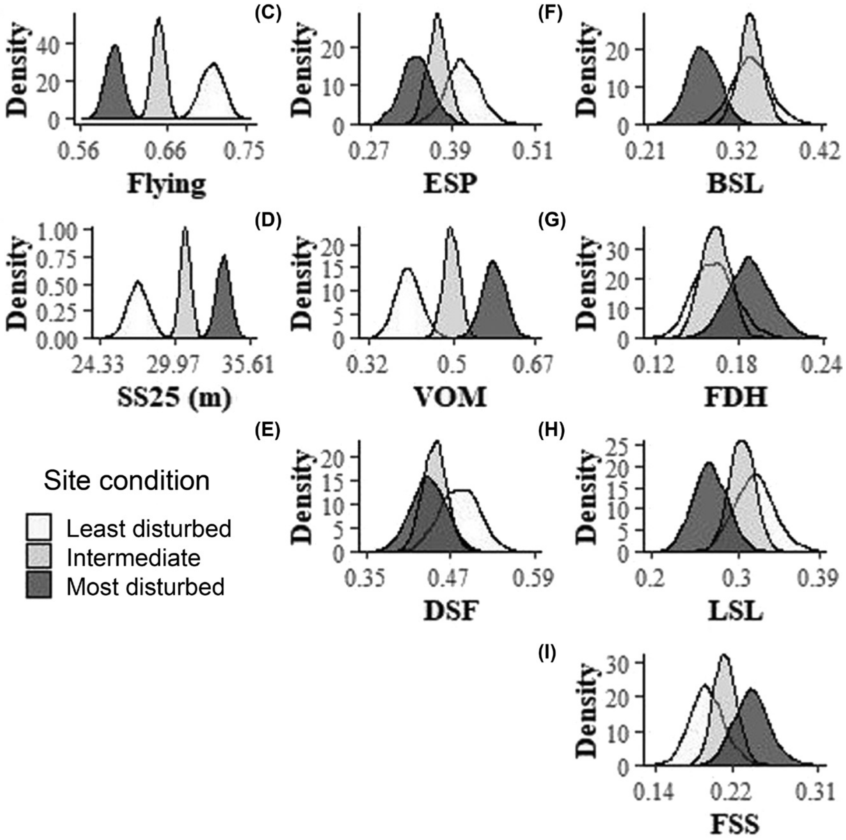

Figure 3. Posterior distributions of the mean for each response variable and for each habitat condition class. White is least disturbed, gray is intermediate and black is most disturbed. Flying = proportion of flying taxa; SS25 = 25% stream signature distance; FDH = female dispersal (high), BSL = body size (large), LSL = life span (long), FSS = flight strength (strong); ESP = emergence synchrony poor; DSF = development speed (fast) and VOM = voltinism (multi); trait definitions are provided in Table 1.

perennial or groundwater dominated systems were typically larger and have long-lived adult phases and sites with lower precipitation were associated with higher frequencies of asynchronous emergence and fast development. Given these relationships, we might expect hydrologically stable reaches to export aquatic insect subsidies that are larger in size and can live longer in terrestrial ecosystems and more arid locations to export subsidies more consistently when there is water in the stream channel. If these trait-states increase an organisms ability to survive and reproduce in their environment (Townsend and Hildrew 1994, Giam et al. 2017), these results could provide insights into how the aquatic insect subsidies might be impacted by climate change, as many flow regimes are predicted to become less stable (Barnett et al. 2008, Mallakpour and Villarini 2015, Blöschl et al. 2017).

Many of the trait–environment relationships we analyzed may be partly explained by interdependence among traits (Hamilton et al. 2020) and therefore difficult to mechanistically interpret or to attribute causation (Verberk et al. 2013). For example, we found the percentage of fine substrate was associated with a decreased frequency of large body size among flying taxa, presumably because smaller substrates do not provide refuge and interstitial habitat for larger taxa (Townsend and Hildrew 1994). We also found substrate size was associated with lower frequencies of long life span, and high female dispersal and higher frequency of multivoltinism. These trait–environment relationships are more difficult to attribute to the availability of refugia provided by substrate size but instead are likely correlated with body size (Resh et al. 1988, Usseglio-Polatera et al. 2000, Verberk et al. 2008, Lancaster et al. 2020). Indeed, univariate trait–environment relationships are known to be challenging to interpret from a strict mechanistic perspective (Poff et al. 2006) and may not accurately describe how trait composition will change in under future conditions (Verberk et al. 2013).

Our results elucidate large-scale patterns in trait composition of flying taxa that could drive regional differences in the characteristics aquatic insect subsidies. For example, the California hydrologic region (HUC 18) was associated with taxa with greater body size, female dispersal ability and longer life span. Larger bodied individuals may yield a larger quantity of subsidy to terrestrial consumers and individuals that live longer as adults, or fly further before ovipositing, may be more likely to be consumed further from the stream (McKie et al. 2018) Similarly, terrestrial consumers in the Great Basin (HUC 16) could have access to aquatic insect subsidies for longer periods of time because flying insects in benthic communities typically develop quicker and emerge irregularly throughout the year. Collectively, the geographical patterns we detected in the trait composition of benthic macroinvertebrate communities could provide insights into the large scale variation in the use of aquatic insect subsidies by terrestrial consumers detected in other studies (Lafage et al. 2019).

