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Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a worldwide meta-analysis

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Abstract. Cross-boundary fluxes of organisms and matter, termed “subsidies,” are now recognized to be reciprocal and of roughly equal importance for both aquatic and terrestrial systems, even if terrestrial input to aquatic ecosystems has received most attention. The magnitude of aquatic-to-terrestrial subsidies is well documented, but the drivers behind these subsidies and their utilization by terrestrial consumers are characteristically local-scale studies, limiting the inferences that can be drawn for broader geographic scales. We therefore built and analyzed a database of stable isotope data extracted from 21 studies worldwide, to identify both landscape-scale (catchment) and local-scale (100-m riparian zone) variables that may affect the diet of terrestrial predators in riparian ecosystems. Our meta-analysis revealed a greater magnitude of aquatic-to-terrestrial subsidies (>50%) than previously reported, albeit with large geographic and inter-annual variations. Moreover, we demonstrated a large effect of landscape-scale factors on aquatic-to-terrestrial subsidies, particularly anthropogenic land use and tree cover. Local human population was the only relevant factor at the local scale. We also found that studies on landscape-scale and anthropogenic land use effects on aquatic-to-terrestrial subsidies are strongly under-represented in the ecological literature, which limits the general inferences that can currently be drawn about landscape effects. We suggest that landscape-scale studies could improve our understanding of how land use and environmental change might influence future patterns of biodiversity and ecosystem function.

Key words: anthropogenic land use; aquatic subsidies; diet; human population; stable isotopes; terrestrial predators.

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INTRODUCTION

Decades of research have demonstrated and quantified the tight linkages between aquatic and terrestrial ecosystems (Fisher and Likens 1973, Bartels et al. 2012). Cross-boundary fluxes connecting ecosystems, usually termed “subsidies” (Polis et al. 1997b), can be organisms, energy, or nutrients. Terrestrial-to-aquatic subsidies in the form of litter and organic matter are essential for aquatic ecosystem function (reviewed by Tank et al. 2010), and terrestrial prey subsidies also

have important effects on riverine food webs (Polis and Hurd 1996, Nakano and Murakami 2001, Erős et al. 2012, Gustafsson et al. 2014). More recently, research has focused on aquatic-to-terrestrial subsidies (Baxter et al. 2005, Schindler and Smits 2017). Although the amount (biomass) of terrestrial-to-aquatic prey subsidies often is greater than the reverse, their overall contribution to the carbon budget of predators is similar (Bartels et al. 2012). Thus, the most recent picture to emerge is that of tightly coupled, roughly reciprocal aquatic–terrestrial ecosystems.

One of the remaining key challenges for understanding the ecology of cross-boundary fluxes is to determine at which scales and to what extent the structure of the surrounding terrestrial landscape affects the magnitude and the importance of aquatic-to-terrestrial subsidies (Marcarelli et al. 2011). At the local scale (100-m buffer), landscape structure has an impact on predator diet by facilitating or preventing subsidies from entering recipient ecosystems (Greenwood 2014, Muehlbauer et al. 2014). At the landscape (catchment) scale, ecosystem size and land use effects on riparian ecosystem food webs were poorly studied (Marczak et al. 2007, Schindler and Smits 2017), except for the recent studies of McHugh et al. (2010), Jackson and Sullivan (2017), Stenroth et al. (2015), and Carlson et al. (2016). Land use, at local and landscape scales, influences the composition and biomass of both aquatic insect communities (via water quality, terrestrial subsidies, and canopy cover: Dolédec et al. 2006, Schindler and Smits 2017) and predator communities (Hendrickx 2007, Lafage et al. 2015a). On the other hand, ecosystem size, by integrating the effects of spatial heterogeneity, disturbance, and productivity, is a strong predictor of food chain length (Sabo et al. 2010). To gain a better understanding of broader-scale ecological processes, comparative studies of subsidy transfer between aquatic-terrestrial ecosystems at the catchment scale are needed.

