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

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8

9 Abstract

10 Cross-boundary fluxes of organisms and matter, termed "subsidies", are now recognized 11 to be reciprocal and of roughly equal importance for both aquatic and terrestrial systems, 12 even if terrestrial input to aquatic ecosystems has received most attention. The magnitude 13 of aquatic to terrestrial subsidies is well documented, but the drivers behind these 14 subsidies and their utilization by terrestrial consumers are characteristically local scale 15 studies, limiting the inferences that can be drawn for broader geographic scales. We 16 therefore built and analyzed a database of stable isotope data extracted from 21 studies 17 worldwide, to identify both landscape and local scale variables that may affect the diet of 18 terrestrial predators in riparian ecosystems. Our meta-analysis revealed a greater 19 magnitude of aquatic-to-terrestrial subsidies (> 50%) than previously reported, albeit with 20 large geographic and inter-annual variations. We demonstrated a large effect of 21 landscape-scale factors on aquatic-to-terrestrial subsidies, particularly anthropogenic land 22 use and tree cover. Local human population was the only relevant factor at the local 23 scale. We also found that studies on landscape-scale and anthropogenic land use effects 24 on aquatic-to-terrestrial subsidies are currently strongly under-represented in the 25 ecological literature. Such studies are needed to improve our understanding of how land

- 26 use and environmental change might influence future patterns of biodiversity and
- 27 ecosystem function.
- 28 Key words: anthropogenic land use, aquatic subsidies, diet, human population, stable
- 29 isotopes, terrestrial predators

30 Introduction

31 Decades of research have demonstrated and quantified the tight linkages between aquatic

32 and terrestrial ecosystems (Fisher and Likens 1973, Bartels et al. 2012). Cross-boundary

33 fluxes connecting ecosystems, usually termed "subsidies" (Polis et al. 1997b), can be

34 organisms, energy, or nutrients. Terrestrial-to-aquatic subsidies in the form of litter and

35 organic matter are essential for aquatic ecosystem function (reviwed by Tank et al. 2010)

36 and terrestrial prey subsidies also have important effects on riverine food-webs (Polis and

37 Hurd 1996, Nakano and Murakami 2001, Erős et al. 2012, Gustafsson et al. 2014). More

38 recently, research has focused on reciprocal subsidies between aquatic and terrestrial

39 ecosystems (Baxter et al. 2005, Schindler and Smits 2017). Although the amount of

40 terrestrial-to-aquatic prey subsidies often is greater than the reverse, their overall

41 contribution to the carbon budget of predators is similar (Bartels et al. 2012). Thus, the

42 most recent picture to emerge is that of tightly-coupled, roughly reciprocal aquatic-

43 terrestrial ecosystems, at least at the local scale at which most studies have taken place.

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

48 has an impact on predator diet by facilitating or preventing subsidies from entering 49 recipient ecosystems (Greenwood 2014, Muehlbauer et al. 2014). At the landscape 50 (catchment) scale, ecosystem size (McHugh et al. 2010, Jackson and Sullivan 2017) and 51 land use (Stenroth et al. 2015, Carlson et al. 2016) have recently more attention. Studies 52 focusing on the effect of ecosystem size and land use on riparian ecosystem food webs, 53 however, remain scarce (e.g. Marczak et al., 2007; Schindler and Smits, 2017). Land use, 54 at local and landscape scales, influences the composition and biomass of both aquatic 55 insect communities (via water quality, terrestrial subsidies and canopy cover: Dolédec et 56 al., 2006; Schindler and Smits, 2017; and predator communities: Hendrickx et al., 2007; 57 Lafage et al., 2015). On the other hand, ecosystem size, by integrating the effects of 58 spatial heterogeneity, disturbance and productivity, is a strong predictor of food chain 59 length (Sabo et al. 2010). To gain a better understanding of broader-scale ecological 60 processes, comparative studies of aquatic-terrestrial ecosystems at the catchment scale 61 are needed. 62 In this study, we conducted a worldwide meta-analysis of studies that have assessed