Extended consequences of anthropogenic impacts

Consistent with other investigations, our results demonstrate that anthropogenic activities could impact aquatic insect subsidy dynamics by altering the trait composition of benthic macroinvertebrate communities (Greenwood and Booker 2016, McKie et al. 2018). We found sites classified as most disturbed had lower proportions of individuals that could fly, and could therefore leave the stream to subsidize terrestrial ecosystems. Proportional data however may not correspond to absolute emergence values. Others have found nutrient additions can increase the abundances of all invertebrate taxa, including those with winged adult phases (Davis et al. 2011, Greenwood and Booker 2016, McKie et al. 2018). Among our sites elevated nitrogen or phosphorous concentrations were a good predictor of site degradation (U.S. EPA 2016b), but absolute abundance values could not be calculated given the survey methods. If anthropogenic activities increase the overall abundance of flying taxa, exceptional emergence events from disturbed sites may be able to offset some anthropogenic nutrient loading in waterways (Stepanian et al. 2020).

The most disturbed sites also had the longest stream signatures which could suggest aquatic insect subsidies are available to consumers living further from the water's edge at these sites. Members of Chironomidae (Diptera) often dominate disturbed sites (but see Serra et al. 2017) and, being generally small bodied taxa, their longer stream signature distance may be due to wind transport (Muehlbauer et al. 2014). Diptera are an exceptionally diverse order, however, and we only included members of Chironomidae to calculate the stream signature due to limitations of data availability in the meta-analysis of Muehlbauer et al. (2014). It is possible that other Diptera taxa could change the potential relationship between the level of disturbance and lateral extent of aquatic insect subsidies. Further we do not know how the condition of the aquatic ecosystem interacts with the permeability of the terrestrial boundary (but see Greenwood 2014, Alberts and Sullivan 2016, Carlson et al. 2016). Clarifying these uncertainties will require increasing the representation of Diptera in traits databases and increasing our understanding of how boundary conditions could alter the spatio-temporal characteristics of aquatic insect subsidies beyond what their traits suggest.

The frequency of trait-states among flying taxa also differed according to disturbance class. High female dispersal, strong flight strength and multivoltinism were more common at the most disturbed sites, suggesting that individuals may be able to travel comparatively further into the terrestrial environment and, because of their shorter generation times, emerge from the stream more often. We also found that large body size, long life span, poorly synchronized emergence and fast development were more common at least disturbed sites. Interestingly, it seems that both least and most disturbed sites could increase the spatial extent and duration of insect subsidies by favoring different trait-states. One should note, however, that high female dispersal in agricultural sites can result from the presence of small-bodied, blood-feeding Diptera (Ceratopogonidae and Simuliidae, McKie et al. 2018) which may be available to a different suite of terrestrial consumers than large bodied taxa (Davis et al. 2011). Thus even though the least and most disturbed sites are associated with traits that increase spatial extent, their subsequent effect on terrestrial consumers may be different. Future research should address the relative importance of, and interactions between, larval traits as indicators of spatial and temporal characteristics of aquatic insect subsidies.

Limitations

Our results are indicative of potential characteristics of aquatic subsidies as they are transported into terrestrial ecosystems by adults. Although adults and their traits are sourced from aquatic communities, emergence rates are likely variable among taxa (Poepperl 2000, Moyo 2020) and location (Gratton and Vander Zanden 2009). The trait–environmental relationships we uncovered however, could be used in tandem with large-scale analyses of aquatic secondary production (Patrick et al. 2019) to refine estimates of aquatic insect deposition (Gratton and Vander Zanden 2009, Bartrons et al. 2013). For example, the proportion of flying taxa in a larval community may constrain the amount of secondary production that can be exported from a stream. Site-specific estimates of the stream signature distance could better capture variation in lateral extent of subsidies in the terrestrial ecosystem.

Additionally, trait–environment relationships were assessed at the genus (or order for stream signature) level, and thus sensitive to the availability of trait data. This could mask variation at lower taxonomic levels (Heino et al. 2013). Resolving these limitations will require increasing our knowledge of the relative intra-generic variability in traits and the number of non-chironomid Diptera represented in traits databases.

Finally, we used univariate models to assess trait environment relationships. Although univariate models permit relatively straightforward and transparent interpretation of the trait–environment relationships (Hamilton et al. 2020), multivariate statistical techniques can assess multiple traits simultaneously (Poff et al. 2010, Heino et al. 2013). Evaluating multiple traits could be insightful for identifying the trait(s) that explain most variation among sites and potentially the most important trait driving differences in spatial and temporal characteristics of subsidies.

Conclusions

Benthic macroinvertebrate communities and their traits vary along natural and anthropogenic gradients within and among drainage basins. Importantly, here we show this variation could potentially impact terrestrial consumers by changing the spatial and temporal characteristics of aquatic insect resource subsidies. Several trait–environment relationships were associated with hydroclimate features. If these relationships are mechanistically grounded they could inform predictions about how the frequency of these traits and the potential linkages between aquatic and terrestrial ecosystems could be impacted by global change (Larsen et al. 2016). More generally, the framework and trait–environment relationships we present may be useful for understanding broad geographical patterns in linkages between ecosystems and promote novel applications of biomonitoring data to address novel questions in macroscale ecology.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h44j0zpj1> (Kopp and Allen 2020).

Acknowledgements – We would like to thank M. Kaspari, J. Kelly, T. Neeson, J. Wu, D. Nelson, M. Busch, J. Heino and two anonymous reviewers for comments on a previous version of this manuscript. We also thank B. McKie for providing data to specify prior distributions for the traits analysis. This manuscript is part of a PhD thesis at the Univ. of Oklahoma.

Funding – DA and DK were supported by the US National Science Foundation (award 1802872, and additional support to DA was provided by award 1754389).

Author contributions

Darin Kopp: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Daniel Allen**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Resources (lead); Supervision (lead); Writing – review and editing (Equal).

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