In this study, we conducted a worldwide meta-analysis of studies that have assessed aquatic-to-terrestrial subsidies using stable isotopes. We quantified the effects of ecosystem size, stream morphology, and land use on aquatic subsidies to terrestrial predators. First, we estimated the overall proportion of aquatic subsidies in the diet of several groups of terrestrial predators and tested whether the proportion of these prey was significantly higher than that of terrestrial prey. We hypothesized that the proportion of aquatic subsidies varied between taxonomic groups of predators, hydrological system type (hydroecoregion), and year. Next, we assessed the relative importance of biotic and abiotic variables at local and landscape scales (100-m buffers and catchments, respectively) for the proportion of aquatic subsidies in the diet of spider and carabid beetle predators. We hypothesized that landscape-scale variables related to anthropogenic

land use would be of at least equal importance in explaining predators' diets as commonly assessed local-scale variables as agricultural and urban catchments are supposed to have the capacity to export more aquatic subsidies (Greenwood and Booker 2016). Sabo et al. (2010) hypothesized ecosystem size was affecting food webs through hydrologic variability, with large ecosystems being more stable and consequently producing more resources. We thus expected a positive relationship between ecosystem size and proportion of aquatic prey in the diet of predators. Similarly, stream meandering was expected to exhibit a positive relationship as increasing exchange surface should increase aquatic prey availability (Sabo and Hagen 2012).

METHODS

Our meta-analysis focused on the use of aquatic subsidies by terrestrial predators. We restricted the subsidies to aquatic organisms actively crossing the boundary between aquatic and terrestrial ecosystems (i.e., macro-invertebrates). All predators consuming aquatic macro-invertebrates were included. In order to get a more accurate estimation of the proportion of aquatic subsidies in the diet of predators, we restricted our meta-analysis to studies using stable isotopes, which integrate the use of prey types over a longer period of time than do stomach content analyses (Tieszen et al. 1983).

Data retrieval

We searched the Web of Science and Google Scholar for studies focusing on riparian habitats and using stable isotopes as a tool to infer the contribution of aquatic prey to the diet of terrestrial predators. The keywords used were "aquatic subsidies" AND "stable isotope" AND "diet", which gave 69 results. From these 69 articles, we refined the selection by screening title and abstract to check for adequacy with our study aims. We then screened the bibliography of the selected studies to find new references and iterated this search procedure until we did not find any new documents. This procedure reduced the 69 papers to 47. At last, a selection of studies was based on the number of sampling sites and replicates in the different studies; that is, we kept studies with at least two sampling sites or studies with repeated

measurements in time and studies including sampling of two predator species.

As studies that used experimental manipulation of subsidies (and using stable isotopes) were very rare, descriptive studies were also included. Studies on predators' diet based on stable isotopes include a great variety of techniques for partitioning the diet between aquatic and terrestrial prey (mainly linear mixing models vs. Bayesian mixing models), and large differences in the assumed isotope fractionation between trophic levels. To overcome this issue, we (re)-calculated the percentage of aquatic prey in the diet of predators using the same Bayesian mixing model and fractionation values. Using the same fractionation values for all studies was essential as Bayesian mixing models may be highly sensitive to the value used (Bond and Diamond 2011). Consequently, we rejected studies in which the mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for consumers and prey per sampling site could not be extracted. The final data set consisted of 21 studies (Appendix S1: Table S1). Data were retrieved from tables, supplementary material, and figures (using WebPlotDigitizer) or by contacting the authors.

Response variable

The proportion of aquatic subsidies in predators' diet was inferred using two-source Bayesian mixing models. Inputs to the models were means and standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of aquatic and terrestrial preys with fractionation values recommended by McCutchan et al. (2003). Our choice between Post (2002) and McCutchan et al. (2003) was motivated by the fact that only the latter provides specific values for fluid-feeders, which represent most of the organisms included in our study. In some studies, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were only available for basal sources (algae and terrestrial litter). In these cases, trophic fractionation was estimated using the per trophic step fractionation multiplied by the estimated number of trophic transfers between the consumer and basal resources. This number was estimated as the difference between the consumer $\delta^{15}\text{N}$ and mean basal resource $\delta^{15}\text{N}$ divided by 3.4‰ (McHugh et al. 2010, Jackson and Sullivan 2017). When raw data for stable isotope were available for consumers, we used the *simmr* package (Parnell et al. 2013, Parnell

2016) to infer the proportion of aquatic vs. terrestrial subsidies in diet. When only means and standard errors were available, we used a modified version of the JAGS models used by Parnell et al. (2013) to include standard error of the consumer isotope values as a prior of the model. Source aggregation (terrestrial vs. aquatic) was made before running partitioning models, as the number of sources included in models was variable between studies. This choice was justified to allow us to compare diets (Stock et al. 2018). As most of the species included in our study were generalist predators, we chose not to give any prior (in the Bayesian model) to the proportion of aquatic prey in diet (Stock et al. 2018).