63 aquatic-to-terrestrial subsidies using stable isotopes. We quantified the effects of 64 ecosystem size, stream morphology and land use on aquatic subsidies to terrestrial 65 predators. First, we estimated the overall proportion of aquatic subsidies in the diet of 66 several groups of terrestrial predators, and tested whether the proportion of these prey 67 was significantly higher than that of terrestrial prey. We hypothesised that the proportion 68 of aquatic subsidies varied between taxonomic groups of predators, hydrological system 69 type (hydro-ecoregion) and year. Next, we assessed the relative importance of biotic and 70 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
- 72 beetle predators. We hypothesised that landscape-scale variables related to anthropogenic
- 73 land use would be of at least equal importance in explaining predators' diets as
- 74 commonly-assessed local-scale variables.

75 Methods

76	Our meta-analysis focused on the use of aquatic subsidies by terrestrial predators. We
77	restricted the subsidies to aquatic organisms actively crossing the boundary between
78	aquatic and terrestrial ecosystems (i.e. macro-invertebrates). All predators consuming
79	aquatic macro-invertebrates were included. In order to get a more accurate estimation of
80	the proportion of aquatic subsidies in the diet of predators, we restricted our meta-
81	analysis to studies using stable isotopes, which integrate the use of prey types over a
82	longer period of time than do stomach content analyses (Tieszen et al. 1983).
83	Data retrieval
84	We searched the Web of Science and Google Scholar for studies focusing on riparian
85	habitats and using stable isotopes as a tool to infer the contribution of aquatic prey to the
86	diet of terrestrial predators. The keywords used were "aquatic subsidies" AND "stable
87	isotope" AND "diet", which gave 69 results. From these 69 articles we refined the
88	selection in several steps. First, a selection was made based on words in the title and a
89	second one on words in the abstract. We then screened the bibliography of the selected
90	studies to find new references and iterated this search procedure until we did not find any
91	new documents. This procedure reduced the 69 papers to 47. At last, a selection of
92	studies was based on the number of sampling sites and replicates in the different studies,
93	i.e. we kept studies with at least two sampling sites or studies with repeated
94	measurements in time and studies including sampling of two predator species.
95	As studies using experimental manipulation of subsidies (and using stable isotopes) were
96	very rare, descriptive studies were also included. Studies on predators' diet based on

97	stable isotopes include a great variety of techniques used to partition the diet between
98	aquatic and terrestrial prey (mainly linear mixing models vs Bayesian mixing models),
99	and great differences in the assumed isotope fractionation between trophic levels. To
100	overcome this issue we (re)-calculated the percentage of aquatic prey in the diet of
101	predators using the same Bayesian mixing model and fractionation values. Using the
102	same fractionation values for all studies was essential as Bayesian mixing models may be
103	highly sensitive to the value used (Bond and Diamond 2011). Consequently, we rejected
104	studies in which the mean and standard deviation of $\delta 13C$ and $\delta 15N$ for consumers and
105	prey per sampling site could not be extracted. The final data set consisted of 21 studies
106	(Table 1). Data were retrieved from tables, supplementary material, figures (using
107	WebPlotDigitizer) or by contacting the authors.
108	Response variable

108 <u>Response variable</u>

109 The proportion of aquatic subsidies in predators' diet was inferred using two-source 110 Bayesian mixing models. Inputs to the models were means and standard deviations for 111 δ 13C and δ 15N of aquatic and terrestrial preys with fractionation values recommended 112 by McCutchan et al. (2003). In some studies, $\delta 13C$ and $\delta 15N$ values were only available 113 for basal sources (algae and terrestrial litter). In these cases, trophic fractionation was 114 estimated using the per trophic step fractionation multiplied by the estimated number of 115 trophic transfers between the consumer and basal resources. This number was estimated 116 as the difference between the consumer $\delta 15N$ and mean basal resource $\delta 15N$ divided by 117 3.4‰ (McHugh et al. 2010, Jackson and Sullivan 2017). When raw data for stable 118 isotope were available for consumers, we used the simmr package (Parnell et al. 2013, 119 Parnell 2016) to infer the proportion of aquatic vs terrestrial subsidies in diet. When only