Predictors

The catchment draining to each sampling location was delineated using QGIS 2.18.18 (Quantum GIS Development Team 2017) and GRASS (GRASS Development Team 2017) plugin *r.watershed* from a 30 m resolution digital elevation model (Shuttle Radar Topography Mission [SRTM] 1 Arc-Second Global, LP DAAC). Predictors were extracted at local (100-m buffer) and landscape (catchment) scales. Local scale was defined as 100-m buffer as it corresponds to the approximate distance for which aquatic subsidies are still at half of their maximum level (stream signature, sensu Muehlbauer et al. 2014) for all species included in our study. Catchment was chosen as the relevant landscape scale as previous studies already highlighted the importance of catchment in shaping riparian food webs (Sabo and Power 2002). At the landscape scale, the predictors were catchment perimeter-to-area (a function of size, shape, and fractal irregularity or folding of the edge: Polis et al. 1997a); meandering ratio over 1 km upstream; percentage cover of agriculture, forests, non-forested natural habitats (bare ground, herbaceous, shrubs), open waters (lakes and meadows), and urban areas; mean percent tree cover (a measure of canopy cover); and mean human population. At the local scale, the predictors were river width, land use class, mean percent tree cover, and mean human population. The variables were selected to reflect potential exchange surface (perimeter-to-area, meandering), terrestrial input in the aquatic system (percent tree cover), land use, and human-related pressure (% urbanization covers and human population).

Land use data were extracted from GLCNMO v3 (Tateishi et al. 2014). Percent tree cover was extracted from PTC V2 (Geospatial Information Authority of Japan, Chiba University, and collaborating organizations). Mean human population was extracted from Gridded Population of the World, Version 4 (Center for International Earth Science Information Network 2016). River width and meandering ratio were extracted under GIS using Google Maps satellite imagery. To take into account the possible influence of climate, location, and local biodiversity, each sampling site was assigned to a freshwater ecoregion (Abell et al. 2008).

Statistical analysis

First, we used the proportion of aquatic subsidies in the diet minus 0.5 (i.e., deviation from a 50% aquatic/50% terrestrial diet) as an effect size to test for differences between proportion of aquatic and terrestrial subsidies in the diet of the terrestrial predators. We used a random-effect model with effect size as a response and freshwater ecoregion, sampling year, and taxonomic group of the predators as random factors. Publication bias was checked, and considered minor, using a funnel plot. We used the metafor package (Viechtbauer 2010) with restricted maximum-likelihood estimator to test the effect size.

Second, using partial least-square regression (PLS) on mean percentage of aquatic subsidies in the diet per sampling site, we tested which combination of landscape and local variables best explained the proportion of aquatic subsidies in predators' diet. Given the low number of studies available for some predator groups (Appendix S1: Table S1), we only performed one PLS for spiders and one for carabid beetles. Freshwater ecoregion and sampling year were also included in the model as moderators (variables potentially affecting the strength and direction of the relationship between predictors and response variable). Partial least-square regression extracts orthogonal components (latent variables maximizing the explained variance in the dependent variables) from a set of variables (Eriksson et al. 2006). It is particularly useful when dealing with correlated predictors (Carrascal et al. 2009), which is often the case for land use variables. The number of components to be kept was determined based on Q^2 value with an M-fold cross-validation

approach. Eriksson et al. (2006) recommend a "variable importance on the projection" (VIP) >1 for identifying the most important predictors. Predictors with $0.8 < VIP < 1$ explain only some variation in the model and predictors with $VIP < 0.8$ are considered non-explicative. Weights of the variables (loading values) describe the direction and strength of the relationship between predictor and dependent variables. The PLS was performed using mixOmics package for R (Le Cao et al. 2017). As we expected different scale effects according to taxonomic group, the PLS was performed separately for each group.

RESULTS

Dataset description

Among the 21 studies included, two were not used in the PLS because we could not locate the sampling sites with enough accuracy. Spiders and carabid beetles were the two most studied groups whose diets were estimated in 51.3% and 41.6% of the studies, respectively. The studies were mainly located in the northern hemisphere with cold or temperate climates (Fig. 1; Appendix S1: Table S1). A strong bias toward small, forested catchments with very low human population density and urbanization extent was also observed (Fig. 2; Appendix S2: Fig. S1). Conversely, very few studies were located along rivers with very large catchments or/and high human population.

Predator's reliance on aquatic subsidies

The contribution of aquatic subsidies to predator diets was significantly higher than 50% (effect size = 0.07, CI 95%: 0.013–0.13; Fig. 3). Our random-effect model accounted for 94.75% of the heterogeneity in diet ($Q = 207.5$, $df = 19$, $P < 0.001$). Residual heterogeneity was significant ($Q_E = 63.5$, $df = 3$, $P < 0.0001$) and mostly attributed to between-study variability ($I^2 = 95.3\%$), justifying the use of random factors. A significant overall effect of moderators ($Q_M = 272.7$, $df = 23$, $P < 0.001$) was observed. Sampling year and freshwater ecoregion both had a significant effect ($Q_M = 76.4$, $df = 4$, $P < 0.001$ for year and $Q_M = 168.8$, $df = 15$, $P < 0.001$ for ecoregion). Even if differences can be important between regions and year, no clear pattern was visible (Fig. 4). The predator taxonomic group effect was not significant ($Q_M = 7.88$, $df = 4$, $P = 0.096$).



Fig. 1. Map of the selected studies.

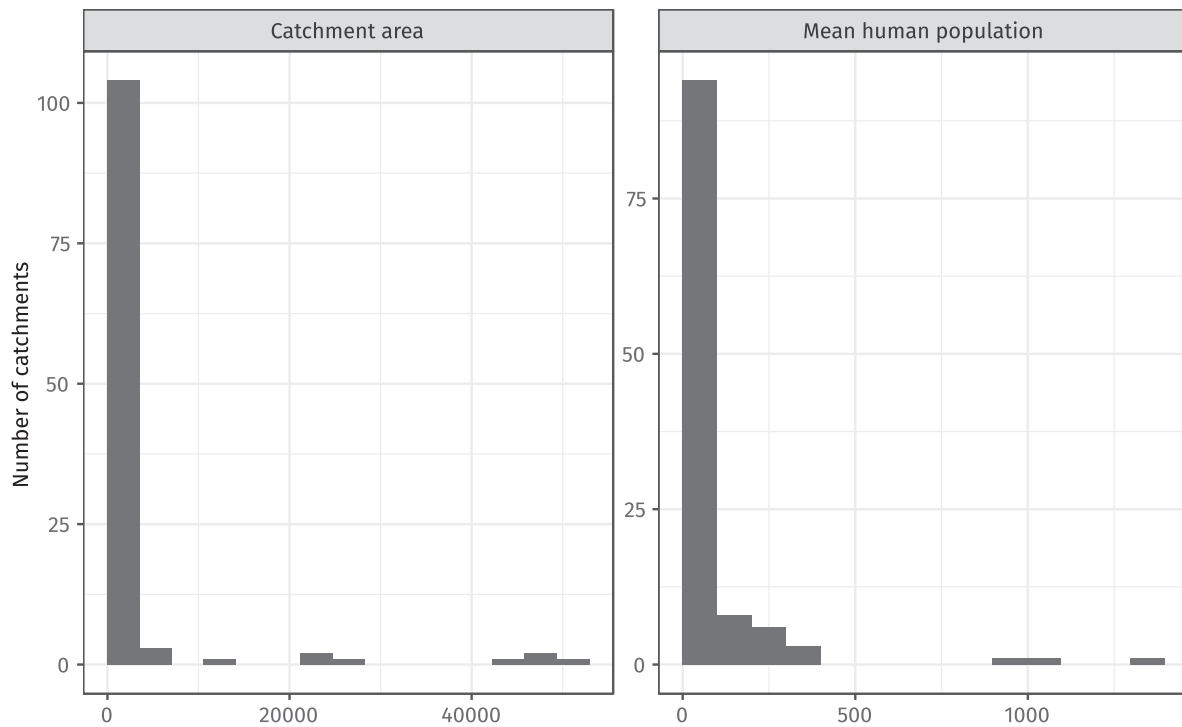


Fig. 2. Histogram of catchment area and mean human population size in the catchments.

Predictors of aquatic subsidies contribution

In the PLS regression model for spiders (two components: 17.5% and 10.1% of variance explained), the mean human population at both

local scale and landscape scale and the percentage of agriculture at the landscape scale were the most important variables related to a high proportion of aquatic prey in the diet. In contrast, the percentage