120	means and standard errors were available we used a modified version of the JAGS
121	models used by Parnell et al. (2013) to include standard error of the consumer isotope
122	values as a prior of the model. Source aggregation (terrestrial vs aquatic) was made a
123	priori as the number of sources included in models was variable between studies, which
124	is problematic for <i>a posteriori</i> aggregations if one wants to compare diets (Stock et al.
125	2018). We chose not to give any prior to the proportion of aquatic preys in diet
126	(generalist diets) which means that all possible combinations of proportions of aquatic
127	and terrestrial preys were likely a priori (Stock et al. 2018).
128	Predictors
129	The catchment draining to each sampling location was delineated using QGIS 2.18.18
130	(Quantum GIS Development Team 2017) and GRASS (GRASS Development Team
131	2017) plugin r.watershed from a 30 m resolution digital elevation model (Shuttle Radar
132	Topography Mission (SRTM) 1 Arc-Second Global, LP DAAC). Predictors were
133	extracted at local (100 m buffer) and landscape (catchment) scales. At the landscape
134	scale, the predictors were catchment perimeter-to-area (a function of size, shape, and
135	fractal irregularity or folding of the edge: Polis et al., 1997a); percentage cover of
136	agriculture, forests, non-forested natural habitats (bare ground, herbaceous, shrubs), open
137	waters (lakes and meadows) and urban areas; mean percent tree cover (a measure of
138	canopy cover); and mean human population. At the local scale, the predictors were river
139	width; meandering ratio over 1 km upstream; land use class; mean percent tree cover; and
140	mean human population.

141	Land use data were extracted from GLCNMO v3 (Tateishi et al. 2014). Percent tree cover
142	was extracted from PTC V2 (Geospatial Information Authority of Japan, Chiba
143	University and collaborating organizations). Mean human population was extracted from
144	Gridded Population of the World, Version 4 (Center for International Earth Science
145	Information Network, 2016). River width and meandering ratio were extracted under GIS
146	using google maps satellite imagery. To take into account the possible influence of
147	climate, location and local biodiversity, each sampling site was assigned to a freshwater
148	ecoregion according (Abell et al. 2008).
149	Statistical analysis
150	We used the proportion of aquatic subsidies in the diet minus 0.5 as an effect-size to test
151	for differences between proportion of aquatic and terrestrial subsidies in the diet of the
152	terrestrial predators. Freshwater ecoregion, sampling year and taxonomic group of the
153	predators were included in the model as fixed factors. We used the metafor package
154	(Viechtbauer 2010) with restricted maximum-likelihood estimator to test the effect-size.
155	The selection of landscape and local variables best explaining the proportion of aquatic
156	subsidies in predators' diet was done using partial least square regression (PLS) on mean
157	% of aquatic subsidies in the diet per sampling site. Given the low number of studies
158	available for some groups (Table 1), the PLS were only performed for spiders and
159	carabid beetles. Freshwater ecoregion and sampling year were also included in the model
160	as moderators. PLS regression extracts orthogonal components (latent variables
161	maximizing the explained variance in the dependent variables) from a set of variables
162	(Eriksson et al. 2006) and are particularly useful when dealing with correlated predictors
163	(Carrascal et al. 2009), which is often the case for land use variables. The number of

164	components to be kept was determined based on Q ² value with a M-fold cross-validation
165	approach. Eriksson et al. (2006) recommend a 'variable importance on the projection'
166	(VIP) greater than 1 for identifying the most important predictors. Predictors with
167	$0.8 \le VIP \le 1$ explain only some variation in the model and predictors with $0.8 \le VIP$ are
168	considered non-explicative. Weights of the variables (loading values) describe the
169	direction and strength of the relationship between predictor and dependent variables. The
170	PLS were performed using mixOmics package for R (Le Cao et al. 2017). As we
171	expected different scale effects according to taxonomic group, the PLS were performed
172	separately for each group.
173	Dataset and code are available on the Open Science Framework repository

174 (DOI 10.17605/OSF.IO/T6EYP).