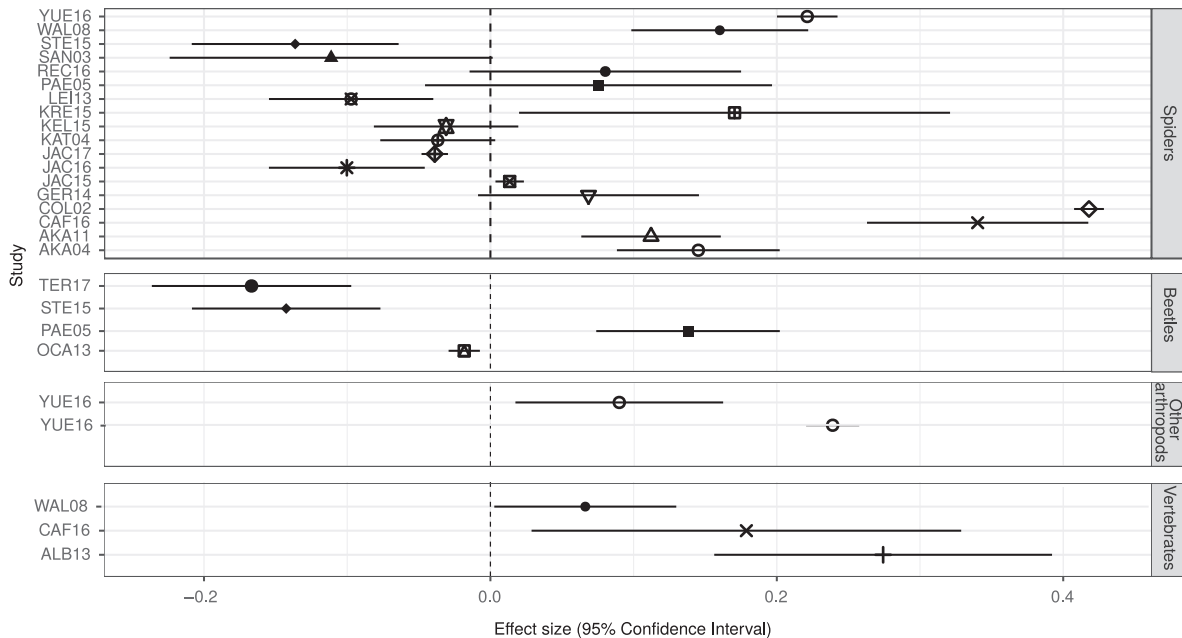


Fig. 3. Forest plot showing the overall effect size (observed proportion of aquatic prey in diet – 0.5). Signs and bars denote means and 95% confidence intervals of the effect sizes. Single studies are coded according to Appendix S1: Table S1.

of non-forested natural habitats and open waters were related to low percentage of aquatic prey in the diet (Fig. 5a). Despite high loading value, the percentage of open waters was weakly correlated to the percent of aquatic prey in the diet. Variables selected on the second components were identical.

In the PLS regression model for carabid beetles (two components: 32.9% and 21.4% of variance explained), percent tree cover, forests, and water bodies at the landscape scale were the most important variables for low proportion of aquatic prey. The percentage of non-forested natural habitats, urban areas, and agriculture at the landscape scale and the river width of the local scale were most important variables for high proportion of aquatic prey (Fig. 5b).

DISCUSSION

Our study extends recent findings that demonstrate high levels of aquatic-to-terrestrial subsidies in riparian ecosystems (Bartels et al. 2012), improving both the resolution of subsidy quantification, and allowing inferences at broader ecological scales. Our meta-analysis also provides evidence of widespread effects of anthropogenic land use on

riparian food webs. These effects seem to be prevalent at the landscape scale, probably the most relevant scale for understanding the role of aquatic-terrestrial linkages for land management practices, such as proposed land use conversion or biodiversity conservation (Carpenter and Biggs 2009). Despite the general pattern of high aquatic subsidies use by terrestrial predators, we also documented significant inter-annual and geographic variations in these subsidies, largely driven by hydrologic cycles and ecoregion, respectively.

We found the diet of riparian predators to be highly dependent on aquatic subsidies (>50%, overall effect size = 0.07). This estimation, not suffering from mixing-model and discrimination-factor biases (Bond and Diamond 2011), is considered fairly robust. This suggests that, in general, the proportion of aquatic subsidies in predator diets may be even higher than the 40% reported in Bartels et al.'s (2012) meta-analysis. We could not find any significant effect of predator taxonomic group, which might be due to the small number of studies dealing with groups other than carabid beetles and spiders. Nevertheless, spiders represent the most abundant terrestrial arthropod predator group found on every life-supporting