175 **Results**

176 Dataset description

177 The final dataset resulted in 21 studies representing 159 sampling sites and 400 diets

178 (Table 1). This corresponds to almost half of the studies initially selected. Twenty-six

179 studies could not be used, mainly because they did not report data in a suitable format

180 and quality for analysis of diet partitioning. Among these 21 studies, two were not used

in the PLS because we could not locate the sampling sites with enough accuracy. Spiders

- 182 and carabid beetles were the two most studied groups whose diets were estimated in
- 183 51.3% and 41.6% of the studies, respectively. The studies were mainly located in the
- 184 northern hemisphere with cold or temperate climates (Fig. 1 and Table 1).

185 Study site locations were strongly biased toward small forested catchments with very low

- 186 human population density and urbanization extent and located mainly in the northern
- 187 hemisphere (Fig. 2 and 3). Conversely, a few studies were also located in rivers with very
- 188 large catchments or/and high human population.
- 189 Predator's reliance on aquatic subsidies
- 190 The contribution of aquatic subsidies was significantly higher than 50% (effect size =
- 191 0.07, CI 95%: 0.013 0.13: fig. 4). Our model accounted for 95.3% of the heterogeneity
- in diet (R^2 =95.3, Q= 207.5, df = 19, p < 0.001) with a significant overall effect of
- 193 moderators ($Q_M = 272.7$, df = 23, p < 0.001). 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 = 168.8, df
- 195 15, p < 0.001 for ecoregion). The predator taxonomic group effect was not significant
- 196 $(Q_M = 7.88, df = 4, p = 0.096)$, whereas the test for residual heterogeneity was significant
- 197 ($Q_E = 63.5$, df = 3, p < 0.0001), and most of the unaccounted variance is due to residual
- 198 heterogeneity (I2=95.3%).

199 Predictors of aquatic subsidies contribution

200 In the PLS regression model for spiders (two components: $R^2 = 0.394$ and $R^2 = 0.460$),

the mean human population at both local scale and landscape scale as well as the

202 percentage of agriculture at the landscape scale were the most important variables related

- to a high proportion of aquatic prey. In contrast, the percentage of non-forested natural
- habitats and open waters were related to low percentage of aquatic prey (fig 5). Despite
- high loading value, the percentage of open waters was weakly correlated to the percent of

aquatic prey in the diet.

In the PLS regression model for carabid beetles (two components: $R^2 = 0.112$ and $R^2 = 0.041$), 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. 6).

212 Discussion

213 Our study extends recent findings that demonstrate high levels of aquatic-to-terrestrial 214 subsidies in riparian ecosystems (Bartels et al. 2012), improving both the resolution of 215 subsidy quantification, and allowing inferences at broader ecological scales. Our meta-216 analysis also provides some of the strongest evidence to date of widespread effects of 217 anthropogenic land use on the riparian food webs. These effects seem to be prevalent at 218 the landscape scale, probably the most relevant scale for understanding the role of 219 aquatic-terrestrial linkages for land management practices, such as proposed land use 220 conversion or biodiversity conservation (Carpenter and Biggs 2009). Despite the general 221 pattern of high aquatic subsidies use by terrestrial predators, we also documented 222 significant inter-annual and geographic variations in these subsidies, largely driven by 223 hydrologic cycles and ecoregion, respectively.

224 We found the diet of riparian predators to be highly dependent on aquatic subsidies (>

50%, overall effect size = 0.07). Since we re-computed diet partitioning from raw data to

reduce mixing-model and discrimination-factor biases (Bond and Diamond 2011), our

estimate is likely the most robust to date. 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. 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.

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

236 (ecoregion) variation in aquatic-to-terrestrial subsidies across the broad geographic scale

237 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.