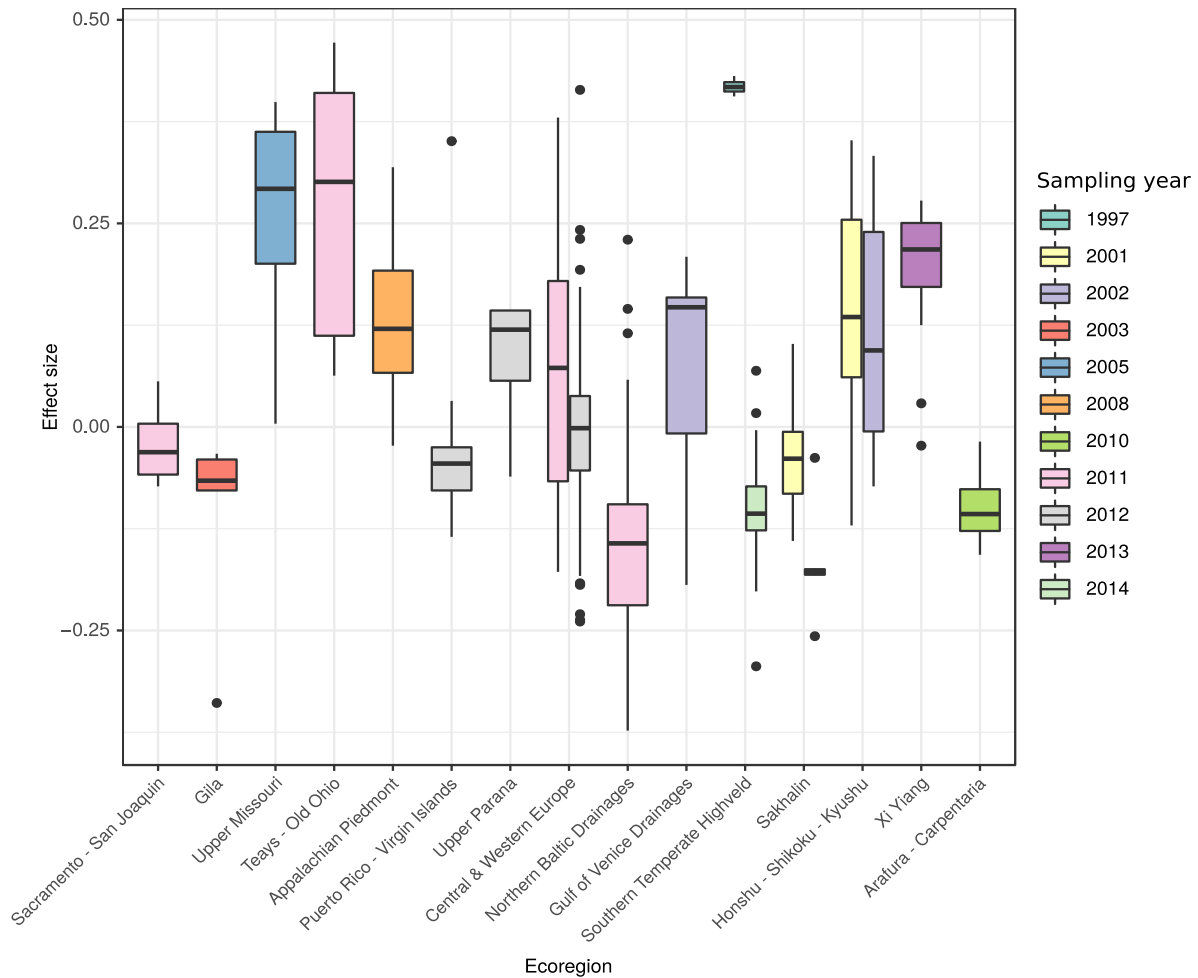


Fig. 4. Boxplot of the mean effect size (observed proportion of aquatic prey in diet – 0.5) per ecoregion. Colors correspond to sampling year.

land mass (Turnbull 1973, Riechert 1984) and both spiders and carabid beetles are found in very high densities in riparian ecosystems (Hering and Plachter 1997, Paetzold et al. 2005). Given the wide geographic spread of our analysis and the pattern of high proportion of aquatic-derived carbon across the study sites, it seems likely that most predator taxa in riparian systems rely on these subsidies for more than 50% of their diet. Nevertheless, it is important to keep in mind that a large proportion of the carbon coming from the aquatic system may be derived from terrestrial input brought back to the terrestrial ecosystem by adult aquatic insects (Kraus and Vonesh 2012).

Perhaps unsurprisingly, we also found significant temporal (inter-annual) and spatial

(ecoregion) variation in aquatic-to-terrestrial subsidies across the broad geographic scale of our study. Inter-annual climate-driven effects on stream hydrology (droughts vs. floods) may have important impacts on aquatic and riparian communities (Power et al. 2008, Lafage et al. 2015b, Lafage and Pétillon 2016), and on aquatic and terrestrial food webs (Marks et al. 2000, O'Callaghan et al. 2013). Thus, inter-annual variation in hydrologic conditions acts as a filter on functional traits of species and determines, for example, functional length of the riparian food chains. The significant effect of ecoregion on aquatic-to-terrestrial subsidies is probably due to region-specific differences in species communities, driven by both physical and ecological processes (Abell et al. 2008). It has

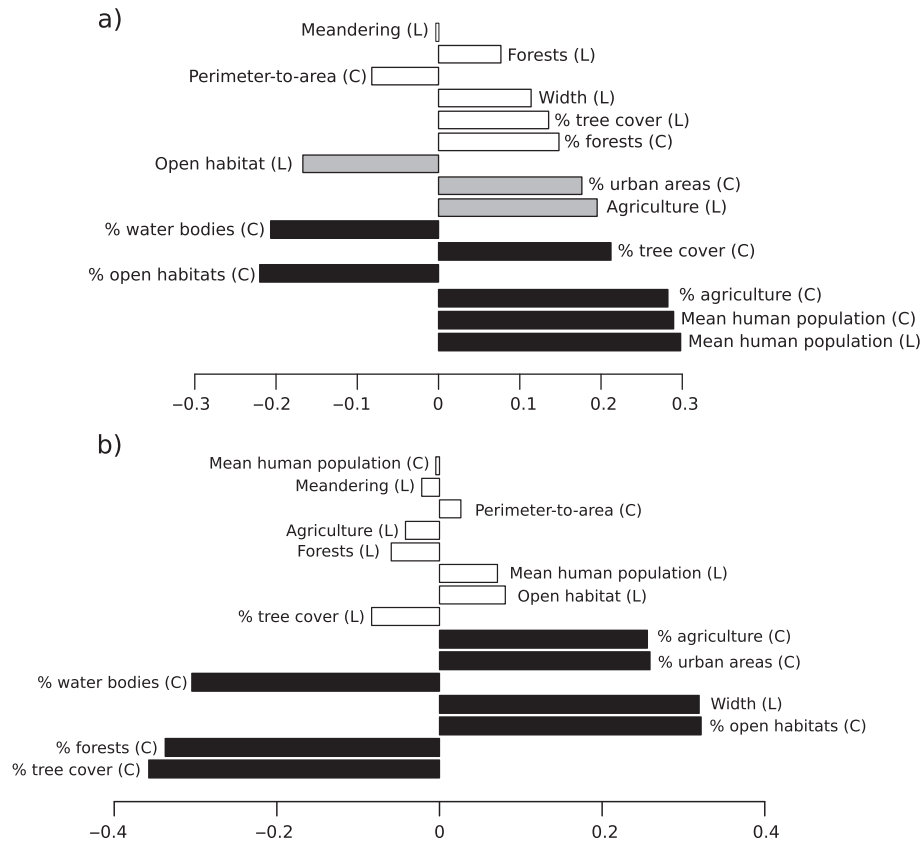


Fig. 5. The variable weights of the first component in the partial least-square models for proportion of aquatic prey in spider (a) and carabid beetles (b) diet. Positive weights indicate a positive relationship between the predictor and response variables and vice versa. Variables with white bars are non-significant (variable importance on the projection [VIP] < 0.7). Variables with gray bars are significant with low explicative power ($0.8 < \text{VIP} < 1$). Variables in black are significant and are the most contributing variables ($\text{VIP} > 1$). (L): Local scale (100m buffer); (C): Landscape scale (catchment).

been suggested that aquatic subsidy composition (especially through changes in species traits) is a key factor for resource use in the recipient system (Stenroth et al. 2015). Also, changes in predator communities might result in changes in species richness and functional diversity affecting the ability of predators to capture aquatic preys (e.g., for birds see Philpott et al. 2009). Significant differences in ecosystem functioning between ecoregions might also have a large impact. For instance, large differences in terrestrial and aquatic productivity (Bunn et al. 2006) and in carbon processing (Tiegs et al. 2019) might influence prey availability and carbon signature, cascading to predator's isotopic signature. Besides, variation in hydrological regime between ecoregions might strongly affect transfer of subsidies in space and

time (e.g., flooding regime and prey pulses; Bartels et al. 2012).