239 2008, Lafage et al. 2015b, Lafage and Pétillon 2016), and on aquatic and terrestrial food

240 webs (Marks et al. 2000, O'Callaghan et al. 2013). Thus, inter-annual variation in

241 hydrologic conditions act as a filter on functional traits of species and determines e.g.

functional length of the riparian food chains. The significant effect of ecoregion on

243 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

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,

247 changes in predator communities might result in changes in species richness and

248 functional diversity affecting the ability of predators to capture aquatic preys (e.g. for

birds: Philpott et al. 2009).

250 Numerous studies have demonstrated the importance of landscape-scale processes on

ecological status (e.g. Allan, 2004) and macro-invertebrate communities (aquatic:

Lammert and Allan, 1999; Richards et al., 1996, terrestrial: Hendrickx et al., 2007;

253 Lafage et al., 2015a). The relative importance of landscape- versus local-scale factors,

however, is still under debate (Sandin and K. 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 local

vegetation (Tagwireyi and Sullivan, 2016), land use (Stenroth et al., 2015) and stream

259 morphology (Iwata 2007, Muehlbauer et al. 2014). Our results could be related to the low

260 resolution of our vegetation-related local variables, which were extracted from satellite

261 data within a 100 m buffer. Nevertheless, variables related to stream morphology were

262 not selected, although habitat geometry has been found to be the best predictor of trophic

263 flow rate across habitat boundaries (Polis et al. 1997a).

264 At the landscape scale, ecosystem size did not explain the proportion of aquatic-terrestrial 265 subsidies in predator diets. This may be due to the fact that the importance of ecosystem 266 size and the direction of its relationship to predator diets can be system-specific, as 267 conflicting relationships have been reported (Iwata, 2007, Stenroth et al. 2015, Jackson 268 and Sullivan 2017). In our study, agricultural land use and urbanization, however, did 269 have strong and consistent effects on terrestrial consumer diet which might be driven by 270 either direct or indirect effects. First, by decreasing water quality, agriculture and 271 urbanization usually directly affect the composition and quantity of aquatic subsidies 272 (Carlson et al. 2016), shifting towards more and smaller species and resulting in better 273 prey availability for smaller terrestrial predators (Stenroth et al. 2015). Second, land use 274 changes may affect the amount and quality of terrestrial-to aquatic subsidies thereby

indirectly influencing reciprocal aquatic-to-terrestrial subsidies (Nakano et al. 1999, Krellet al. 2015).

277 Habitat openness had opposite effects on spider and carabid diets so that spiders relied 278 more on aquatic subsidies in forested catchments whereas carabids did the opposite. 279 Riparian carabid beetles are usually small flattened winged species (O'Callaghan et al. 280 2013) more likely to capture small preys favored by open habitat (Carlson et al. 2016). 281 Conversely, typical riparian spiders in forested catchment are large web-building spiders 282 (e.g. *Tetragnatha sp.*) that are able to catch and consume large flying preys favored by 283 forested habitats. Several studies have highlighted body size-trophic level linkages (e.g. 284 (Cohen et al. 2003). A positive relationship between prey body-size and *Tetragnatha* use 285 of aquatic subsidies has been previously demonstrated (Tagwireyi and Sullivan 2015). 286 Finally, both groups' uses of aquatic subsidies were negatively related to the percentage 287 of lakes at the landscape scale. Jonsson et al. (2018) recently found black fly larvae 288 autochthony to be positively related to the lake proportion in river. In our case, it is most 289 likely a geographical artefact. Sites located in Sweden presented the largest proportion of 290 lakes and the smallest proportion of aquatic subsidies in predator's diet. 291 The literature on insect emergence is heavily biased towards small streams (Muehlbauer

et al. 2014, Schindler and Smits 2017). We found the same pattern, plus a geographical
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.
- 300 Studies are also needed on southern hemisphere streams.
- 301 Our study is the first worldwide meta-analyses to use exclusively stable isotope studies in
- 302 order to better integrate the temporal component of terrestrial predator diets. We
- 303 demonstrated a high reliance (more than 50%) of terrestrial predators on aquatic subsidies
- 304 across broad geographic regions, despite large geographic and inter-annual variations.
- 305 We further demonstrated a large effect of anthropogenic land use at the catchment scale
- 306 across geographic regions. Linking these two key findings suggests that more attention to
- 307 broad-scale landscape patterns is warranted to improve our understanding of how these
- 308 cross-boundary energy flows affects biodiversity and ecosystem function of tightly
- 309 coupled aquatic-terrestrial systems.