Numerous studies have demonstrated the importance of landscape-scale processes on ecological status (Allan 2004) and macro-invertebrate communities (aquatic: Lammert and Allan 1999, Richards et al. 1996; terrestrial: Hendrickx 2007, Lafage et al. 2015a). The relative importance of landscape- vs. local-scale factors, however, is still under debate (Sandin and Johnson 2004, Stoll et al. 2016). In our study, the proportion of aquatic subsidies in terrestrial predator diets was almost exclusively related to landscape-scale variables, the only significant local variable being human population. This was surprising, as many studies have highlighted the role of vegetation (Tagwireyi and Sullivan 2016), land use (Stenroth et al. 2015),

and stream morphology (Iwata 2007, Muehlbauer et al. 2014, Sabo and Hagen 2012) at the local scale. Our results could be related to the low resolution of our vegetation-related local variables, which were extracted from satellite data within a 100-m buffer. Nevertheless, variables related to stream morphology were not selected, although habitat geometry has been found to be the best predictor of trophic flow rate across habitat boundaries (Polis et al. 1997a).

At the landscape scale, ecosystem size did not explain the proportion of aquatic–terrestrial subsidies in predator diets. This may be due to the fact that the importance of ecosystem size and the direction of its relationship to predator diets can be system-specific, as conflicting relationships have been reported (Iwata 2007, Stenroth et al. 2015, Jackson and Sullivan 2017). In our study, agricultural land use and urbanization at the landscape scale, however, did have strong and consistent effects on terrestrial consumer diet, which might be driven by either direct or indirect effects. First, by increasing autotrophic productivity (through nutrient inputs and lower shading; Harding et al. 1999), agriculture and urbanization usually directly affect the composition, traits, and quantity of aquatic prey (Carlson et al. 2016, McKie et al. 2018), shifting toward more and smaller species and resulting in better prey availability for smaller terrestrial predators (Stenroth et al. 2015). Second, land use changes may affect the amount and quality of terrestrial-to-aquatic subsidies, thereby indirectly influencing reciprocal aquatic-to-terrestrial subsidies (Nakano et al. 1999, Krell et al. 2015). Nevertheless, the observed bias in studies dealing with riparian food webs toward forested small streams is limiting the generalization of our results.

Habitat openness had opposite effects on spider and carabid diets so that spiders relied more on aquatic subsidies in forested catchments whereas carabids did the opposite. Riparian carabid beetles are usually small, flattened, winged species (O'Callaghan et al. 2013) more likely to capture small preys favored by open habitat (Carlson et al. 2016). Conversely, typical riparian spiders in forested catchment are large web-building spiders (e.g., *Tetragnatha* spp.) that are able to catch and consume large flying preys favored by forested habitats. Several studies have highlighted body size–trophic level

linkages (Cohen et al. 2003). A positive relationship between prey body size and *Tetragnatha* use of aquatic subsidies has been previously demonstrated (Tagwireyi and Sullivan 2015).

Finally, both groups' uses of aquatic subsidies were negatively related to the percentage of lakes at the landscape scale. Jonsson et al. (2018) recently found black fly larvae autochthony to be positively related to the lake proportion in river catchment probably as a result of longitudinal resource transfers (i.e., transport of lake production). In our case, it is most likely a geographic artifact. Sites located in Sweden presented the largest proportion of lakes and the smallest proportion of aquatic subsidies in predator's diet. Otherwise, the proportion of catchment presenting open waters was fairly small. As for agricultural cover at the landscape scale, generalization of our results is limited by this bias in the available studies.

The literature on insect emergence is heavily biased toward small streams (Muehlbauer et al. 2014, Schindler and Smits 2017). We found the same pattern, plus a geographic bias, for studies on predators' diet using stable isotopes. Most of the studies we used were located in the northern hemisphere, in small-forested catchments with low proportions of agriculture or urbanization (except for studies specifically dealing with the impact of these land use-related variables). As agriculture represents the main land use type in many developed catchments (Allan 2004) and urban land use exerts a disproportionately large influence on aquatic systems (Paul and Meyer 2001), we call for the development of studies on large rivers, and on catchment impacted by agriculture and urbanization. Studies are also needed on southern hemisphere streams.

Our study is the first worldwide meta-analysis to use exclusively stable isotope studies in order to better integrate the temporal component of terrestrial predator diets. We demonstrated a high reliance (more than 50%) of terrestrial predators on aquatic subsidies across broad geographic regions, despite large geographic and inter-annual variations. We further demonstrated a large effect of anthropogenic land use at the catchment scale across geographic regions. Linking these two key findings suggests that more attention to broad-scale landscape patterns is warranted to improve our understanding of how these cross-boundary energy flows affect

biodiversity and ecosystem function of tightly coupled aquatic–terrestrial systems.

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DATA AVAILABILITY

Dataset and code are available on the Open Science Framework repository (<https://doi.org/10.17605/osf.io/t6eyp>).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2697/full>