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Table 1. Characteristics of the studies used for the meta-analysis. Climate is extracted from Peel et al. (2007) and ecoregion from Abell et al. (2008)

Reference	Code	Group	Nb diets	Country	Sampling year	Nb sites	Climate	Ecoregion
Akamatsu et al. 2004 – Ecol. Res.	AKA04	Spiders	22	JPN	2001	3	Cold, Without dry season, 3 Hot summer	Honshu - Shikoku - Kyushu
Akamatsu & Toda 2011 – Environ. Pollut.	AKA11	Spiders	28	JPN	2002		Cold, Dry winter, Hot 5 summer	Honshu - Shikoku - Kyushu
Alberts et al. 2013 – Sci. Total Environ.	ALB13	Birds	8	USA	2011	11	Cold, Without dry season, Hot summer	Teays - Old Ohio
Mccaffery & Eby 2016 - Freshw. Biol.		Spiders	4	USA	2005	Z	Cold, Without dry season, 4 Warm summer	Upper Missouri
Mccaffery & Eby 2016 - Freshw. Biol.	CAF16	Mouse	4	USA	2005	2	Cold, Without dry season, Warm summer	Upper Missouri
Collier et al. 2002 – Freshw. Biol.	COL02	Spiders	4	ZAF	1997	2	Temperate, Dry winter, 2 Warm summer	Southern Temperate Highveld
Gergs et al. 2014 – Freshw. Biol.	GER14	Spiders	18	GER	2011	ç	Temperate, Without dry 9 season, Warm summer	Central & Western Europe
Jackson et al. 2015 – Freshwater. Sci.	JAC15	Spiders	11	USA	2011	11	Temperate, Dry summer, Warm summer	Sacramento - San Joaquin
Jackson et al. 2016 – Ecol. Evol.	JAC16	Spiders	12	ZAF	2014	. (Temperate, Dry winter, 6 Warm summer	Southern Temperate Highveld
Jackson et al. 2017 - Can. J. Fish. Aquat. Sci.	JAC17	Spiders	36	USA	2011	30	Temperate, Dry summer,) Hot summer	Sacramento - San Joaquin

Kato et al. 2004 – Ecol. Res.	KAT04	Spiders	13 JPN	2001	Cold, Without dry season, 2 Warm summer	Sakhalin, Hokkaido, & Sikhote - Alin Coast
Kelly et al. 2015 – PeerJ	KEL15	Spiders	17 PRI	2012	1 Tropical rainforest	Puerto Rico - Virgin Islands
Krell et al. 2015 – Limnologica	KRE15	Spiders	6 DEU	2012	Temperate, Without dry 3 season, Warm summer	Central & Western Europe
Leigh et al. 2013 – Inl. Waters	LEI13	Spiders	4 AUS	2010	4 Arid steppe, Hot	Arafura - Carpentaria
O'Callaghan et al. 2013 – PloS One	OCA13	Beetles	174 GBR	2012	Temperate, Without dry 14 season, Warm summer	Central & Western Europe
Paetzold et al. 2005 – Ecosystems	PAE05	Spiders	4 ITA	2002	Temperate, Without dry 1 season, Warm summer	Gulf of Venice Drainages
Paetzold et al. 2005 – Ecosystems	PAE05	Beetles	4 ITA	2002	Temperate, Without dry 1 season, Warm summer	Gulf of Venice Drainages
Paetzold et al. 2005 – Ecosystems	PAE05	Ants	1 ITA	2002	Temperate, Without dry 1 season, Warm summer	Gulf of Venice Drainages
Recalade et al. 2016 – J. Anim. Ecol.	REC16	Spiders	4 BRA	2012	Temperate, Dry winter, Ho 1 summer	t Upper Parana
Sanzone et al. 2003 – Oecologia	SAN03	Spiders	5 USA	2003	1 Arid steppe, Hot	Gila
Stenroth et al. 2015 – Freshw. Biol.	STE15	Spiders	19 SWE	2011	Cold, Without dry season, 10 Cold summer	Northern Baltic Drainages
Stenroth et al. 2015 – Freshw. Biol.	STE15	Beetles	10 SWE	2011	Cold, Without dry season, 10 Cold summer	Northern Baltic Drainages
Terui et al. 2017 – Ecol. Res.	TER17	Spiders	1 JPN	2014	Cold, Without dry season, 4 Warm summer	Sakhalin, Hokkaido, & Sikhote - Alin Coast

Terui et al. 2017 – Ecol Res.	TER17 Beetles	5 JPN	2014	Cold, Without dry season, 4 Warm summer	Sakhalin, Hokkaido, & Sikhote - Alin Coast
Walters et al. 2008 – Ecol. Appl.	WAL08 Spiders	12 USA	2008	Temperate, Without dry 4 season, Hot summer	Appalachian Piedmont
Walters et al. 2008 – Ecol. Appl.	WAL08 Herptile	4 USA	2008	Temperate, Without dry 4 season, Hot summer	Appalachian Piedmont
Yuen et al. 2016 Biotropica	YUE16 Spiders	18 HKG	2013	Temperate, Dry winter, Ho 3 summer	t Xi Yiang
Yuen et al. 2016 Biotropica	YUE16 Odonata	6 HKG	2013	Temperate, Dry winter, Ho 3 summer	t Xi Yiang
Yuen et al. 2016 Biotropica	YUE16 Hemiptera	10 HKG	2013	Temperate, Dry winter, Ho 3 summer	t Xi Yiang

Figure captions

Figure 1: Map of the selected studies. White symbols are studies that were rejected on data quality grounds (see text for details).

Figure 2: Plot of the percentage cover of each land use class in catchments per study.

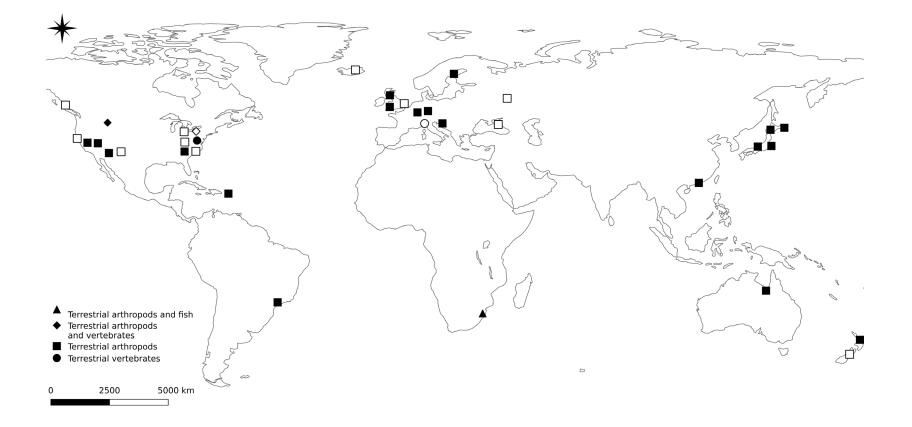
Figure 3: Histogram of catchment area and mean human population size in the catchment.

Figure 4: Forest plot showing the overall effect-size (observed proportion of aquatic prey in diet minus 0.5). Squares and bars denote means and 95% confidence intervals of the effect sizes, while the size of the squares reflects the weight of each study. Single studies are coded according to Table 1.

Figure 5: The variable weights of the first component in the PLS models for proportion of aquatic prey in spider diet. Positive weights indicate a positive relationship between the predictor and response variables and vice versa. Variables white bars are non-significant (VIP < 0.7). Variables with grey bars are significant with low explicative power (0.8 < VIP < 1). Variables in black are significant and are the most contributing variables (VIP > 1).

Figure 6: The variable weights of the first component in the PLS models for proportion of aquatic prey in the carabid beetle diet. Positive weights indicate a positive relationship between the predictor and response variables and vice versa. Variables white bars are non-significant (VIP < 0.7). Variables with grey bars are significant with low explicative power (0.8 < VIP < 1). Variables in black are significant and are the most contributing variables (VIP > 1).

Figure 1



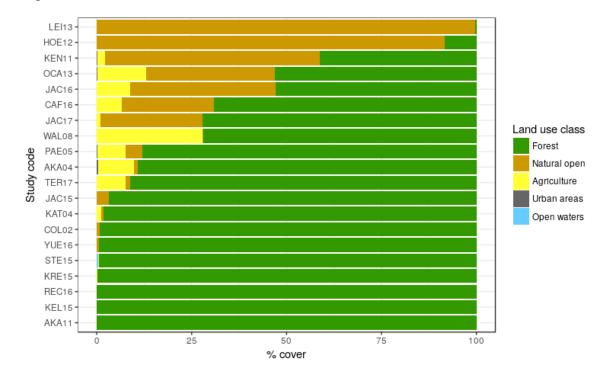
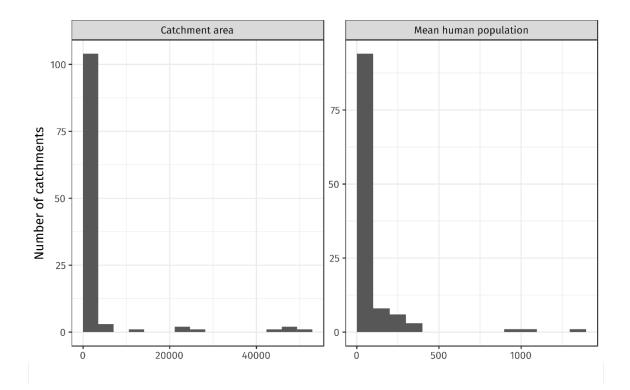


Figure 2







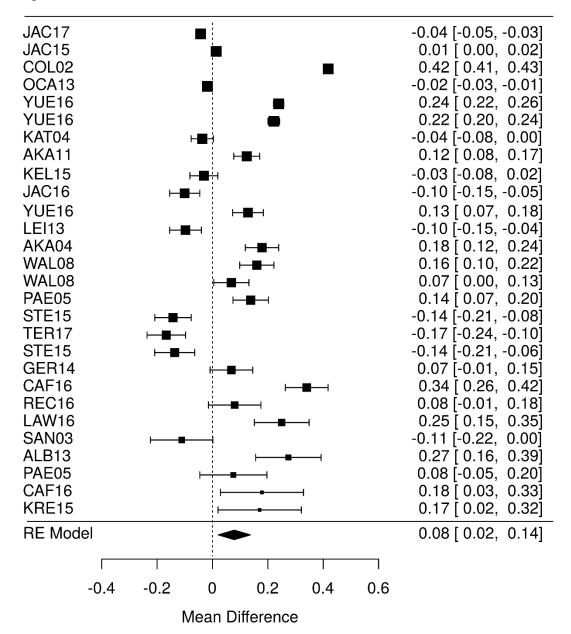


Figure 5

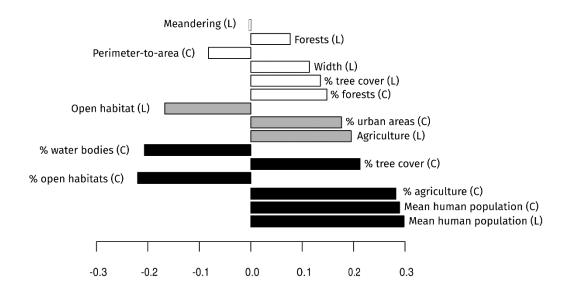


Figure 6

